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FEATURES OF THE SYSTEM OF ANTIOXIDANT PROTECTION OF THE PLANT ORGANISM

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Introduction

The dynamic influence of environmental factors requires a high resistance from the body, which is manifested in both adaptation and immune resistance. The pro-oxidant-antioxidant system of all living organisms is very sensitive to the influence of any environmental factors and is a marker of stability at the molecular level[1]. The high-quality composition of food products and their influence on the general resistance of the body are extremely relevant for a person[2]. On the other hand, the maintenance of a high immune status of plants is also determined by the indicators of the pro-oxidant-antioxidant system and is of great practical importance when carrying out selection work to breed plant varieties characterized by high immune resistance and adaptive capacity. Taking into account all of the above, the study of the system of antioxidant protection (AOP) of plants is urgent, relevant and has a significant practical perspective.

The system of antioxidant protection of plants includes the prevention of the formation of reactive oxygen species (ROS), their inactivation, the interruption of the chain of ROS reactions, the inactivation of products of free radical peroxide oxidation (FRPO), and the repair of damage[3]. Antioxidants (AO) are represented by antioxidant enzymes and low-molecular compounds that do not have enzymatic activity[4].

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1. Features of the enzyme antioxidant system of the plant organism

The most important enzymatic AO present in all cells and organs of plants are superoxide dismutase, catalase, a number of peroxidases, enzymes of the ascorbate-glutathione cycle and cytochrome oxidase[5].

Superoxide dismutase (SOD, ES 1.15.1.1) catalyzes the reaction of disproportionation of O_2^- to molecular oxygen and hydrogen peroxide: $2{\bullet}O_2^- + 2H^+ \rightarrow H_2O_2 + O_2$. The mechanism of action of SOD was established by K. Asada in 1966 and is based on the sequential reduction and oxidation by superoxide of the metal cation of the active center of the enzyme[6]: $СОД\text{-}Me^{n+} + {\bullet}O_2^- \rightarrow СОД\text{-}Me^{(n-1)+} + O_2$; $СОД\text{-}Me^{(n-1)+} + {\bullet}O_2^- + 2H^+ \rightarrow СОД\text{-}Me^{n+} + H_2O_2$. A characteristic feature of plant cells is the presence of all three isoforms: Cu-Zn-SOD, Mn-SOD and Fe-SOD. SOD is the first line of defense against ROS, which interrupts the FRPO chain at the initiation stage and accelerates the dismutation of ${\bullet}O_2^-$ (inducer of other ROS) by 10^4 times[7]. An increase in SOD activity is observed in conditions of water deficit and overwetting of the soil, during heat shock, cooling, salt stress, UV radiation, intense lighting, treatment with ozone, heavy metal salts, abscisic acid, during inoculation with pathogens, which is associated with the activation of latent forms SOD and the synthesis of new ones in response to the release of ROS under stressful conditions. It should be noted that plants resistant to adverse factors, in contrast to sensitive ones, are characterized by higher SOD activity and less pronounced oxidative damage[8].

A decrease in SOD activity is associated with the long-term and intensive effect of the above-mentioned stress factors and aging, which is explained by the depletion of the enzyme pool due to its increased use for ${\bullet}O_2^-$ dismutation, an imbalance in the synthesis and destruction of SOD by inactivation of the AFO enzyme.

Regulation of SOD activity is carried out at the level of transcription (under the influence of stressors), translation (depending on the amount of

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substrate) and through post-translational modification. Components of the signal transduction pathway involved in the activation of SOD and the regulation of its gene expression are AFO, Ca^{2+}-ions, NO, glutathione, phytohormones (abscisic acid) and salicylic acid and melatonin [6].

Catalase (ES 1.11.1.6) is a heme-containing tetrameric enzyme of the class of oxidoreductases that catalyzes the breakdown of hydrogen peroxide with the formation of molecular oxygen and water: $2H_2O_2 \rightarrow O_2 + 2H_2O$, thus breaking the superoxide conversion chain: $\bullet O_2^- \rightarrow H_2O_2 \rightarrow \bullet OH$. Thiol disulfide exchange is carried out in the active center of the enzyme, as the Fe^{2+} ion is coordinated by 4 Nitrogen atoms of heme pyrroles, histidine and sulfur or water, which are substituted for the substrate; during the catalytic cycle, ferrum changes the +2, +3 oxidation states with the formation of a chelate center in a porphyrin or protein. Plant catalases contain only one protohemin group, while animal catalases contain four. Catalase is one of the main enzymes that destroy ROS, and one of the most active enzymes[9]. Now the amino acid sequence of 74 different catalases has been decoded, among which 30 belong to plants, which are divided into III classes: I – utilize H_2O_2 formed in the process of photorespiration, localized in peroxisomes, expressed in leaves in the light, isolated from cotton, tobacco, Arabidopsis, corn; II – isolated from the vascular tissue of Arabidopsis, corn, tomato, potato; III – eliminates H_2O_2 formed in the process of α-, ώ-, β-oxidation of fatty acids, expressed in glyoxysomes and active in germinating seeds and sprouts of cotton, Arabidopsis, corn[10].

Regulation of enzyme activity is carried out at the gene level by H_2O_2 or melatonin, protection against high concentrations of the substrate is provided by the participation of NADPH: each subunit of the catalase tetramer is able to bind NADPH, which prevents the inactivation of the enzyme under the influence of H_2O_2. There is a relationship between SOD and catalase activity, as SOD supplies the substrate for catalase, which generates oxygen for the cell. Free and membrane-bound (reserve) forms of the enzyme are known, a decrease in the activity of the latter is a sign of the development of a pathological process[11].

Peroxidases are a group of oxidoreductases that act on hydrogen peroxide as an acceptor. Peroxidase catalyzes the oxidation of various substrates by hydrogen

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peroxide with the formation of oxidation products of these substrates and water. Catalase splitting of H_2O_2 into H_2O and O_2 is a special case when one H_2O_2 molecule is a peroxidase substrate, and the second is an oxidant, an electron acceptor. Polyphenols in the free state or in the form of glucosides, tannins and aromatic amines are the most common substrates on which peroxidase acts in plant tissues. Peroxidase can also function as an oxidase, channeling the oxidation of the substrate due to molecular oxygen in the absence of H_2O_2. Cofactors of the reaction are Mn^{2+} and a number of phenols[12].

Peroxidase is functionally related to diphenoloxidase, participates in metabolic reactions of polyphenol synthesis, coupled with the activity of flavin enzymes, ensures the normal course of oxidative processes under the influence of stress factors, in particular pathogenic[13]. Activation of peroxidase under the influence of infection is a characteristic biochemical response that determines plant resistance. De novo synthesis of peroxidase is induced under the influence of toxins released by infectious agents. At the same time, new isoenzymes are synthesized that are not present in the native tissue. Peroxidase plays a role in the use of oxygen resources of the cell: when the aeration of plant organs is reduced, the activity of peroxidase increases. Peroxidase is present in plant mitochondria, where it can catalyze the oxidation of menadiol to menadiane (vitamin K3). Vitamins of group K are involved in electron transport and oxidative phosphorylation. Peroxidase can function as an anaerobic dehydrogenase or $NADH{\cdot}H^+$-cytochrome-c-reductase, which indicates the possible functioning of peroxidase as an electron carrier in the electron transport chain of mitochondria. Peroxidase of chloroplasts performs the functions of both peroxidase and oxidase. The $NADP{\cdot}H^+$-oxidase effect of peroxidase is more pronounced compared to its ability to catalyze the oxidation of ordinary substrates of peroxidation[14].

Peroxidases are heme-containing glycoproteins that use different substrates as donors, depending on which they are divided into III groups: ascorbate peroxidase, guaiacol peroxidase, and glutathione peroxidase. ***Ascorbate peroxidase*** (ES.1.11.1.11) reduces H_2O_2 during oxidation of AA, is present in chloroplasts, cytosol, mitochondria, peroxisomes, apoplast in various isoforms, some of which are associated with membranes (thylakoid, peroxisomal). It has a high affinity for the substrate, eliminating H_2O_2 at the

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lowest concentrations. As part of the ascorbate-glutathione cycle, it plays a major role in controlling the level of H_2O_2 in plant cell compartments[15]. ***Guaiacol peroxidase*** (ES.1.11.1.7) reduces H_2O_2 by oxidizing phenolic compounds. Present in cell walls and vacuoles, it participates in the biosynthesis of lignin, directing peroxide to the formation of crosslinks between phenolic components. It is activated by the invasion of pathogens, the action of ozone and UV radiation. In cell walls, it is able to show a pro-oxidant effect. ***Glutathione peroxidase*** (ES.1.11.1.9) uses reduced glutathione as a hydrogen donor, potentially able to eliminate lipid peroxides and H_2O_2 ($2GSH + H_2O_2 \rightarrow GSSG + 2H_2O$; $2GSH + ROOH \rightarrow GSSG + ROH + H_2O$), but for plants, H_2O_2 reduction reactions direct use of GSH is either not characteristic at all or is of low efficiency. The reason is the low affinity of the enzyme to H_2O_2. A characteristic feature of plant GSH-peroxidase is that it does not contain any of its forms. The enzyme is localized in the cytosol, chloroplasts, and peroxisomes. NAD-peroxidase (ES 1.11.1.1) is also known; NADP-peroxidase (ES 1.11.1.2); fatty acid peroxidase (ES 1.11.1.3); cytochrome peroxidase (ES 1.11.1.5***)***[3,9].

Peroxidase inhibitors can be all substances capable of forming compounds with Ferrum that open at least one of the six coordination bonds in the hemoprotein chelate complex, or make it impossible for peroxides to access Ferrum and thus reversibly or irreversibly inactivate the enzyme.

The plant cell also contains *glutathione-S-transferase* (ES 2.5.1.18) and *glutathione reductase* (GSH-reductase; ES 1.6.4.2). Glutathione-S-transferase inhibits the initiation of lipid peroxidation, catalyzes the conjugation reactions of GSH with toxins – organic xenobiotics – herbicides ($ROH + GSH \rightarrow RSG + H_2O$; $RCl + GSH \rightarrow RSG + HCl$), directing less toxic conjugates to the vacuole and cellular wall, where they can be stored until the natural death of an organ or plant. GSH-reductase is an intracellular flavoprotein that maintains a high level of reduced glutathione due to the following reaction: $NADPH + H^+ + GSSG \rightarrow NADPH^+ + 2GSH$[16].

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2. Features of the system of low molecular weight antioxidants of the plant organism

The most important non-enzymatic low-molecular antioxidants of the plant organism are ascorbic acid, α-tocopherol, reduced GSH, carotenoids, flavonoids and isoprene.

Ascorbic acid (AA, 2,3-enediol-1,4-lactone-L-gulonic acid, vitamin C) is the most common metabolite and key antioxidant of all cellular compartments of plants, where ROS formation occurs. Its synthesis begins with UDP-glucose and is characterized by the fact that, unlike animals, only initial and intermediate reactions occur in plants in the cytosol, and the final stage takes place on the inner membrane of mitochondria[17].

AA is a precursor of many compounds of plant metabolism and a cofactor of enzymes, affects cell growth, morphogenesis, synthesis of ethylene, gibberellins, anthocyanin; non-enzymatically reduces oxidized tocopherol, folic acid, converting it into tetrahydrofolic acid; restores Fe^{+3} to Fe^{+2}, which is necessary for the introduction of iron into transferrin and the regeneration of Fe-containing oxidases in hydroxylation reactions, is a protector of carcinogenesis, although its excess has a pro-oxidant effect. AA, as one of the main antioxidants, is a potential donor of hydrogen atoms and electrons used to reduce H_2O_2 and free radicals [18].

AA is stable only in an acidic environment, its content changes with the age of plants, seasonally and during long-term storage. There are four enzyme systems involved in the oxidation of AA. This is a specific oxidase AA-oxidase (ES 1.10.3.3), cytochrome system, polyphenol oxidase (ES 1.14.18.1) in the presence of polyphenols and peroxidase in the presence of H_2O_2. The content of AA in flower petals increases in proportion to the intensity of their color. AA is practically absent in the seeds of plants, but during germination, when intensive metabolism begins, the formation of AA increases rapidly. Vegetative organs of the plant contain more AA and less dehydroascorbic acid in proportion to the amount of light. In most plants, a high content of AA is observed in unripe fruits and decreases as they ripen. A lot of AA accumulates in microspores during pollen formation.

The content of AA is the highest in photosynthesizing leaves (up to 10-50 mM), which transport it through the phloem to the acceptor organs – buds, fruits, roots. Thus, chloroplasts contain a significant amount of AA, which in

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[18] Paciolla C.; Fortunato, S.; Dipierro, N.; Paradiso, A.; De Leonardis S. Vitamin C in Plants: From Functions to Biofortification. Antioxidants. 2019. 8(11), 519. doi.org/10.3390/antiox8110519

terms of mass is not inferior to the content of chlorophyll, and expressed in moles even exceeds it. It is known that AA contributes to the biosynthesis of chlorophyll and its restoration in the dark, increases the phosphorylation of isolated chloroplasts, stabilizes the photophosphorylation of fragments of photosynthetic membranes, which will contribute to the enhancement of photochemical activity and photophosphorylation.

With the participation of AA, resistance of plants to adverse environmental factors is formed: low temperature, radiation, invasion of pathogens, etc. The level of endogenous AA serves as a test that characterizes the resistance of plants[19].

Thus, listing the main processes in which AA participates: photosynthesis, respiration, growth, development, flowering, persistence, genome expression, vegetative and reproductive differentiation, water exchange, regulation of enzymatic activity, biosynthetic and biophysical processes, nitrogen fixation, nitrite reduction, non-enzymatic reduction of tocopherol, stimulation of metabolic reactions associated with the exchange of nucleic acids and protein synthesis, in the protective reactions of plants, participation in the functioning of the AO systems of chloroplasts, mitochondria, peroxide, cytosol and apoplast – it can be argued that AA includes almost all aspects of plant life and is one of the most important multifunctional compounds of autotrophs.

Another key AO of plant cells is reduced ***glutathione*** (GSH, γ-Glu-Cys-Gly). GSH is synthesized mainly in the cytosol and chloroplasts from glutamate, cysteine, and glycine in two ATP-dependent reactions catalyzed sequentially by γ-Glu-Cys synthetase and glutathione synthetase. The intensity of synthesis is determined by the level of FRPO. GSH in plant cells has a fairly high content (0.2-10 mM). GSH is a source, reservoir and transport form of reduced Sulfur, as well as a key participant in the processes related to the detoxification of heavy metals, xenobiotics and excretory products of metabolism[20].

GSH as a cofactor participates in glyoxalase and maleylacetoacetate-isomerase reactions, in the oxidation of formaldehyde to formate, transports amino acids through the membrane, as a nucleophilic agent forms conjugates with electrophiles, is a substrate for the synthesis of phytochelatins, low molecular weight peptides that neutralize heavy metal compounds. As an AO, glutathione can donate thiogroup hydrogen to ROS and organic radicals, reduce disulfide groups of proteins and dehydroascorbic acid, is a necessary component for maintaining the ascorbate reactions of the glutathione cycle, as a pro-oxidant in

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[19] Rietjens IM, Boersma MG, Haanm Ld, Spenkelink B, Awad HM, Cnubben NH. et al. The pro-oxidant chemistry of the natural antioxidants vitamin C, vitamin E, carotenoids and flavonoids. Environ Toxicol Pharmacol. 2002. 11:321–33. DOI: 10.1016/s1382-6689(02)00003-0

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excess it itself forms a radical, that is, it can be a source of radicals. During oxidation, two GSH molecules donate hydrogen atoms, forming oxidized glutathione (GSSG): 2GSH + 2•OH = $2H_2O$ + GSSG. The reverse reaction is catalyzed by the enzyme GSH-reductase when NADPH is used: GSSG + НАДФН + H^+ → 2GSH + + $НАДФ^+$. In a normally functioning cell, the main GSH pool is in a reduced state, and only in seeds that are at rest is all GSH oxidized. Oxidized GSH inhibits membrane ATPases, hexokinase, glucose-6-phosphate dehydrogenase, phosphorylation and nuclear synthesis of RNA[21].

Tocopherols (vitamins of group E) are important AO of plant cells, synthesized exclusively by plants and phototrophic microorganisms. Known α-, β-, γ– and σ-tocopherols. α tocopherol, which is synthesized by enzymes localized on the inner membrane of chloroplasts, dominates in photosynthetic tissues; in other tissues, γ-tocopherol prevails, the most of which is in the seeds of oil crops. The σ-form of tocopherol exhibits the greatest AO effect. All tocopherols are lipid-soluble amphipathic compounds with a chromane core and an isoprene hydrocarbon chain immersed in the lipid layer of the membrane, stabilizing it. The antioxidant properties of tocopherols are determined by the relay transfer of a radical from the membrane through the hydrocarbon chain to the chroman nucleus, which is both a hydrogen donor of phenolic nature and a radical inhibitor that inactivates $^1O_2$, $•O_2^-$, •OH, hydrocarbon and peroxide radicals directed both from the membrane and and from the cytoplasm. Non-enzymatic reduction of the chroman nucleus is carried out by AA[19]. Tocopherol is synthesized in plants through mevalonic acid and tyrosine conversion. It is mostly found in vegetable oils (rosehip, walnut, sea buckthorn), where it protects lipids and carotenoids from oxidation, in wheat germ, green vegetables. Tocopherol binds the products of phospholipase hydrolysis, increases the microviscosity of membranes, enhances the synthesis of GSH and the activity of GSH-reductase, supports oxidative phosphorylation, the content of ubiquinone and ETC enzymes of mitochondria. As AO, it is 7 times more active than AA[19, 21].

Flavonoids (vitamins of the P group) are a group of phenolic compounds that use the Hydrogen atom from the OH group of the aromatic ring to eliminate free radicals. Flavonoids include anthocyanidins, flavones, flavonols, chalcones, and aurones. As AO, flavonoids reactivate sulfhydryl

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[21] Radyuk M.S., Domanskaya I.N., ShcherbakovR.A., Shalygo N.V. Effect of low above-zero temperature on the content of low-molecular antioxidants and activities of antioxidant enzymes in green barley leaves. Russ. J. Plant Physiol. 2009. 56(2) : 175-180. https://doi.org/10.1134/S1021443709020058

groups, GSH, AA and tocopherols. The synthesis of flavonoids is activated by stressors[22].

Carotenes and ***xanthophylls*** are mandatory components of the photosynthetic apparatus of plants, and one of its main protectors. They have a π-system of conjugated multiple bonds through which an unpaired electron is transported. As AO, they actively compete for AFO with polyunsaturated fatty acids, inactivating singlet oxygen and accepting AFO with the formation of peroxides[23].

Isoprene is a volatile compound that is formed in chloroplasts during the synthesis of carotenoids with the participation of the enzyme isoprene synthase, ATP and NADPH. AO properties are due to the ability to inactivate ROS and prevent necrosis under the influence of O_3 and extreme temperatures.

It should be noted that the mechanisms of AOP of plants from ROS are not limited only to the activity of AO enzymes and the content of low molecular weight AO, so, for example, it is possible to modify the activity of the pro-oxidant enzyme peroxidase: with an excess of H_2O_2 in the apoplast, the peroxidase activity is switched to catalase. In such conditions, H_2O_2 is used as an oxidizing and reducing substrate. Another mechanism of AOP is the activation of an alternative (cyanide-resistant) electron pathway and an increase in the content of polyfunctional low-molecular-weight protectors (proline, polyamines, sugars) in plants, and the synthesis of a fairly wide range of stress proteins[24].

Melatonin (N-[2-(5-Methoxyindol-3-yl-l)ethyl]acetamide) is a derivative of tryptophan, in the body of animals it is a hormone, neurotransmitter, cytokine, stimulator of the immune system, which exhibits anti-geriatric, anti-carcinogenic, anti-stress and antioxidant effects . Melatonin in higher plants was first discovered by the Japanese scientist M. Hattori in 1995, who also experimentally determined the level of melatonin in 24 edible plants and noted its highest content in the herbaceous variety Festuca arundinacea. M. Hattori proved that plant melatonin is able to bind to mammalian melatonin receptors, which is extremely important because it indicates that animals can replenish their endogenous supply of this biologically active substance by consuming appropriate plant food. This conclusion is valid for humans as well and opens up prospects for the natural introduction of phytomelatonin into the body instead of its less effective synthetic analogues. Another researcher

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[23] Kreslavski V. D., Allakhverdiev S. I., Los D. A., Kuznetsov V. V. Signaling role of reactive oxygen species in plants under stress // Russ. J. Plant Physiol. 2012. 59. P. 141–154. DOI:10.1134/S1021443712020057

[24] Gill, S. S., Tuteja, N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol. Biochem. 2010. 48, 909–930. doi: 10.1016/j.plaphy.2010.08.016

F.A. Badria in 2002 published data on determining the level of melatonin in medicinal and agricultural plants[25].

According to the works of F.A. According to Badria, onion (0.299 ng/g), white cabbage (0.309 ng/g), carrot (0.494 ng/g), barley (0.873 ng/g) and wheat (1.878 ng/g) have the highest melatonin content among agricultural plants.

Chinese researcher Zhang Chen in 2003 conducted a comparative analysis of melatonin content in 108 Chinese medicinal herbs and found that more than half of the research plants contained melatonin in excess (more than 10 ng/gm). After analyzing the therapeutic effect of these plants, the scientist established that all of them are used to treat diseases associated with the influence of free radicals. Tettamanti Cerabolini established in 2000 that the high content of melatonin in alpine medicinal plants is associated with their protection against the harmful effects of UV radiation and ozone in high-altitude conditions. Recently, the number of publications on the content of melatonin in almost all plants has been increasing. A high level of melatonin is necessary to protect seeds from environmental factors such as UV radiation, drought, extreme temperatures, and chemical pollution.

Melatonin inhibits gene expression of pro-oxidant enzymes Nitrogen (II) oxide synthase and lipoxygenase, can be a ligand in chelate complexes of metal ions of variable valence, producing ROS. Melatonin is also a natural cyclooxygenase inhibitor.

Melatonin, as a donor of electrons and hydrogen atoms, inactivates $^1O_2$, $•O_2^-$, H_2O_2 and •OOH, •OH, •NO and the product of its reaction with $•O_2^-$, ONOO. Melatonin is a synergist of thiol (GSH), phenolic antioxidants (vitamins E and P), AA, but, unlike them, it is amphiphilic, so it is an antioxidant in the aqueous and lipid phases of the body. By reacting with two hydroxyl radicals, melatonin forms cyclic 3-hydroxymelatonin, which is a marker of oxidative stress, and 6-hydroxymelatonin, the antioxidant properties of which are better expressed than those of melatonin. As an indirect antioxidant, melatonin stimulates the activity of antioxidant enzymes – GSH-peroxidase, GSH-reductase, glucose-6-phosphate dehydrogenase, catalase, increases the content of i-RNA SOD and glutathione enzymes in cells.

Melatonin reduces the expression of lipoxygenase (5-LOG, 12 LOG, 12-13 LOG), NO-synthase. Melatonin reduces the production of MDA and 4-hydroxyalkenals, inhibits peroxide and radiation damage. Accumulating in cell nuclei, it has a genoprotective effect. The well-expressed ability of melatonin to restore oxidized guanine (8-oxoguanine) in DNA. Melatonin is reductively regenerated by AA, but unlike other low-molecular reducing

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[25] Badria F.A. Serotonin, tryptamine and melatonin in some Egyptian food and medicinal plants. J. Med. Food. . 2002. Vol. 5, № 3. P. 153–157.

antioxidants, which with O_2 and metal ions of variable valence generate ROS, melatonin is not a pro-oxidant[26].

Cytochrome oxidase (ferrocytochrome *c*, O_2-oxidoreductase, complex IV, ES 1.9.3.1.) is a lipid-containing hemoprotein containing 2 a-type hemes, each of which includes an Iron atom coordinated with four Nitrogen atoms in the tetrapyrrole system of the porphyrin and 2 Cuprum atoms in the prosthetic group. Cytochrome oxidase is the terminal part of the respiratory chain of mitochondria, which catalyzes the transfer of four electrons from coenzyme Q through cytochrome to oxygen, which combines with H^+ to form water: $4H^+ + 4e^- + O_2 \rightarrow 2H_2O$. The enzyme is tightly bound to the inner membrane of mitochondria, inhibited by cyanide and Carbon (II) oxide (in the dark).

Cytochrome oxidase has the highest affinity for oxygen among all other oxidases. Depending on the type of plants, the vegetation period, and external conditions, the maximum activity of cytochrome oxidase is at 1,5 and 6.5% O_2. Higher oxygen concentrations do not increase the activity of this enzyme, and in most cases even inhibit it. So, for example, multi-layered parenchyma, which has a limited supply of oxygen, is characterized by a saturated activity of cytochrome oxidase.

Cytochrome oxidase was found in isolated plastids, and its activity depends on the state of the plastid structure. Cytochrome oxidase is involved in the synthesis of chlorophyll. If in animal tissues cytochrome oxidase is a mandatory component of the respiratory chain, then in plant tissues this enzyme is not the only terminal oxygenase, its functions in plants can also be performed by ascorbinate oxidase, diphenol oxidase system, flavin oxidases and others. Cytochrome oxidase is a marker of the intensity of FRPO, since peroxide destruction of membranes reduces the activity of the enzyme. The release of cytochrome c from the mitochondrial chain triggers the process of apoptosis[27].

CONCLUSIONS

Thus, generation of ROS and synthesis of AO accompanies all physiological and pathological processes of the body. The impact on the body of environmental factors of biogenic and abiogenic origin is reflected in the

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state of its pro-oxidant-antioxidant balance, the violation of which is the cause of most disorders.

The enzymatic link of the antioxidant protection system includes SOD, catalase, peroxidases, enzymes of the ascorbate-glutathione cycle. The most important low-molecular antioxidants of the plant organism are AA, α-tocopherol, reduced GSH, carotenoids, flavonoids and isoprene. The result of the interaction of ROS, their transformation products, low molecular weight and enzymatic antioxidants is a change in the activity of cytochrome oxidase.

The distribution of antioxidants in the plant cell is uneven and is determined by the localization of sources of ROS generation. Thus, their content is highest in chloroplasts and mitochondria, where direct contact of molecules with singlet oxygen and superoxide anion radical was recorded. Powerful generators of prooxidants are lysosomes, peroxisomes and the cell wall, which, accordingly, have a strengthening of the antioxidant line of defense. The presence of glycolytic processes in the cytosol also requires antioxidant compensation.The research of the mechanisms that ensure the pro-oxidant-antioxidant balance opens the perspective of regulation of the body's general reactivity, influence on the processes of adaptation and immune resistance. This is of great practical importance when carrying out selection work on the breeding of plant varieties characterized by high immune resistance and adaptive capacity. Knowledge about the content of antioxidants in food products is no less relevant and practically important for strengthening the protective forces of the human and animal body, developing the rules of rational nutrition under the influence of stressors of any nature.

SUMMARY

The pro-oxidant-antioxidant system of all living organisms is a marker of resistance at the molecular level. The high-quality composition of food products and their influence on the general resistance of the body are extremely relevant for a person. The maintenance of a high immune status of plants is also determined by the indicators of the pro-oxidant-antioxidant system and is of great practical importance when carrying out selection work to breed plant varieties characterized by high immune resistance and adaptive capacity. The most important enzymatic antioxidants present in all plant cells and organs are superoxide dismutase, catalase, a number of peroxidases, and enzymes of the ascorbate-glutathione cycle. The top non-enzymatic low-molecular antioxidants of the plant body are ascorbic acid, α-tocopherol, reduced glutathione, carotenoids, flavonoids and isoprene. Cytochrome oxidase is a marker of the intensity of free radical peroxidation of biopolymers, and therefore a marker of the power of the antioxidant link and an indicator of the pro-oxidant-antioxidant balance.

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