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OXIDATION STRESS IS ADAPTATIVE REACTION INDUCTOR OF WINTER WHEAT PLANTS

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Hydrogen peroxide impact upon the activity of superoxide dismutase (SOD), catalase (CAT), development of lipid peroxidation processes (LP), photosynthetic pigment content and productivity in conditions of field experiment were studied for winter wheat varieties of different ecotypes, namely Stolychna, Polisska 90 – forest-steppe, and Scala-steppe. It was found that hydrogen peroxide action for 24 h induced LP activity, whereas antioxidative enzyme activity dropped at two varieties. Exception was the Stolychna plants that showed decrease in all indexes studied after treatment. In the next phase of ontogenesis (flowering), however, SOD activity increased both in the plants of Polisska 90 and Scala, while CAT and LP activities were close to control in all plants. The data suggest that treatment by hydrogen peroxide stimulated the formation of general unspecific resistance of plants and increased the grain productivity of winter wheat varieties studied.

Key words: winter wheat, hydrogen peroxide, lipid peroxidation, superoxide dismutase, catalase, photosynthetic pigment, productivity

The basic factors for subsequent increase in agricultural productivity will be using biological and ecological knowledge in plant cultivation on the basis of management of ontogenetic and phylogenetic adaptation potential of agrocenoses components (Zhutchenko 2001). A transition to the adaptive plant cultivation will be possible at condition that the plant varieties will be maximally adjusted to the local terms of growing and will effectively use the resources of environment. Various environmental stresses such as drought and other can inhibit plant growth and development, leading to crop reduction. A special attention in adaptive plant cultivation should be accented on variety ability to counteract to abiotic and biotic stressors. A way to solve these problems would be increase nonspecific resistance of plants by induction of general adaptation mechanisms via stressful actions. It is a tool of plant metabolism activation and the adaptation ability increase to other possible stresses impact (Shakirfova 2001). It is now accepted that reactive oxygen species (ROS), particularly H_2O_2 and $O_2^{\bullet-}$, are carefully regulated metabolites capable of signaling and communicating critical information to the cell's genetic machinery. The expression programs following H_2O_2 or $O_2^{\bullet-}$ treatment were essentially identical despite the fact that different ROS are involved. There was a strong induction of genes known to be involved in detoxification of both H_2O_2 and $O_2^{\bullet-}$, such as catalase (CAT), superoxide dismutase (SOD), and glutathione peroxidase, as well as genes involved in oxidative and reductive reactions (e.g. thioredoxin, glutathione reductase, glutaredoxin). Genes moderately induced by ROS and other signals are regulated by different transcription factors, and different upstream signaling pathways

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may govern their response (Scandalios 2005). Evidence appeared concerning hydrogen peroxide participating in induction of separate protective reactions of plants lately (Foyer & Noctor 2005). H_2O_2 is not only a strong oxidizing agent accumulated upon various stress, but also acts as signal molecules in plant response to stress (Desikan *et al.* 2001; Gong *et al.* 2001; Prasad *et al.* 1994). For instance, hydrogen peroxide increased in the leaves of plants, when they were exposed to various stresses (Prasad *et al.* 1994; Uchida *et al.* 2002, 2006). Besides, it can effectively modulate the related gene expression and subsequently lead to the enhancement of plant tolerance to the stress (Azevedo Neto *et al.* 2005; Desikan *et al.* 2001; Hung *et al.* 2005). This compound is produced in response to action of a variety of stress inductors that seems to mediate cross-talk between signaling pathways and contribute to the phenomenon of cross-tolerance (when exposure of plants to one stress offers protection towards another; Gong 2001). Therefore, attempts have been made to use external treatment with hydrogen peroxide in order to enhance stress resistance of plants (He *et al.* 2009; Prasad *et al.* 1994; Wahida *et al.* 2007). Information available evidences H_2O_2-pre-treated seeds exhibited increases in germination rate, net photosynthetic rate, leaf area, and dry weight. The treatment greatly decreased malonyldialdehyde (MDA) and membrane damage rate for wheat varieties, being more effective in variant with tolerant variety. Seed pre-treatment with H_2O_2 reduces cellular membrane damages by drought stress and induces higher expression of antioxidative enzymes such as CAT and ascorbate peroxidase (APX) (He *et al.* 2009). Application of H_2O_2 positively affects the growth of the treated plants; and increment in net photosynthetic rate, stomatal conductance, internal CO_2 and chlorophyll content in the H_2O_2 exposed *Artemisia annua* plants were also noted. A significant upregulation in antioxidant enzymes, viz. CAT, peroxidase (POX) and SOD, was observed as a result of exogenous H_2O_2 treatment when applied foliarly or as soil drench (Aftab *et al.* 2011). It was also found that pre-treating rice seedlings with low levels (<10 μM) of H_2O_2 permitted the survival of more green leaf tissue, and of higher quantum yield for photosystem II at salt and heat stresses. It was also shown that the pre-treatment induces not only active oxygen scavenging enzymes activities but also expression of transcripts for stress-related genes (Orozco-Cárdenas *et al.* 2001). These results suggest that H_2O_2 can increase plant tolerance to various stresses acting as signal molecules for the response (Uchida *et al.* 2002, 2006). In our earlier work, it was also shown that treatment of wheat by hydrogen peroxide optimized the metabolic processes of plant organism and stimulated the development of adaptive reactions (Taran *et al.* 2008). That is why the purpose of our work was to explore the biochemical mechanisms of the induced resistance of winter wheat plants treated with hydrogen peroxide in the process of ontogenesis in field conditions, the basis of which is activation of natural protective mechanisms against action of environmental factors.

MATERIAL AND METHODS

Varieties of Ukrainian breeding (*Triticum aestivum* L.) during 2011–2012 vegetation were used for investigation. The originator of winter wheat variety Polisska 90 is "Institute of Agriculture of NAAS". It is in variety registry of Ukraine since 1994. The variety is established by individual selection from the variety Polisska 87. Variation – erytrospermum. The plant height is 105–110 cm. It is resistant to lodging and frost. The weight of 1,000 grains is 46.5–47.8 g, protein content is 14–15%, and wet gluten content is 30%. It is recommended for cultivation in the forest-steppe and marshy woodlands zones of Ukraine.

The originator of winter wheat variety Stolychna is "Institute of Agriculture of NAAS". The variety was created by the selection from a combination of crossing varieties Polisska 2, Kolosysta and Polisska 90. It is in the variety registry of Ukraine since 2005. Variation – erytrospermum. The weight of 1,000 grains is 48–53 g. Harvest is 7.10–8.25 t/ha, protein content is 12.5%, wet gluten content is 25.0%. The growing season is 295–300 days. The variety is resistant to lodging, drought, and frost. It is recommended for marshy woodlands and forest-steppe zones of Ukraine.

The originator of the winter wheat variety Scala is a private scientific-production association "Bor" (Odessa Institute APV). Variation – erytrospermum. It was created by the selection of varieties Odeska

51, Odeska 66, and Albatross Odeskyj. It is in the variety registry of Ukraine since 2007. The plant height is 74–90 cm, is winter-hardy, and is resistant to drought and diseases. Harvest is 6.22–6.49 t/ha. The weight of 1,000 grains is 41.3–46.0 g, and vegetation period is 270–286 days. The protein content is 13.8–14.1%, and wet gluten content is 29.7–30.3%. It is a strong wheat, recommended for steppe and forest-steppe zones.

Plants were grown in field conditions in the stationary rotation of the National Scientific Centre "Institute of Agriculture" on light loamy grey forest soil. The size of the experimental plot was 10 m^2. For the biochemical studies, samples of 10 plants were selected diagonally from plots. Farming for growing was common for the area. Wheat fertilization system consists of the main fertilizer, fertilizer in rows during planting, and fertilizing during the growing season. Nitrogen fertilizer was applied as dispersion of nitrogen fertilizer granular form in the early spring regrowth of plants (the second stage of organogenesis) at the dose of N30–40 or (20–30% of the design standards for the growing season). The second feeding took place in the same way at the early tubing of plants (the fourth stage of organogenesis) to increase productive tillering at the dose equal to 50% of nitrogen norm per growing season (40–60 kg). Third application was in phase of the "flag" leaf and earing to the grain formation beginning (7^{th}, 8^{th}, and 9^{th} stages of organogenesis).

To study the unspecific resistance development, experimental plants were treated with H_2O_2 in a concentration 1×10^{-4} M twice in the interval of 3 days. Control plants were treated with distilled water. Spraying of plants was performed at spring (tillering stage) when the thickness of the cuticle layer of leaves and stems is thin, which is the pre-condition of acting agent penetration. The discharge of H_2O_2 solution was 1 L/m^2. Within 24 h after treatment, the reaction of plants on the stressor action was explored. Later, in the next ontogenesis stage – flowering – the degree of plant adaptation was determined. Peroxidation of endogenous lipids was evaluated in the supernatant of plant flag leaf tissue homogenates as MDA formation revealed in condensation with thiobarbituric acid (Andreeva *et al.* 1988). Pigment content was determined spectrophotometrically (Porra *et al*. 1989). SOD activity (EC 1.15.1.1) was determined according to Chevari (1985), and CAT activity (EC 1.11.1.6) was determined according to Kumar (1993). H_2O_2 impact upon wheat productivity was estimated after harvest structure elements. The common amount of plants and number of productive stems per run meter (item/run m), number of grains in the ear (item), height of plant (cm), and mass of 1,000 grains (g) (Methods 1971) were determined. The results were treated by the method of variation statistics, and replications of experiments were threefold; the reliability of the difference between the arithmetic mean of indicators was established by variance analysis according to Fisher using the software Anova.

RESULTS AND DISCUSSION

Analysis of the obtained results (Table 1) revealed that hydrogen peroxide did not influence significantly the morphometric indexes of Polisska 90 plants; however the mass of 1,000 grains increased by 9%. The applied treatment induced similar changes at forest-steppe ecotype Stolychna, whereas the mass of 1,000 grains increased by 18% and harvest yield by 15%. In contrast, steppe ecotype variety Scala plants displayed index changes different from the other varieties, and the mass of 1,000 grains increased by 13%. It is necessary to note that in the period of phase of stalk-shooting, there was a natural drought, which appeared to be an additional abiotic stress factor.

At molecular level, oxidative stress (based on MDA as indicator) appeared as significant in case of varieties Scala and Polisska 90, since accumulation of lipid peroxidation (LP) products were detected after 24 h. In contrast, MDA levels decreased in cv. Stolychna. Except for SOD activity in cv. Polisska 90, inhibition of antioxidative enzymes like SOD and CAT was mostly observed in experimental plants (Table 2). Previously, it has been shown that soaking maize seeds in 100 mM hydrogen peroxide solution induced a transient significant decrease in SOD activity within first 24 h. However, soaking seeds with H_2O_2 induced a marked increase in CAT activity (Gondim *et al.* 2010). SODs are ubiquitous metal-binding enzymes that constitute the first-line of defense against ROS. SOD is the major super-

oxide scavenger and plays a key role in cellular defense mechanisms against ROS. It catalyzes the dismutation of superoxide into hydrogen peroxide and molecular oxygen and reduces the risk of $^{\bullet}OH$ formation (Azevedo Neto *et al.* 2005). Since certain dismutases (e.g. Cu, Zn-SOD, and Fe-SOD) can be inhibited by H_2O_2 (Bowler *et al.* 1994; Fridovich 1975; Kwiatowski *et al.* 1985), it is possible that treatment with H_2O_2 might cause decrease in SOD activity observed in two varieties in 24 h. Concerning CAT, it is known that the response of catalase to exogenously applied H_2O_2 varied depending on the isoform balance, exogenous H_2O_2 concentration, and stage of plant development. Two isoforms of wheat catalase, CAT-1 and CAT-2, exhibit an optimum activity at pH 7. When pH was decreased from 7 to 5.6, CAT-1 showed a decreasing affinity for its substrate, whereas the opposite was found for CAT-2. The difference in affinity for hydrogen peroxide as well as the poor stability of CAT-1 in acidic medium suggests that it might have relevance to effectiveness of the two enzymes (Garcia *et al.* 2000). Moreover, it was suggested that fluctuations in H_2O_2 levels may play a significant signaling role in effecting the tissue-specific and temporal expression of the different *Cat* genes in maize (Scandalios *et al.* 1997). Besides, chloroplasts scavenge and eliminate H_2O_2 through several mechanisms that do not necessarily use CAT. One of them is, for example, ascorbate–glutathione cycle, where APX reduces H_2O_2 to form water and dehydroascorbate. Chloroplasts have the capacity to reduce H_2O_2 in other subcellular compartments, too (Asada & Nakano 1980). Thus, CAT activity decrease in first 24 h may be due to changing pH while treating and/or activating another path of scavenging (via the ascorbate–glutathione cycle, for example). A similar result was demonstrated by Simova-Stoilova *et al*. (2008) at drought action – stable MDA content, deep CAT activity decrease, and SOD deviation depending on variety tolerance. Our results further showed that in the phase of flowering, the processes of peroxidation diminished and MDA levels were comparable with control variant meanings. Similarly, most of the observed differences in enzymatic activity disappeared, indicating the creation of new homeostasis.

As it was noted earlier, in the period of phase of stalk-shooting there was an additional abiotic stress factor – natural drought. However, such a stress of given intensity did not influence chlorophyll *a* and *b*

T a b l e 1

Hydrogen peroxide action upon harvest structure elements

Indexes	Productive stem number [item/run m]	Plant height [cm]	Grain number in ear [item]	1,000 grains mass [g]	Grain yield [t/ha]
Stolychna variety					
Control	85.00	108.60	37.70	38.60	7.45
Experiment	76.00	104.30	41.10	45.60	8.57
Difference	9.00^{+}	4.30^{+}	-3.40^{+}	-7.00	-1.12^{+}
Polisska 90 variety					
Control	73.00	93.00	41.10	41.40	5.20
Experiment	76.00	98.00	42.20	45.40	5.60
Difference	-2.70^{+}	-5.00^{+}	-1.10^{+}	-4.00^{+}	-0.40^{+}
Scala variety					
Control	67.00	73.30	31.30	30.10	4.32
Experiment	71.00	78.00	33.00	34.30	4.67
Difference	-4.08^{+}	-4.70	-1.70^{+}	-4.20^{+}	-0.35^{+}
$LSD_{0.05}$	1.50	1.00	1.00	1.10	0.14

$^{+}$indicates significant differences between the values of H_2O_2 treated and control plants ($P = 0.05$)

Table 2

Physiological parameters of wheat leaves after hydrogen peroxide treatment

Stage	Variety	Variant	MDA	SOD	CAT	Pigment content [mg/g DM]		
			µM/g DM	Conventional units	µ MH_2O_2/g DMxmin	chl *a*	chl *b*	Carotenoids
Shooting stage	Stolychna	Control	9.67	15.09	40.35	10.08	2.91	2.09
		Experiment	7.97	8.78	15.19	9.11	2.73	1.85
		Difference	1.70$^+$	6.31$^+$	25.16$^+$	0.97$^+$	0.18$^+$	0.24$^+$
	Polisska 90	Control	10.22	8.89	44.65	8.31	2.44	1.71
		Experiment	11.97	12.72	32.95	9.37	2.70	1.92
		Difference	-1.75$^+$	-3.83$^+$	11.70$^+$	-1.06$^+$	-0.26$^+$	-0.21$^+$
	Scala	Control	9.08	12.50	41.55	8.53	2.45	1.77
		Experiment	11.65	2.92	30.71	8.15	2.26	1.74
		Difference	-2.57$^+$	9.58$^+$	10.84$^+$	0.38$^+$	0.19$^+$	0.03
Flowering stage	Stolychna	Control	7.06	12.50	70.00	10.14	3.16	2.11
		Experiment	7.64	10.40	74.00	9.74	3.13	2.14
		Difference	-0.58$^+$	2.10$^+$	-4.00$^+$	0.40$^+$	0.03	-0.03
	Polisska 90	Control	7.26	14.70	68.00	6.59	1.79	2.24
		Experiment	7.44	17.10	71.00	6.85	1.91	1.81
		Difference	-0.18	-2.40$^+$	-3.00$^+$	-0.26$^+$	-0.12$^+$	0.43$^+$
	Scala	Control	8.24	13.00	69.40	5.87	2.25	1.10
		Experiment	8.71	18.00	73.00	6.54	2.29	1.45
		Difference	-0.47$^+$	-5.00$^+$	-3.60$^+$	-0.67$^+$	-0.04	-0.35$^+$
$LSD_{0.05}$			0.28	1.36	0.20	0.16	0.06	0.05

$^+$indicates significant differences between the values of H_2O_2 treated and control plants ($P = 0.05$)

content at experimental plants. There were some intervarietal differences in the content of photosynthetic pigments. Upon stress, however, the carotenoid levels increased significantly in only Scala plants indicating antioxidant defense.

CONCLUSIONS

The results of investigations performed showed that exogenous hydrogen peroxide affected winter wheat plants in variety peculiarity depended manner. For Stolychna and Scala varieties treated with H_2O_2, the scavenging by SOD was apparently not involved possibly because of inhibition by high H_2O_2 level. In addition, all varieties treated showed decrease in CAT activity. Thus, oxidation balance was likely regulated by other mechanisms (judging upon MDA indexes, especially of Stolychna plants). Treatment with H_2O_2 of both forest-steppe and steppe ecotypes in the concentration of 1×10^{-4} at the beginning of vegetation promoted their adaptation to other environmental stress factor action in different ways and increased general adaptation reactions at later stages of ontogenesis. Taking into account that hydrogen peroxide promoted general unspecific resistance of plants of all varieties studied, we assumed its positive influence on plant productivity. This resistance is obviously not connected with activation of antioxidation enzymes. In common, a strategy of plant adaptation to oxidative stress induced by hydrogen peroxide treatment is directed in support of redox homeostasis restoration, which could be realized by a number of variety-dependent physiological mechanisms.

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