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FORMATION OF PLANTS NONSPECIFIC INDUCED IMMUNITY AT THE BIOGENOUS STRESS

(review)

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Abstract

Because of pesticide pollution and violation of protective reactions in biosystems, the ways to increase a nonspecific natural resistance in plants is relevant. For the recent decades the mechanisms of pathogens-to-plant cell interaction were revealed. To identify chemical signals arising in the spots of plant infection by pathogenic microorganisms, the term «elicitor» was suggested (M. Yoshikawa et al., 1993; M. Thakur et al., 2013). Cell innate immunity is based on the recognition of phytopathogenic surface molecules, which is a primary signal for actuating the complicated network, including induction and phytoimmunity regulation (I. Tarchevskii, 2000). During signaling the essential role is played by proteins and small molecule messengers (salicylic acid and jasmonic acid, hydrogen peroxide, nitric oxide). Salicylic acid is involved in amplification and multiplication of the signals coming from the receptors into the plant cells, which ensures the timely activated protection. The earliest plant organism response to the pathogen introduction is a local generation of reactive oxygen species (oxidative burst), triggering a chain of subsequent defense mechanisms (S. Tyuterev, 2002). A significant increase in the level of reactive O₂ and H₂O₂ has an inhibitory effect on the pathogenic microorganisms. The reactive oxygen species (ROS) are also suggested to play significant role in the membrane lipooxidation, cell wall modification and signal transduction (C. Richael et al., 1999; T. Pietras et al., 1997). A key role in ROS regulation is played by an antioxidant defense system, which function is to slow down and prevent intracellular oxidation of organic substances. In this, the antioxidant enzymes (superoxide dismutase, catalase, peroxidase) and low molecular weight antioxidants (ascorbic acid, glutathione, tocopherol, carotenoids, anthocyanins) are mainly involved (S.S. Gill et al., 2010). A defensive effect of peroxidases is due to oxidation of phenolic compounds to quinones (B. Barna et al.; 1995, E.N. Okey et al., 1997). The correlation was found between peroxidase activity in plant tissues and plant resistance to pathogens (T.B. Kumeiko et al., 2009; N. Radhakrishnan et al., 2009). An increase in catalase activity is a defense reaction in cells during the next stages of biotic stress development (F.M. Shakirova, 2001). Starting from reception of signaling molecules of phytopathogens on the cell membrane all metabolic processes are controlled by resistance genes that regulate complex defense reactions (V. Repka et al., 2004). As a consequence, plants produce large variety of substances, carrying protection functions. The main ones are phytoalexins and PR-proteins (Yu. D'jakov, 2012). Due to stress proteins, the enzymes get activated, the membrane stabilization occurs, the activity of mitochondria and chloroplasts increases, and, therefore, the energy level rises (T. Chirkova, 2002). The data summarized herein are the basis for developing new concept for protection of agricultural crops by means of biologicals with eliciting effect that boost plant immune state.

Keywords: elicitors, phytoalexins, genome, resistance genes, salicylic acid, jasmonate acid, peroxidase, catalase.

Long use of ecotoxic pesticides in intensive agriculture resulted in an increased destabilization of agrocenoses and a decreased plant resistance to pathogens [1]. These obviously need to improve cardinaly the understanding of plant pathogenesis, and, primary, diagnostics of immune state which determines the course of pathological processes and adequate defense measures [2, 3].

Article provides an overview of the data concerning the main regularities of an induced nonspecific immunity and the mechanisms which make it possible to estimate plant resistance to phytopathogens [4-6]. These results make the base for development of new concept in plant defense with a view to promoting agro-

cenose immunity and environmental improvement due to lowering pesticide load by means of immune-stimulating preparations.

The pathathogenic microorganisms being in touch with plants are shown to excrete the compounds providing infestation of plant tissue. Chemical signals produced in the locus where infection occurs are defined as elicitors [2, 7]. Elicitors are the initial signals and triggers of phytoimmunity induction and regulation [8]. Nonspecific cell immunity in plants is based on recognition of surface molecules of phytopathogens, the nonspecific elicitors [9, 10]. Polysaccharides, proteins, polypeptides, glycoproteins, lipid-containing compounds can serve the biogenic nonspecific elicitors [11, 12]. The polysaccharide elicitors from fungal cell wall are mostly studied. Glucans and chitosans possess an expressed elicitor effect [13]. Interaction between elicitors and the receptors of cell plasmalemma is the first step in a signaling chain together with cell response to phytopathogen [14]. A possible number of molecular receptors of the same types can reach few thousands per cell thus providing reliable transmission of information from the elicitors of different chemical structure [4]. Presumably, the Ca^{2+} input and the K^+ и Cl^- output, the membrane depolarization, NADPH-oxidase activation, and cytosol acidation are involved in signal transmission into the cell [15].

Despite the individual mechanism for recognition of each elicitor, the complex of phosphorylation reactions is commonly involved, resulting in transfer of phosphoric acid residue to inner part of a receptor thus activating enzyme which is associated to [16, 17]. Receptors for all elicitors have the same structure and consist of an outer fragment located out of the cell, an intra-membrane fragment and a fragment located in the cytoplasm. The outer N-end of the receptor is elicitor-specific while the inner C-end possesses the specificity to the receptor-associated enzyme determining choice of a signaling system to be involved in interaction.

Transmembrane signaling from the outer receptors into the cell is one of the main mechanisms of metabolic regulation which area basic for intercellular signaling system [18-20]. In this, proteins and relatively small molecular messengers such as salicylic and jasmonic acids, hydrogen peroxide, nitric oxide, etc., prevail, being functional intermediates between the receptors and cell response manifested in metabolic modifications which result in increased immunity in plants [21]. Necrotrophic pathogens can induce jasmonate signaling pathway [14, 22]. Jasmonates are assumed to enhance the elicitors' effects as they are an integral part of signaling system [23, 24]. Plant infection caused by pathogenic microflora is accompanied by ethylene production, the hormone important for increasing plant resistance [31].

Biotrophic microorganisms have been shown to induce the salicylate signaling pathway [7, 25]. Salicylic acid well meet the features of systemic signaling molecules, particularly can easy move over the phloem vessels due to physical characteristics perfectly adjusted to distant transport via the sieve tubes [4, 26-29]. Under the influence of pathogens its level rises tens-folds, and it can induce defense mechanisms in plants [30-32]. Salicylic acid is involved in enhancement and multiplication of the signals from receptors into cell thus guaranteeing relevant defense [14, 33]. Besides, a positive influence of salicylic acid on intracellular molecular processes should be mentioned. It participates in transport of newly synthesized proteins into nucleus, chloroplasts, mitochondria and vacuoles. Salicylic acid activates synthesis, protection and restoration of structures of nucleic acids and proteins important for plant viability [4].

Generation of active oxygen species (AOS) is one of earliest plant cell response to the elicitors [34-37]. Of them, the superoxide anion and hydrogen peroxide are of special importance [38, 39]. The main potential sources of AOS are

NADPH-oxidase, peroxidase, amino oxidase, flavin-containing oxidases, poly-amino oxidases [40, 41]. AOS are assumed to possess a direct antimicrobial effect and be significant for other defense mechanisms, such as membrane lipooxidation, cell wall modification, and signal transduction thus inducing cell resistance or death from oversensitivity [42, 43].

Activation of oxidative burst is a core component of highly amplified and integrated signaling system [41]. These reactions make a base for formation not only local resistance but also induced systemic immunity due to which plant resistance to microorganisms, fungi and viruses increases [44]. Under optimal conditions the AOS are produced in small concentrations mainly in chloroplasts, mitochondria and peroxisomes [45]. Intensive AOS production in cell is a universal nonspecific response to pathogens as any other stressors such as high temperature, drought, frosts, eco-toxicants [46]. Obviously, H_2O_2 and another AOS can be «double agents», either inducing directly an oxidative stress which results in cell destroying and death, or act as signaling molecules which induce molecular, biochemical and physiological reactions contributing to plant adaptation and resistance [47-50]. Salicylic acid is most powerful inducer of AOS [46, 51].

A key role of AOS level regulation in cell belongs to antioxidant defense system of which the main function is to slow down and to prevent oxidation of intracellular organic matters, to protect biological structures, and to provide detoxication of secondary metabolites [52-54]. During initial defense reaction to stress the AOS are neutralized and the free radical chain is interrupted [55]. In this the superoxide dismutase, catalase and peroxidase, etc., are important together with low-molecular antioxidants such as ascorbic acid, glutathione, tocopherols, carotenoids and anthocyanins [56]. For plant viability under different stresses a balanced AOS generation and degradation is crucial [57, 58], therefore catalase and peroxidase involved in AOS degradation and utilization are important, too [59].

In publications there are special references to multiple roles of peroxidases in plant resistance to phytopathogens [60]. An increased level of AOS in plant tissues initiates peroxidase activation and expression of the genes involved in control of induced systemic resistance. Genes determining peroxidase level in tissue are disclosed in many plant species. Peroxidase activation mainly serves to avoid the adverse AOS effects on cell structures. Peroxidases oxidate phenolic compounds to highly reactive quinones [61, 62]. Peroxidase was shown to enhance antibacterial activity of phenols in the presence of hydrogen peroxide. Particularly, it was reported that plant resistance to phytopathogens increases due to more solid plant cell wall as the lignin synthesis is activated by peroxidase. It was also reported that infection was a «catalyst» of some peroxidases. Their activation results in AOS production and is a defense mechanism together with NADPH-oxidase activity. So peroxidases, being a part of signaling system in plant cells, provide defense response which is adequate to the infection.

A direct correlation is revealed between the activity of plant tissue peroxidases and the resistance to pathogens [63-66]. Special attention is paid to peroxidases as an element of superoxide dismutase system for an elicitor signal transduction which, as a result, determines the character of cell response to infection [67, 68]. Peroxidase catalytic systems are considered the most important of biotic defense factors in plant protection against pathogenic microorganisms [69].

Catalases which control H_2O_2 level in plant tissues are also involved in a defense response [70-72]. Under biotic stresses the catalase activity of pathogen indicates its aggressiveness as it represses AOS in host plant tissues thus decreasing biocide effect of H_2O_2 [60, 73]. At the initial phase of pathogenesis it is neces-

sary to put down the catalase activity in plant cells. As a result, the H_2O_2 concentration in the tissues remains enough to kill pathogens. Due to salicylic acid binding catalases the H_2O_2 is accumulated and involved in the immune response [74-76]. Jasmonic acid demonstrates the same activity of catalase inhibiting.

Otherwise, catalase activation is a mechanism of decreasing plant defense potential [77]. As the catalase activity increases, the H_2O_2 level is putting down so that resistance is not developed and, in contrary, the plants become more susceptible to pathogens [78-80]. Since AOS are toxic both to pathogen and the host plant, the intracellular AOS level is controlled stringently by antioxidant system the catalase is a part of [81]. Besides, catalases restrict the AOS lifetime thus preventing their adverse effects in cells. Therefore, an increase in catalase activity is considered a positive defense response toward cell safety when biotic stress is in progress [82, 83]. Though the oxidative stress is an integral part of a developed infection, the enough antioxidant level enables plants to withstand it [12].

All these events are controlled by resistance genes which regulate the defensive mechanisms. Signaling systems and genome are related in two ways. On one side, all enzymes and other proteins are encoded by the genome, on the other side, gene expression or suppression is under control of the signaling systems. These include signal reception, multiplication and transduction to gene promoters, programmed gene expression, control of adequate response in cells, and induced plant immunity to phytopathogen [84, 85]. A number of interrelated metabolic processes are developed due to which the tolerance is expressed and the plant possesses the power to withstand phytopatogenes [86].

Plants can produce a lot of defensive substances, particularly, phytoalexins [12]. To date, there are about 350 these plant antibiotics which are synthesized in response to elicitors [87, 88]. These are mostly lipophilic compounds located around the infected zone. Phytoalexin production is closely related to oversensitivity [89], and, in this, the phytoalexins are accumulated intensively in the necrotized cells where they kill phytopathogens due to expressed antibiotic activity.

PR-proteins related to pathogenesis are synthesized in plant tissue as a response to fungal, bacterial and viral infection [90-92]. For instance, the β -1,3-glucanases can destroy cell walls in fungi, and also the suppressors are blocked due to them. Chitinases are involved significantly in nonspecific induced resistance to phytopathogens. The expression of chitinases and β -glucanases are usually correlates with plant tolerance to biotic stressors.

Reported mechanisms of plant immunity are tightly linked to intracellular metabolic processes of restoring energy which was used for immunization. Due to stress proteins' action the enzyme systems becomes more powerful, the stabilization of cell membranes occurs, and the functional activity of mitochondria and chloroplasts rises, resulting in more energy production [93]. Changes in intracellular metabolism make a biochemical basis for a nonspecific plant tolerance to different stressors [94].

Recently, phytoimmune correction due to the treatment with elicitors used to form reliable immunogenic agrocenoses with high adaptability and reproduction rate is considered promising for cultivated crops [1, 4, 12, 13, 51]. Particularly, in All-Russian Research Institute for Agricultural Microbiology (St. Petersburg) the concept of chitosan-based preparation has been developed. In this concept the chitosan is a nonspecific resistance inducer used together with a few more ingredients. A novelty consists in using signaling molecules to widen the range of defensive reactions, particularly, to intensify the AOS production, and to promote octadecanoid pathway of antibiotic synthesis in plants the same as salicylate pathway. It results in similar efficiency against necrotrophic and biotrophic organisms which attack plants. Different preparations under the Chi-

tozars trade name have been developed for the stimulation of plant tolerance to fungi, bacteria and viruses [14]. In a view of activating natural mechanisms of plant tolerance to biotic stresses, Immunocitofit and Bioduks, the commercial preparations based on arachidonic acid and its derivatives, have been developed. These compounds stimulate the phytoalexins production in plant tissues providing increase in tolerance to phytopathogens. Immunity activated by arachidonic acid or the arachidonic acid-based biologicals is bimodal in character depending on used concentration of the elicitor, so that at low level it causes a long systemic resistance and reliable defensive effect, while only a short local induction occurs when the concentration is higher. Developed immunostimulants are being used widely in crop farming [13].

Studying more detail about the effects of salicylic acid as a key factor of plant immunity resulted in practical recommendations according to its use for the defense stimulation [4]. High stimulating activity is characteristic to Albit, the preparation of poly- β -butyric acid. It induces a systemic resistance to wide range of diseases. After the treatment with Albit, significant biochemical and physiological changes are observed due to induced immune response. Particularly, the peroxidase activity and salicylic acid level rise reliably. Cytological study reveals a significant increase in the number of mitochondria in protoplasts. After sensitization the polymorphic leucoplasts are detected around the nucleus, and the production of carotenoids, terpenoids and phenols increases in the tissues. Besides, Albit suppresses diseases due to promoting high immune state in plants for a long time [51].

A special feature of the inducers is their ability to sensitize the plant to further infestations. Activation of tolerance mechanisms along with specific physiological and biochemical impact on cell nucleus determine the rate and the type of cell response. This event is «recorded» in epigenetic programming thus providing prompt response under repeated attacks of the pathogen [12]. Moreover, at least 2-fold decrease in pesticide level must be regarded too as a significant positive effect of elicitors which contribute to improvement of environmental condition and functions of agro-ecosystems.

Thus, a concept of nonspecific induced immunity in plants is quite well developed. According to this concept, the mechanisms involved in plant immunity formation are i) the interaction between signaling molecules produced by phytopathogen and the receptors in plant cell membrane; ii) signal transduction through intercellular signaling system; iii) expression of resistance genes which activate the defense mechanisms, such as oversensitivity, synthesis of key enzymes, signaling molecules, proteins, phytoalexins. Also the levels of salicylic and jasmonic acids, phytoalexins, peroxidase and catalase activity in tissues must be assayed to estimate plant response to the biogenic stress. Due to eliciting biologicals and optimized plant protection measures it is possible to boost immune state of plants thus making agroecosystems environmentally friendly.

REFERENCES

1. Egorov E.A. *V sbornike nauchnykh trudov GNU SKZNIISiV. Tom 2* [In: Proc. GNU SKZNIISiV, V. 2] Krasnodar, 2013: 48-52.
2. Yoshikawa M., Yamaoka N., Takeuchi Y. Elicitors: their significance and primary modes of action in the induction of plant defense reactions. *Plant Cell Physiol.*, 1993, 34(8): 1163-1173.
3. Dmitriev A.P. *Fiziologiya rastenii*, 2003, 50(3): 465-474.
4. Tarchevskii I.A. *Signal'nye sistemy kletok rastenii* [Signaling systems of plant cells]. Moscow, 2002.
5. Kessmann H., Kuhl A., Stahle Csech U., Oostendorp M., Staub T., Ruess W., Normeyer D., Rayals J. Systemisch aktivierte Resistenz in Pflanzen (SAR): Molekulare Grundlagen. *Mitt. Biol. Bundesanst. Land- und Forstwirtschaft*, 1996, 321: 259.
6. Mittler R., Del Pozo O., Meisel L., Lam E. Pathogen-induced programmed cell

- death in plants, a possible defense mechanism. *Dev. Genet.*, 1997, 21(4): 279-289 (doi: 10.1002/(SICI)1520-6408(1997)21:4%3C279::AID-DVG5%3E3.0.CO;2-4).
7. Thakur M., Sohal B.S. Role of elicitors in inducing resistance in plants against pathogen infection: a review. *ISRN Biochemistry*, 2013: 1-10 (doi: 10.1155/2013/762412).
 8. Hahn M.G. Microbial elicitors and their receptors in plants. *Annu. Rev. Phytopathol.*, 1996, 34: 387-412 (doi: 10.1146/annurev.phyto.34.1.387).
 9. Garcia-Brugger A., Lamotte O., Vandelle E., Bourque S., Lecourieux D., Poinssot B., Wendehenne D., Pugin A. Early signaling events induced by elicitors of plant defenses. *Mol. Plant-Microbe Interact.*, 2006, 19(7): 711-724 (doi: 10.1094/MPMI-19-0711).
 10. Shkalikov V.A. *Immunitet rastenii* [Plant immunity]. Moscow, 2005.
 11. Dmitriev A.P. *Tsitologiya i genetika*, 2002, 36(3): 58-68.
 12. Tyuterev S.L. *Nauchnye osnovy indutsirovannoi ustoichivosti rastenii* [Induced tolerance in plants]. St. Petersburg, 2002.
 13. D'yakov Yu.T. *Fundamental'naya fitopatologiya* [Fundamental phytopathology]. Moscow, 2012.
 14. Tyuterev S.L. *Zashchita i karantin rastenii*, 2005, 4: 21-26.
 15. Pugin A., Guern J. Mode of action of elicitors: Involvement of plasma membrane functions. *C. R. Acad. Sci., Ser. 3*, 1996, 319(11): 1055-1061.
 16. Boyes D.C., McDowell J.M., Dang J.L. Plant pathology: Many roads lead to resistance. *Curr. Biol.*, 1996, 6(6): 634-637 (doi: 10.1016/S0960-9822(09)00435-7).
 17. Xing Ti, 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*, 1997, 9(2): 249-259 (doi: 10.1105/tpc.9.2.249).
 18. Tarchevskii I.A. *Fiziologiya rastenii*, 2000, 47(2): 321-331.
 19. Yarullina L.G., Ibragimov R.I. *Kletochnye mekhanizmy formirovaniya ustoichivosti rastenii k gribnym patogenam* [Cell mechanisms of plant resistance to pathogenic fungi]. Ufa, 2006.
 20. Heil M., Bostock R.M. Induced systemic resistance (ISR) against pathogens in the context of induced plant defences. *Annals of Botany*, 2002, 89(5): 503-512 (doi: 10.1093/aob/mcf076).
 21. van Loon L.C., van Strien E.A. The families of pathogenesis-related proteins, their activities, and comparative analysis of PR-1 type proteins. *Physiological and Molecular Plant Pathology*, 1999, 55(2): 85-97 (doi: 10.1006/pmpp.1999.0213).
 22. Hanania U., Furman N., Ron M., Zamir D., Eshed Y., Avni A. High affinity binding site for a fungal elicitor (EIX) exists only in plants responding to the elicitor. *Plant Physiol.*, 1997, 114: 42.
 23. Ding C.K., Wang C.Y., Gross K.C., Smith D.L. Jasmonate and salicylate induce the expression of pathogenesis-related-protein genes and increase resistance to chilling injury in tomato fruit. *Planta*, 2002, 214(6): 895-901 (doi: 10.1007/s00425-001-0698-9).
 24. Il'inskaya L.I., Gorenburg E.V., Chalenko G.I., Ozeretskoyanskaya O.L. *Fiziologiya rastenii*, 1996, 43(5): 713-720.
 25. Vimala R., Suriachandrasekhar M. Induced resistance in bhendi against powdery mildew by foliar application of salicylic acid. *Journal of Biopesticides*, 2009, 2(1): 111-114.
 26. Alvarez A.L. Salicylic acid in machinery of hypersensitive cell death and disease resistance. *Plant Mol. Biol.*, 2000, 44: 429-442 (doi: 10.1023/A:1026561029533).
 27. Anderson M.E. Glutathione. In: *Free radicals: a practical approach* /N.A. Punchard, F.J. Kelly (eds.). Oxford Univ. Press, Oxford, 1996.
 28. Bartling D., Radzio R., Steiner U., Weiler E.W. A glutathione S-transferase with glutathione-peroxidase activity from *Arabidopsis thaliana*. Molecular cloning and functional characterization. *Eur. J. Biochem.*, 1993, 216(2): 579-586 (doi: 10.1111/j.1432-1033.1993.tb18177.x).
 29. Chamnongpol S., Willekens H., Moeder W., Langebartels C., Sander-mann H., van Montagu M., Inze D., van Camp W. Defense activation and enhanced pathogen tolerance induced by H₂O₂ in transgenic tobacco. *PNAS USA*, 1998, 95(10): 5818-5823 (doi: 10.1073/pnas.95.10.5818).
 30. Seskar M., Shulaev V., Raskin I. Endogenous methyl salicylate in pathogen-inoculated tobacco plants. *Plant Physiol.*, 1998, 116(1): 387-392 (doi: 10.1104/pp.116.1.387).
 31. Meuwly Ph., Summermatter K., Coquoz J.L., Buchala A., Molders W., Metraux J.-P. Accumulation of salicylic acid in cucumber, *Arabidopsis* and potato plants infected with pathogens. In book: *Mater. 15th Int. Bot. Congr. Yokogama*, 1993: 395.
 32. Chivasa S., Murphy A.M., Naylor M., Carr J.P. Salicylic acid interferes with tobacco mosaic virus replication via a novel salicylhydroxamic acid-sensitive mechanism. *Plant Cell*, 1997, 9(4): 547-557 (doi: 10.1105/tpc.9.4.547).
 33. Shirasu K., Nakajima H., Rajasekhar V.K., Dixon R.A., Lamb C. Salicylic acid potentiates an agonist-dependent gain control that amplifies pathogen signals in the activation of defense mechanisms. *Plant Cell*, 1997, 9(2): 261-270 (doi: 10.1105/tpc.9.2.261).
 34. Lamb C., Dixon R.A. The oxidative burst in plant disease resistance. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 1997, 48: 251-275 (doi: 10.1146/annurev.arplant.48.1.251).
 35. Mehdy M.C. Active oxygen species in plant defense against pathogens. *Plant Physiology*, 1994, 105(2): 467-472.
 36. Wojtaszek P. Oxidative burst: an early plant response to pathogen infection. *Biochem. J.*,

- 1997, 322(3): 681-692 (doi: 10.1042/bj3220681).
37. Grant J.J., Loake G.J. Role of reactive oxygen intermediates and cognate redox signaling in disease resistance. *Plant Physiol.*, 2000, 124(1): 21-30 (doi: 10.1104/pp.124.1.21).
 38. Gessler N.N., Aver'yanov A.A., Belozerskaya T.A. *Biokhimiya*, 2007, 72(10): 1342-1364.
 39. Troshina N.B. *Perekis' vodoroda kak regulyator ustoichivosti rastenii i kallusov pshenitsy k gribnym patogenam. Avtoreferat doktorskoi dissertatsii* [H₂O₂ as a regulator of wheat plant and callus resistance to pathogenic fungi. DSci Thesis]. St. Petersburg 2007.
 40. Huckelhoven R., Kogel K.H. Reactive oxygen intermediates in plant-microbe interactions: Who is who in powdery mildew resistance. *Planta*, 2003, 216: 891-902.
 41. Lamb C., Dixon R.A. The oxidative burst in plant disease resistance. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 1997, 48: 251-275 (doi: 10.1146/annurev.arplant.48.1.251).
 42. Richael C., Gilchrist D. The hypersensitive response: A case of hold or fold. *Physiol. and Mol. Plant Pathol.* 1999, 55(1): 5-12 (doi: 10.1006/pmpp.1999.0209).
 43. Pietras T., Malolepsza U., Witusik A. Udział nadtlenku wodoru i reaktywnych postaci tlenu wytwarzanych przez oksydazę NADPH w odporności roślin przeciwko patogenom. *Wiad. Bot.*, 1997, 41(3-4): 43-50.
 44. Huckelhoven R., Kogel K.-H. Untersuchungen zur Rolle reaktiver Sauerstoffspezies in der induzierten Resistenz von Gerste gegenüber dem Echten MehltauPilz. *Mitt. Biol. Bundesanst. Land- und Forstwirtschaft*, 1998, 357: 148.
 45. Kreslavskii V.D., Los' D.A. *Fiziologiya rastenii*, 2012, 59(2): 163-178.
 46. Desikan R., Mackerness S.A.-H., Hancock J.T.,Neill S.J. Regulation of the *Arabidopsis* transcriptome by oxidative stress. *Plant Physiol.*, 2001, 127: 159-172 (doi: 10.1104/pp.127.1.159).
 47. Galvez-Valdivieso G., Mullineaux P.M. The role of reactive oxygen species in signaling from chloroplasts to the nucleus. *Physiol. Plant.*, 2010, 138(4): 430-439 (doi: 10.1111/j.1399-3054.2009.01331.x).
 48. Jaspers P., Kangasjarvi J. Reactive oxygen species in abiotic stress signaling. *Physiol. Plant.*, 2010, 138(4): 405-413 (doi: 10.1111/j.1399-3054.2009.01321.x).
 49. Vranova E., Inze D., van Breusegem F. Signal transduction during oxidative stress. *J. Exp. Bot.*, 2002, 53(372): 1227-1236 (doi: 10.1093/jexbot/53.372.1227).
 50. Kreslavskii V.D., Lyubimov V.Yu., Kotova L.M. *Fiziologiya rastenii*, 2011, 58(2): 262-267.
 51. Ryabchinskaya T.A., Kharchenko G.L., Sarantseva N.A., Bobreshova I.Yu., Zlotnikov A.K. *Vestnik zashchity rastenii*, 2008, 2: 34-41.
 52. Apel K., Hirt H. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu. Rev. Plant Biol.*, 2004, 55: 373-399 (doi: 10.1146/annurev.arplant.55.031903.141701).
 53. Kolupaev Yu.E. *Vestnik Khar'kovskogo natsional'nogo agrarnogo universiteta. Seriya Biologiya*, 2007, 3: 6-26.
 54. Kuznetsov V.I., Dmitrieva G.A. *Fiziologiya rastenii* [Plant physiology]. Moscow, 2005.
 55. Shao H.-B., Chu L.-Y., Lu Z.-H., Kang C.-M. Primary antioxidant free radical scavenging and redox signaling pathways in higher plant cells. *Int. J. Biol. Sci.*, 2008, 4(1): 8-14 (doi: 10.7150/ijbs.4.8).
 56. Mullineaux P.M., Karpinski S., Baker N.R. Spatial dependence for hydrogen peroxide-directed signaling in light-stressed plants. *Plant Physiol.*, 2006, 141(2): 346-350 (doi: 10.1104/pp.106.078162).
 57. Gill S.S., Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol. Biochem.*, 2010, 48(12): 909-930 (doi: 10.1016/j.plaphy.2010.08.016).
 58. Foyer C., Lopez-Delgado H., Dat J.F., Scott I.M. Hydrogen peroxide- and glutathione-associated mechanisms of acclimatory stress tolerance and signaling. *Physiol. Plant.*, 1997, 100: 241-245 (doi: 10.1111/j.1399-3054.1997.tb04780.x).
 59. Chumakov A.E., Zakharova T.I. *Vredonosnost' boleznei sel'skokhozyaistvennykh kul'tur* [Harmfulness of crop diseases]. Moscow, 1990.
 60. Bolwell G.P., Daudi A. *Reactive oxygen species in plant-pathogen interactions. signaling and communication in plant: Book 2. Reactive oxygen species in plant signaling* /F. Baluska, J. Vivanco (eds.). Berlin, Heidelberg, 2009.
 61. Barna B., Adam A.L., Gullner G., Kiraly Z. Role of antioxidant systems and juvenility in tolerance of plants to diseases and abiotic stresses. *Acta phytopathol. et entomol. Hung.*, 1995, 30(1-2): 39-45.
 62. Okey E.N., Duncan E.J., Sirju-Charran G., Sreenivasan T.N. *Phytophthora* canker resistance in cacao: Role of peroxidase, polyphenoloxidase and phenylalanine ammonia-lyase. *J. Phytopathol.*, 1997, 145(7): 295-299 (doi: 10.1111/j.1439-0434.1997.tb00404.x).
 63. Khorosheva T.M., Suslova T.A., Noritsina M.V., Lysova L.A. V sbornike: *Zashchita rastenii ot vreditel'ei i boleznei* [In: Plant protection against pests and diseases]. Saratov, 1996: 70-76.
 64. Kumeiko T.B., Ol'khovskaya T.A. *Risovodstvo*, 2009, 14: 55-58.

65. Radhakrishnan N., Balasubramanian R. Salicylic acid induced defense responses in *Curcuma longa* (L.) against *Pythium aphanidermatum* infection. *Crop Protect.*, 2009, 28(11): 974-979 (doi: 10.1016/j.cropro.2009.07.010).
66. Graskova I.A., Kuznetsova E.V., Voinikov V.K. *Izvestiya Irkutskogo gosudarstvennogo universiteta. Seriya Biologiya. Ekologiya*, 2008, 1(1): 44-48.
67. Graskova I.A. Borovskii G.B. *Fiziologiya rastenii*, 2004, 51(5): 692-697.
68. Medvedev S.S. *Fiziologiya rastenii* [Plant physiology]. St. Petersburg, 2012.
69. Tarchevskii I.A. *Fiziologiya rastenii*, 2000, 47(2): 321-331.
70. Chen G., Asada K. Ascorbate peroxidase in tea leaves occurrence of two isozymes and differences in their enzymatic and molecular properties. *Plant Cell Physiol.*, 1989, 30: 987-998.
71. Meloni D.A., Oliva M.A., Martinez C.A., Cambraia J. Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. *Environ. Exp. Bot.*, 2003, 49(1): 69-79 (doi: 10.1016/S0098-8472(02)00058-8).
72. Nunez M., Mazzafera P., Mazorra L.M., Siquira W.J., Zullo M.A.T. Influence of a brassinosteroid analogue on antioxidant enzymes in rice grown in culture medium with NaCl. *Biol. Plant.*, 2003, 47(1): 67-70 (doi: 10.1023/A:1027380831429).
73. Shetty N.P., Jorgensen H.J.L., Jensen J.D., Collinge D.B., Shetty H.S. Roles of reactive oxygen species in interaction between plants and pathogen. *Eur. J. Plant Pathol.*, 2008, 121(3): 267-280 (doi: 10.1007/s10658-008-9302-5).
74. Repka V., Fisherova I., Silharova K. Methyl jasmonate is a potent elicitor of multiple defense responses in grapevine leaves and cell-suspension cultures. *Biol. Plant.*, 2004, 48(2): 273-283 (doi: 10.1023/B:BIOP.0000033456.27521.e5).
75. Hung K.T., Hsu Y.T., Kao C.H. Hydrogen peroxide is involved in methyl jasmonate-induced senescence of rice leaves. *Physiol. Plant.*, 2006, 127(2): 293-303 (doi: 10.1111/j.1399-3054.2006.00662.x).
76. Liu Yu., Pan Ts. Kh., Yan Kh.R., Liu Yu.Yu., Khuan V.D. *Fiziologiya rastenii*, 2008, 55(6): 851-862.
77. Maksimov I.V., Sorokan' A.V. *Fiziologiya rastenii*, 2011, 58(2): 243-251.
78. Ozertskovskaya O.L., Vasyukova N.I. *Fiziologiya rastenii*, 2006, 53(4): 546-553.
79. Titova S.A. *Vliyanie fitopatogennykh mikroorganizmov na enzimaticheskuyu aktivnost' rasteniya-khozyaina Glycine max (L.) Merr. i Glycine soja Sieb. et Zucc. Avtoreferat kandidatskoi dissertatsii* [Enzymatic activity in *Glycine max* (L.) Merr. and *Glycine soja* Sieb. et Zucc. as influenced by phytopathogenic microorganisms. PhD Thesis]. Blagoveshchensk, 2014.
80. Semenova E.A., Titova S.A., Dubovitskaya L.K. *Fundamental'nye issledovaniya*, 2011, 4(12): 708-711.
81. Avetisyan G.A., Babosha A.V. *Byulleten' Glavnogo botanicheskogo sada*, 2013, 4: 30-36.
82. Pakhomova V.M. *Tsitologiya*, 1995, 37(1): 66-91.
83. Shakirova F.M. *Nespetsificheskaya ustoichivost' rastenii k stressovym faktoram i ee regulyatsiya* [Plant non-specific tolerance to stresses and its regulation]. Ufa, 2001.
84. Grechkin A.N. *Bioorganicheskaya khimiya*, 2000, 26(10): 779-781.
85. De Wit P.J.G.M. Fungal avirulence genes and plant resistance genes: unraveling the molecular basis of gene-for-gene interactions. *Adv. Bot. Res.*, 1995, 21: 147-185 (doi: 10.1016/S0065-2296(08)60012-9).
86. Lykova N.A. *Effekt prevegatsii. Ekologicheskie posledstviya* [Effect of pre-vegetation. Environmental consequences]. St. Petersburg, 2009.
87. Hammerschmidt R. Phytoalexins: what we have learned after 60 years? *Ann. Rev. Phytopathol.*, 1999, 37: 28-36 (doi: 10.1146/annurev.phyto.37.1.285).
88. Kuc J. Phytoalexins, stress metabolism and disease resistance in plants. *Ann. Rev. Phytopathol.*, 1993, 33: 275-297 (doi: 10.1146/annurev.py.33.090195.001423).
89. Perkovskaya G.Yu., Kravchuk Zh.N. *Fiziologiya rastenii*, 2004, 51(5): 680-685.
90. Broekaert W.E., Terras F.R.G., Cammue B.P.A., Osborn R.W. Plant defensins: novel antimicrobial peptides as component of the host defense systems. *Plant Physiol.*, 1995, 108(4): 1353-1358 (doi: 10.1104/pp.108.4.1353).
91. Huub J.M., Linthorst J.M., Van Loon L.C. Pathogenesis-related proteins in plants. *Critic. Rev. Plant Sci.*, 1991, 10(2): 123-150 (doi: 10.1080/07352689109382309).
92. Selitrennikoff C.P. Antifungal proteins. *Appl. Environ. Microbiol.*, 2001, 67(7): 2883-2894 (doi: 10.1128/AEM.67.7.2883-2894.2001).
93. Chirkova T.M. *Fiziologicheskie osnovy ustoichivosti rastenii* [Physiological bases fro plant resistance]. St. Petersburg, 2002.
94. Koshkin E.I. *Fiziologiya ustoichivosti sel'skokhozyaistvennykh kul'tur* [Physiology of cultivated plant resistance]. Moscow, 2010.