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## CROP PRODUCTION

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### PHYSIOLOGICAL ROLE OF SIGNAL SYSTEMS IN THE FORMATION OF LEGUME-RHIZOBIAL SYMBIOSIS

Review

#### Abstract

The literary and own data on participation and interrelation bacterial Nod-factor signaling and components calcium, NADPH oxidase and NO synthase signaling systems of a plant on preinfectious and infectious stages of formation of legume- rhizobium symbiosis are generalized. The physiological role of Nod factor, reactive oxygen species (ROS), reactive nitrogen species (RNS), calcium ( $Ca^{2+}$ ), NADPH-oxidase and nitric oxide (NO) and their cross influence on the processes determining formation of symbiotic structures on roots of the plant-host is considered.

**Keywords:** legume-rhizobial symbiose, ROS, RNS, Nod factors signaling,  $Ca^{2+}$ -signal system, NADPH oxidase.

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### ФИЗИОЛОГИЧЕСКАЯ РОЛЬ СИГНАЛЬНЫХ СИСТЕМ В ФОРМИРОВАНИИ БОБОВО-РИЗОБИАЛЬНОГО СИМБИОЗА

Обзор

#### Аннотация

Обобщены литературные и собственные данные о физиологической роли бактериальной Nod-факторной сигнальной системы и компонентов кальциевой, NADPH-оксидазной и NO-сигнальных систем растения на преинфекционной и инфекционных стадиях формирования бобово-ризобияльного симбиоза. Раскрыта физиологическая роль бактериального Nod-фактора, активных форм кислорода (АФК), активных форм азота (АФА), кальция ( $Ca^{2+}$ ), NADPH-оксидазы и оксида азота (NO) и их перекрестное влияние на процессы, определяющие формирование симбиотических структур в корнях растения-хозяина

**Ключевые слова:** бобово-ризобияльный симбиоз, активные формы кислорода (АФК) и азота (АФА), Nod-факторный сигналинг,  $Ca^{2+}$ -сигнальная система, NADPH-оксидаза.

#### 1. Introduction

Legumes (*Fabaceae*) and nodular bacteria (rhizobia) of various species (*Azorhizobium*, *Allorhizobium*, *Bradyrhizobium*, *Mezorhizobium*, *Rhizobium*, *Sinorhizobium*) form mutualistic symbiosis generating root nodules, where rhizobia fix atmospheric nitrogen ( $N_2$ ) at the expense of energy resources of host plant, in exchange to accessible mineral nitrogen ( $NH_3$ ). Symbiosis between rhizobia and legumes is a unique biological phenomenon; acquisition of theoretical knowledge on it would contribute to practical results – higher yields of legumes and other cultivated plants, enhancement of soil nitrogen fertility, preservation of ecological stability of soil medium [6].

Formation of legume-rhizobial symbiosis is a function of successful infection of legumes roots with rhizobia and formation of symbiotic structures, which are complex processes performed by nodular bacteria under rigid control of host plant [44], [62], [65], [84], [85], [2]. In fact, it is a molecular dialogue between two partners involving specific bacterial compounds including certain response of host plant, such as ionic changes ( $K^+$ ,  $Cl_2^-$ ,  $Ca^{2+}$ ,  $H^+$ ), cytoplasm alkalization,  $Ca^{2+}$  oscillation and gene expression that result in bacterial invasion and nodule formation [24], [86]. Participants of this molecular dialogue between two organisms are signal systems: bacterial Nod-factor (NF-system), и plant systems - calcium, NADPH-oxidase, NO-synthase and their components – reactive oxygen species (ROS) and reactive nitrogen species (RNS). The present review will cover

literary data and the authors' results as evidence of participation of the stated signal systems and their components in legume-rhizobial symbiosis at the initial stages of its formation.

## 2. Nod -factor signal system

Bacterial invasion in plant cells is characterized by primary interaction on cytoplasmic membrane of bacterial compound(s) and plant receptor(s), which further results in activation (in case of pathogenesis) or inactivation (in case of mutualistic symbiosis) of plant protective systems. The cascade of responses involved in the processes includes different systems: from functioning of signal molecules to gene expression, synthesis of new proteins and protective compounds. Understanding of morphological, physiological, biochemical and genetic peculiarities of these processes has been a primary task of experimental biology in the last few decades. Significant advances have been made in the study of pathogenesis [30]. Mutualistic symbiosis has been extensively researched by various specialists who gained considerable achievements in this domain of biology [8]. Nevertheless, participation of signal systems in the formation of legume-rhizobial symbiosis does not provide a complete picture of their role in functioning of this unique biological phenomenon [54].

Nodular bacteria in rhizosphere or those adsorbed on root surface recognize their specific plant flavonoids (daidzein, genestein, coumestrol, naringenin and others), thus inducing transcription of nodular *nod*-genes (nodulation genes). This process comprises expression of *nod* gene, the product of which is directly linked to flavonoids [49]. The protein, product of *nod* gene is a transcription activator of other bacterial *nod*-genes [39], which are responsible for synthesis of specific signal molecules - lipochitooligosaccharides called rhizobial Nod-factors (NF). It should be noted that NF molecular skeleton is a chitooligosaccharide (N-acetyl-D-glucosamin with  $\beta$ -1, 4 bonds), which acts as an elicitor of fungal pathogens and initiates plant protective response. Legumes have been found to differentiate lipochitooligosaccharides from chitooligosaccharides due to the fact that principal NF skeleton has modifications differing in various rhizobial species mainly in length and saturation degree of lateral residues of fatty acids [48]. That is why lateral NF chains are considered to specifically interact with plant receptor and this molecular complex of two organisms performs signal transduction and directs organisms' metabolism towards mutualistic co-existence [48]. NF complex chemical structure may be presumed to determine rhizobia specificity to host legumes.

NF induces various responses in host plant, starting from the change in membrane potential, depolarization of nodular hair plasmalemma [34], [40] through to formation of nodular primordia [58]. These signal molecules are perceived by epidermal plant cells, the plasmalemma of which locates an elaborate multicomponent receptor complex –Nod-factor (s) receptors (NFR) – receptor-like kinases (RLK). One of them - a LysM RLK protein – contains extracellular lysine motifs (LysM), the other one – leucine rich repeat (LRR RLK) – is rich in leucine repetitions (Ferguson et al., 2010). Thus, in *Lotus japonicum* such receptors of LysM are presented by protein kinases LjNFR5 and LjNFR1, in peas - PsSYM10/PsSYM2, in alfalfa – MtLYK3/MtLYK4 [84]. LRR RLK proteins may be exemplified in *Lotus japonicum* by LjSYMRLK, in alfalfa - MtDMI2 [88].

Presence of two (or more?) [84] receptors in epidermal cells is due to their different roles in triggering signal paths inducing rhizobial infection of plants in epidermal cells is accounted for by their different role in initiation of activity of signal paths leading to rhizobial infection of plant and formation of root nodules [72], [74], [96], [13]. LRR RLK are presupposed to participate in the original initiation of bacterial invasion paths (root hair deformation, infection threads formation), and LysM RLK may play a key role in further development of signal cascade leading to organogenesis of the nodule in cortex and pericycle cells. But at the same time LysM RLK activation is apparently necessary for LRR RLK functioning [37].

Thus, molecular interaction between NF and RLK is a major prerequisite for start-up of genetic infection and nodulation processes in legume roots nodulation. These events are preceded by pre-infection responses of host plant to NF action that is restructuring of cytoskeleton, swelling and twisting of root hair tip and formation of radially directed cytoplasmic bridges – preinfection threads – in external cortical cells. Then inside the deformed root hair a bacterial microcolony is formed to perform local hydrolysis of root hair cell wall. At this point the root hair stops its external growth and begins to grow inside forming tubular invagination of cell wall and membrane - infection thread (IT), in which bacteria are propagated and transported to cortex cells.

IT formation is coordinated with nodule morphogenesis in juxtaposing cortical tissues. NF-signaling participation in these events has been proven in tests with mutant organisms [48]. Characteristics were given to specific genes involved in NF-signaling and to transcription factors (for instance, proteins NIN, RPG, ERN, CYCLOPS, CERBERUS), required for nodule primordium formation; genes playing a direct part in infecting, actine restructuring, synthesis of early proteins-nodulins (ENODs), secretion and other events were also identified [37]. It was proven that cytokinin, the receptor of which – histidine kinase (*MtCRE1/LjHK1*) is activated by calmodulin-dependent kinase (CCaMK), takes place in the initiation of cortical cells division [50], [37].

Apart from the stated functions, Nod-factor signal system may participate in inactivation of macrosymbiont protective systems, in particular, in inhibition of chitinase synthesis and activation of hydrolases. With this in view, the role of Nod-signal system is connected here with the modification of hormonal response of host plant during formation of nodule meristem and regulation of changes in macrosymbiont gene apparatus [84].

Rhizobial infection enhances nitrate absorption by pea roots, which, presumably, might be connected with activation of anion channels on plant cell plasmalemma [11]. At the same time published data witness that both rhizobia and nitrates contribute to synthesis in roots of Q-compound presenting linked peptides – CLAVATA3/ESP (CLE) [127]. Peptide Q (CLE) participates in autoregulation of root nodules formation and under rhizobial infection is transferred to the plant surface part, and in case of nitrates remains in the roots. Q linking to a plant receptor LRR RLK in roots or surface organs presumably initiates synthesis of a compound (factor) producing inhibiting effect on nodules formation (in case of nitrates) or performing autoregulation of nodule formation via reverse (systemic) response induced in leaves.[37].

Therefore, bacterial Nod-factor signal system is a primary trigger of physiological processes changing the direction of host plant metabolism and leading to formation of symbiotrophic organism. It might be the same system that initiates signal transfer for long distances, which is related to formation of system resistance [3]. Based on this, rhizobial infection may be interpreted

as an external factor causing formation of system resistance against undesirable for host plants external impacts, which agrees with the opinion of other authors [99], [62]

It should be also noted that host plant uses protective reactions against rhizobia as well provided symbiotic interaction paths are disturbed, for instance, in the case of use of rhizobial and plant mutants [2]. Besides Nod-factor signal system, a significant role in legume-rhizobial interactions is ascribed to other bacterial (rhizobial) signal compounds: exopolysaccharides (EPS), lipopolysaccharides (LPS), capsular polysaccharides (KPS) and cyclic  $\beta$ -glucanes [16]. Probable plant receptors interacting with Nod-factor may be lectins [35], [111]. Interaction of rhizobial EPS with lectins may be due to specificity of rhizobia to host plant [100]. On the whole Nod-factor signal system may be viewed as a unique mechanism for nodule formation, whereas many other systems are common for non-related mutualistic symbiosis and plant protection against pathogens [8].

### 3. $\text{Ca}^{2+}$ -signal system during symbiosis

Presently  $\text{Ca}^{2+}$  is considered as omnipresent regulator of cell functions and change in its level in the cell serves a trigger for many physiological responses. Activity of  $\text{Ca}^{2+}$  is considered to be affecting membranes permeability, cytoplasm movement, enzymes activity, secretion, cell division. It plays a key role in regulation of vitally important processes related to cell development and differentiation, hormone signals transduction, tropisms, programmed cell death and plant resistance to stress [17], [75], [10], [66].  $\text{Ca}^{2+}$ -signal enhances due to its interaction with diverse proteins, which can afterwards accomplish ion transportation, regulatory and other functions, and maintain low  $\text{Ca}^{2+}$  level in cell organelles. The amount of  $\text{Ca}^{2+}$ -containing proteins in plants is fairly high: *Arabidopsis* contains over 150 [123]. Tight interdependence of calcium with NO and ROS in the cells of various organisms has been proven [63], [101].

Increase in  $\text{Ca}^{2+}$  ions concentration in cytoplasm is one of the earliest cell reactions to various stress impacts. However, this increase is of short-term character and is quickly replaced with the drop of its content in cytoplasm, which is apparently an indispensable condition of this signal system functioning.  $\text{Ca}^{2+}$  level rise and drop in protoplasm shows in the form of calcium spiking – singular fluctuations of calcium ions level, oscillations (repeated spikes in the form of rhythmical changes in calcium concentration in cytoplasm and organelles) and  $\text{Ca}^{2+}$  waves propagating in the cell. This phenomenon recently named “ $\text{Ca}^{2+}$ -signature” characterizes fluctuations of intracellular calcium by such parameters as the following: amplitude, frequency, and pulse duration [116]. These processes proceed due to membrane transport, activation of secondary intermediaries of  $\text{Ca}^{2+}$ -linking proteins, for instance,  $\text{Ca}^{2+}$ -ATPases, kinases, protein-sensors) and other processes [75]. Specific role here is played by calmodulin (CaM) and protein kinases, which depend on  $\text{Ca}^{2+}$  and perform phosphorylation of proteins – factors of transcription regulation [5, p.103-113, 101].

$\text{Ca}^{2+}$ -spikes constitute a significant component of Nod-factor signal system affecting deformation of root hair and formation of infection thread (IT) [76]. During legume-rhizobial symbiosis NF provokes rapid (1 minute after NF impact) calcium ions transport to cytoplasm via plasmalemma and membrane depolarization [24], [106]. Nevertheless, NF interaction with plant receptor on the surface of epidermal cells of root hair proceeds at least through two signal paths: one of them involves  $\text{Ca}^{2+}$ -spikes, which leads to gene expression, synthesis of proteins-nodulines and nodule organogenesis. The other one, related to root hair deformation, does not involve  $\text{Ca}^{2+}$ -spikes [77] (Miwa et al., 2006). NF, LysM-RLK,  $\text{Ca}^{2+}$ -spikes, CCaMK, NIN (transcription factor), cytokinin, histidin-kinase (*MtCRE1/LjHK1*) participate in the first signal path (NSP 1/2) leading to synthesis of nodulin-proteins (Enod40 and others) in epidermis and division of cortical cells. The second path is initiated by NF and LRR-RLK [84]. In the study by Miwa et al. (2006) employing mutants a genetic analysis of signal symbiotic paths (NSP1/2) in *Lotus japonicus* is investigated and genes participating in  $\text{Ca}^{2+}$ -flow initiation in cytoplasm and emergence of  $\text{Ca}^{2+}$ -spikes are analyzed. It was found that only two genes (*Nfr1* u *Nfr5*) under the influence of NF initiate calcium flow into cytoplasm, hair root deformation and infection. Expression of the other five genes (*SymRK*, *Castor*, *Pollux*, *Nur133*, *Sym24*) results in the emergence of calcium oscillations, activation of calmodulin-dependent kinase, synthesis of NIN-proteins and nodule organogenesis.

$\text{Ca}^{2+}$ -signal system functioning initiation under the influence of cytoplasmic  $\text{Ca}^{2+}$  is of short-term character: rapid  $\text{Ca}^{2+}$ -flow takes place only within 5 minutes after root treatment with purified NF ( $10^{-8}$  M) [106]. Then  $\text{Ca}^{2+}$ -flow is quickly replaced with decrease in its content, which is apparently an indispensable condition of signal systems functioning. Oscillations in concentration of cytosol  $\text{Ca}^{2+}$  are observed approximately 10-15 minutes after the NF impact of NF on  $\text{Ca}^{2+}$  flow ([33]Ehrhard et al., 1996). It should be noted that induction of  $\text{Ca}^{2+}$  flow into cytoplasm and  $\text{Ca}^{2+}$ -spikes requires different NF concentrations: in the first case they are to be 2-3 orders higher than in the second case [106]. This may evidence different NF sensitivity to plant receptors responsible for triggering processes modulating calcium signal functions.

$\text{Ca}^{2+}$ -spikes formation takes place with participation of ion channels proteins (CASTOR, POLLUX) and nucleoporines (NUP85, NUP133), and activation of  $\text{Ca}^{2+}$ -calmodulin-dependent kinase (CCaMK), is initiated by rhythmical changes in  $\text{Ca}^{2+}$  concentration in cytoplasm and organelles. Mutation by  $\text{Ca}^{2+}$ -spikes inhibits organogenesis of nodules in *Lotus japonicus*, which is deleted by previously activated form of CCaMK [59]. Similar fluctuations in  $\text{Ca}^{2+}$  concentration cause, with participation of activated CCaMK, phosphorylation of proteins – transcription factors, further transduction of NF-signal leading to expression of symbiotic genes in the nucleus.

Though calcium functions in a plant organism are relatively well studied, there are still moot issues concerning interaction of this molecule with other signal compounds, for example, reactive oxygen species (ROS) and reactive nitrogen species (RNS) at the initial stages of legume-rhizobial symbiosis [54]. This will be discussed in the chapter “Interaction of signal systems during formation of legume-rhizobial symbiosis”.

#### 4. ROS role in symbiosis

ROS and RNS formation in the course of symbiotic interaction development is a major factor of affinity of early plant response to pathogen and symbiotroph infection [89], [32]. These compounds constitute a basis of functioning of two signal systems – NADPH oxidase and NO synthase [5]. It should be noted that investigations linked to the study of ROS and RNF role in symbiotic relations of organisms as compared to pathogenesis, at the moment do not present a complete picture of dependence of legume-rhizobial symbiosis formation on these molecules. The role of these compounds at the initial stages of legume-rhizobial and arbuscule-mycorrhizal interaction formation is discussed in a number of publications [19], [46], [19], [52], [18]. ROS and antioxidant compounds participation in functioning of root nodules is reflected in the studies by Becana and other [20], [61], [78].

Literary data confirm that ROS ( $O_2^{\cdot-}$ ,  $H_2O_2$ ) may perform signal and other functions at early stages of symbiosis [90, 79]. Thus,  $H_2O_2$  in alfalfa infection threads participates in cross-linking of arabin-galactan-protein-extensins, thus enhancing IT matrix density [2]. In semi-aquatic legume *Sesbania rostrata*  $H_2O_2$  is involved in signal path related to nodule formation of the plant stem [60].

Intense ROS formation in plants takes place in photosystem, peroxisomas, plasmalemmas, mitochondria respiratory chain and other cell structures, where reactive oxygen compounds are generated due to single-electron reduction of  $O_2$  in respiratory chain and other non-enzyme and enzyme reactions [9], [43], [7]. One of the primary ROS sources during phytopathogenesis is NADPH oxidase of peroxisomas and plasmalemma [80], [5], [68]. There was identified a strong relation between ROS formation and calcium entrance into cytoplasm under the impact of biotic and abiotic stressors and  $Ca^{2+}$  and ROS role as key components of single signal network [66]. Both signal and cytotoxic roles of ROS under the influence of diverse stress factors may be considered proven [7]. To survive, plant organisms have to maintain a certain balance between these functions (pro-oxidant-antioxidant equilibrium) [118], [103]. Antioxidant and signal systems are key players here. The former deactivates ROS excess, the latter with the help of ROS ensures triggering of the organism protective mechanisms. Specificity of plant organism response to ROS depends on many factors – chemical peculiarities of ROS, their generation location, plant development stage, impact of stress factors on the organism and interaction with other signal molecules (nitrogen oxide, phytohormones, salicylic and jasmonic acids, lipid and phenolic exchange products).

A significant source of ROS generation in plants is NADPH oxidase localized on cell plasmatic membrane, which with participation of superoxide-dismutase enzyme (SOD), generates signal molecules –  $O_2^{\cdot-}$  and  $H_2O_2$ . Inhibition of NADPH oxidase activity results not only in reduction of ROS generation, but to hindering IT formation in the course of symbiotic relations between alfalfa and *Sinorhizobium meliloti* [87], [24]. Functional activity of NADPHN-oxidase is supposed to be one of constituents of ROS formation mechanism regulation at the initial staged of legume-rhizobial interaction [91]. This is confirmed by the data of Lohar with coauthors [70], [71], who showed that NADPHN-oxidase transcripts accumulation in alfalfa roots coincides with the change in  $H_2O_2$  content in the first hours after seedling inoculation with rhizobia. On the other hand, treatment of alfalfa seedling with purified NF entails inhibition of  $H_2O_2$  formation [102], which, according to the authors, is related to plant protective response. Decrease in  $H_2O_2$  and salicylic acid generation decrease during inoculation of pea seedlings with rhizobia is also reported by other authors [51], who explain this fact by functioning of protective-regulatory mechanism in formation of legume-rhizobial symbiosis [52]. Controversy of the data on  $H_2O_2$  content change in macrosymbiont during interaction with rhizobia may, apparently, be also explained by different duration of the tests that is by time dependence of  $H_2O_2$  level in macrosymbiont.

ROS, along with jasmonic acid and ethylene, is considered to act as a negative regulator of legume-rhizobial symbiosis formation [42]. These compounds take part in protective mechanisms of host plant. Protective response of pea host plant has been shown to be more pronounced in case of incompatible rhizobial interaction, which is evidently connected with the restriction of rhizobial infection distribution [125]. Nevertheless, rhizobial infection can regulate the content of cytotoxic compounds, such as  $H_2O_2$  and NO in the roots. Thus, according to the data of [11] the peak of hydrogen peroxide accumulation during inoculation of pea seedlings by rhizobia is observed 30 minutes after inoculation, and during further exposures (1, 2, 6, 24 and 48 h) hydrogen peroxide content decreases in the roots and does not differ from control. The analysis of these data shows that drastic increase in  $H_2O_2$  content (2.6 times) 30 minutes after the impact on rhizobia roots, apparently, characterizes non-specific plant response to pathogenic and symbiotic microorganisms. With longer exposure to biotic factors, a specific response of the organism seems to be observed, which is characterized either by enhancement of ROS synthesis by the plant (such as in the case of exposure to avirulent pathogen), or by depression of synthesis – as in the case virulent pathogenesis and symbiotic bacteria. In the latter case host plant “recognizes” microorganisms as “its own” and “takes off” protective barriers, “allowing” infection. However, certain protective responses of the plant are induced also during nodule development [45]. It was demonstrated that in alfalfa many IT stop to grow even in the case of compatible symbiotic relations due to development of supersensitive response (SSR) in root cortex cells [112]. But even if rhizobia initially suppressed host plant protective responses and penetrated root tissues, the infection process may stop at later stages. Thus, it has been established that 90% of infection threads formed in alfalfa root hairs terminate their growth and get destroyed. The death of infection threads results from SSR taking place in the cells during phytopathogenesis with ROS participating as key components. Thus, according to Vasse et al. [112], individual infection threads with rhizobia in them perish and contain substances characteristic of cell SSR under phytopathogenesis (phenols, PR-proteins, etc.). In alfalfa there were found  $O_2^{\cdot-}$  and  $H_2O_2$  in the matrix of some infection threads surrounding bacteria [108]. It was shown that nodulation of lateral roots of tropical semi-aquatic plant *Sesbania rastrata* is accompanied by  $H_2O_2$  and ethylene generation [60]. Both processes are initiated by NF. Increase of  $H_2O_2$  content in alfalfa seedlings and drop in the activity of antioxidant enzymes at the early stages of infection were observed by Bueno with coauthors [19] in the tests with mutant *Sinorhizobium meliloti*, which is defective by Nod-factor synthesis. The increased  $O_2^{\cdot-}$  generation by pea seedlings takes place in case of interaction between plant and incompatible strain *Rhizobium leguminosarum* bv. *phaseoli* (French beans strain) and rises in the first 24 hours after pea roots inoculation with compatible strain *Rhizobium leguminosarum* bv. *Viceae* [4]. Bacterial antioxidant

enzyme SOD catalyzing dismutation reaction of  $O_2^{\cdot-}$  in  $H_2O_2$ , is necessary for normal rhizobial infection and nodulation in legumes [108]. According to Lohar et al. [70] the change in morphology of root hairs in response to rhizobial infection is accompanied by temporary fluctuations in hydrogen peroxide concentration, which the authors relate to the necessity of ROS availability for the processes leading to deformation of root hairs and further invasion of nodular bacteria.

As previously stated, initial stage of plant interaction with pathogenic and symbiotic microorganisms have common features [130]. Hydrogen peroxide is necessary for expression of *rip1* gene encoding synthesis of early alfalfa nodulin – peroxidase [97], as well as for substrate for peroxidase catalyzing lignin and callose synthesis, for cell wall strengthening against bacterial invasion. According to Glyan'ko et al., [52], the activity of soluble peroxidase in pea roots in response to inoculation decreases in the root sector, which is susceptible to rhizobial infection and increases in non-susceptible sector. No similar regularity was found by the authors for non-nodular pea mutant, in which peroxidase activity did not change in response to rhizobial infection in both root sectors. The authors believe that reduction in peroxidase activity facilitates rhizobia penetration in the root, and its increase in non-susceptible sector is likely to have a direct anti-bacterial effect directed towards systemic distribution of rhizobia and plant root protection from excessive infecting. The phenomenon of systemic resistance to rhizobial infection in other sectors of legume roots after preliminary root infecting was reported in other publications as well [27].

Modulation of macrosymbiont metabolism under the impact of microsymbiont and showing in ROS accumulation proves SSR (Super Sensitivity Reaction) of host plant cells. This, apparently, confirms ROS participation in the regulation of infecting processes and nodulation during symbionts' interaction. However, according to Vasil'eva et al. [114], [115], in other organs of host plant - in pea epicotyl, rhizobia infection is followed by ROS accumulation in the form of  $O_2^{\cdot-}$  and  $H_2O_2$ . The authors hypothesize that in this case macrosymbiont develops "systemic induced resistance", which is exhibited in other plants in case of their infecting by non-pathogenic microorganisms [94]. Such a resistance in a legume emerging in response to rhizobia penetration is presumably aimed to prevent rhizobia (and other bacteria) penetration into surface organs and is triggered by a signal system, which might be similar to the one functioning in case of plant infecting with non-pathogenic microbes with jasmonic acid involved [95]. Wave nature of ROS ( $H_2O_2$ ) functioning in plant cells is reported in the publications by Miller et al. [81], [82], which draw evidence of presence in Arabidopsis cells at the genetic level of ROS-waves functioning as a systemic long-distance signal – from one cell to another and from one organ to another, related to formation of systemic resistance to stressor impact. According to Steinhorst and Kudle [101], the major participant of these processes is NADPH oxidase (RbohD-oxidase) – ROS generator, whose activity is linked with  $Ca^{2+}$ -signal and  $Ca^{2+}$ -regulated kinases.

Systemic acquired resistance is known to be formed with participation of salicylic acid, whose synthesis is tightly connected with another signal molecule – hydrogen peroxide [98]. The probability of salicylic acid participation in legume-rhizobial symbiosis was discussed in a number of publications [83], [21], [46], [51], [109]. If exogenously entered into plants, salicylic acid negatively affected formation and functioning of legume-rhizobial symbiosis [1], [83]. Under normal physiological conditions the synthesis of salicylic acid in macrosymbionts is apparently regulated at the gene level with NF rhizobia involved. Thus, mutation in rhizobial strain by NF or alfalfa inoculation with incompatible rhizobial strain resulted in drastic accumulation of salicylic acid in the roots ensuring this acid functioning as a signal molecule initiating protective responses in macrosymbionts, which hinders infection and nodulation processes [21]. In other words, Nod-factor decreases the intensity of salicylic acid synthesis in host plant, thus entailing blocking of mediated by it signal mechanism related to macrosymbionts' protective responses [83], [19], [109] demonstrated that reduction of endogenous level of salicylic acid in *Lotus japonicus* and *Medicago truncatula* through the expression of transgenic enzyme salicylate-hydrolase intensifies infection and nodulation of legumes with determinant and non-determinant nodule types. The authors hypothesize a significant role of salicylic acid in protective responses of host plant in the course of symbiosis formation.

## 5. Nitric oxide (NO) role in symbiosis

NO is classed as a biologically active compound within the group of reactive nitrogen form, which, besides NO, comprises peroxynitrite ( $OONO^-$ ) and other low-molecular N-compounds –  $NO_2^-$ ,  $NO^-$ ,  $NO^+$ ,  $NO_2^{\cdot}$ -radical. NO and  $OONO^-$ -modified compounds - S-nitrosothiols, nitrotyrosine containing and other proteins considered as compounds participating in nitrosative stress. RNS role in the processes of symbiotrophic interaction of organisms, in particular, plants, microbes, fungi, remains one of the least studied issues. Investigation of this question mostly focuses on NO as a molecule-based radical with a wide spectrum of biological activity [53], [73].

NO presence in alfalfa nodules has been experimentally proven [22]. The authors believe that NO generation in nodules takes place with participation of NO-synthase, but not nitrate- or nitrite-reductase. NO function as a negative regulator of  $N_2$ -fixation in nodules is hardly probable [126]. NO complex with leghemoglobin has been shown to be present in mature functioning soy nodules with nitrates absence in the medium [14], [128]. According to Yamamoto and Kanayama. [124], with high  $NO_3^-$  content in soy plants, bacteroids synthesize NO, which is linked to leghemoglobin forming nitrosyl-leghemoglobin. This may lead to inhibition of oxygen transfer to bacteroids resulting in the reduction of nitrogenase activity and further nodules degradation. Tests in vitro demonstrated inhibiting action of NO on soy nodules nitrogenase [110]. Nitrogen oxide may participate in the regulation of activity of two genes of  $N_2$ -fixation: *nifA* and *fixK* via forming a complex with membrane-linked protein FixL involved in the regulation of nitrogen fixation in *um meliloti*. This protein is a  $O_2$ -sensor activated at low, and inactivated at high  $O_2$  concentrations. NO, as well as  $O_2$  is assumed to participate in the regulation of FixL activity and therefore, that of nitrogen fixation [47]. The studies of demonstrated that leghemoglobin *in vivo* may form with NO nitrosil complexes with heme and non-heme iron [12]. This, according to the author, excludes nitrogen oxide from redox-cycle of free-radical oxidation reactions. Presence of non-symbiotic hemoglobin in different plant organs, including soy, was reported by Andersson et al. [129]. Expression of cytokinin receptor gene *LjHb1* was also shown to be accompanied by enhancement of synthesis of non-symbiotic hemoglobin in the roots of *Lotus japonicum* [104]. The function of nonsymbiotic hemoglobin in legumes (unlike leghemoglobin function in nodules) has not been sufficiently studied. Interesting data were obtained by Yan et al. [117] during investigation of

the role of micro-RNA (miRNAs) in legume-rhizobial integration, when miR172 expression results in synthesis in transgenic soy roots of non-symbiotic hemoglobin, which, in the authors' opinion, plays an important role in the regulation of nodule formation. The role of non-symbiotic hemoglobin in this case might be to detox NO producing negative impact on symbiosis, and to modulate NO level in the course of symbionts' interaction [113], [104], [105].

## 6. Interaction of signal systems during formation of legume-rhizobial symbiosis

The crucial part of legume-rhizobial symbiosis problem is the interaction between signal molecules –  $\text{Ca}^{2+}$ , ROS and RNS under normal physiological conditions and particularly under unfavorable biotic and abiotic factors. Numerous studies of ROS involvement in plant signaling also confirm their interaction with  $\text{Ca}^{2+}$  [64], [23], [92], [15], [38], [67], [101]. ROS have been shown to activate  $\text{Ca}^{2+}$ -channels, which are engaged in establishment of apical calcium gradient [93], [25] and are a signal mechanism leading to polar growth of root hair [41], [131]. Close interaction of rhizobial NF-signal system with  $\text{Ca}^{2+}$ -spikes and the influence of the latter on the induction of infecting and nodulation genes have been proven [76]. Early ROS generation and distribution were found to be tightly interrelated not only with  $\text{Ca}^{2+}$ -signaling, but also with ATP in legume root hairs [24]. However, interrelation between ROS and  $\text{Ca}^{2+}$  is ambivalent. The experiments with alfalfa mutant *dmi* confirmed that,  $\text{Ca}^{2+}$ -oscillations are not required for ROS modulation or root hair deformation [26], [102], [107], [36], [70].  $\text{Ca}^{2+}$ -flow is rapid only within 5 minutes after treatment by NF ( $10^{-8}$  M) [102] and it takes place much earlier than ROS modulation in the roots begins (20-40 minutes after treatment with NF) [107], [70]. Therefore, modulation of  $\text{Ca}^{2+}$ -flow does not coincide in time with ROS modulation and root hair deformation during legume-rhizobial symbiosis.

There are available results of the tests, where calcium causes ROS generation, while in other tests ROS foster  $\text{Ca}^{2+}$  entrance to cytosol. Mutual enhancement of ROS and calcium activity as messengers of a single signal system is possible [75], [66]. In legume-rhizobial symbiosis роль the role of these compounds is likely to be primarily in plant metabolism regulation conditioned to reconfiguration of metabolism at the level of mutualistic interaction and prevention of triggering protective reactions against symbiotic partner – rhizobia.

ROS and RNS interaction mechanisms are an important issue. It has been sufficiently studied for phytopathogenesis, when systemic resistance is acquired based on cell SSR and its further death. As shown by the studies, host plant cell death with SSR results from simultaneous activity of ROS and RNS. Proportional content in the cell of NO,  $\text{O}_2^-$ ,  $\text{H}_2\text{O}_2$  and  $\text{OONO}^-$  determines cell SSR to phytopathogen invasion or elicitors' impact on the plant [31], [121], [120]. This phenomenon, however, has not been explored in case of legume-rhizobial interaction.

ROS were found to play a key role in regulation of polar growth of root hair, *Fucus* zygotes and pollen tubes through their ability to regulate  $\text{Ca}^{2+}$ -channels engaged in the establishment of apical calcium gradient [93], [25]. Modern views on calcium and nitrogen oxide link in signal systems under pathogenesis are summed up in the review by Jeandroz et al. [63], where specific attention is paid to interaction on cytoplasmic membrane of bacterial compound (MAMP) and plant receptor (PRR) leading to enhancement of calcium inflow to cytosol through  $\text{Ca}^{2+}$ -channels (CNGCs) followed by cytosol calcium influence on NO synthesis and nitrogen oxide impact on genes expression and  $\text{Ca}^{2+}$  outflow from intra-cellular organelles to cytosol.

ROS and  $\text{Ca}^{2+}$  have been proven to be major signal elements of the mechanism of regulation of membrane NADPH oxidase activity in plants. Plant NADPH oxidase is designated as Rboh (respiratory burst oxidase homologs) and is a homolog of  $\beta$ -subunit (gp91phox) of phagocytes NADPH oxidase. Rboh has N-terminal sector connecting  $\text{Ca}^{2+}$  ions by two motifs (EF-hand). Cytosol calcium flows are supposed to activate  $\text{Ca}^{2+}$ -dependent protein-kinases (CDPK), which phosphorylate N-terminal sector of Rboh and therefore, activate the enzyme [60]. All these data speak in favor of  $\text{Ca}^{2+}$  regulating role in plant NADPH oxidase activity [55]. NADPH oxidase localized on plasmalemma is activated when organisms are affected by abiotic and biotic factors [56]. ROS formed through the activation of this enzyme protect the plant from pathogens via participation in cell super-sensitivity reaction, systemic acquired and induced resistance, strengthening of cell wall as a mechanical barrier on the path of infection [122].

Regulation of NADPH oxidase activity may also involve NO participation via S- nitrosilation of cysteine (Cys 890) enzyme, which leads to the loss of enzyme activity and reduction of ROS generation [119]. As Marino et al. [79] demonstrate, alfalfa NADPH oxidase is engaged in functioning of alfalfa nodules. The tests with NADPH oxidase inhibitor (diphenyleneiodonium chloride) hinders ROS reaction in the roots, root hair deformation, formation IF [70], [87].

The interaction of signal systems ( $\text{Ca}^{2+}$ , ROS, RAS, NO, etc.) is a major problem in the initial stages of bean-rhizobial symbiosis in normal physiological conditions for plant growth and especially in adverse biotic and abiotic factors. Calcium is necessary for the functioning of the NADPH oxidase -generator of ROS, there is evidence of the need for calcium for the functioning of the plant enzyme that generates NO in reaction with L-arginine [28]. But on the other hand, the abundant infection is able to reduce the level of NO,  $\text{H}_2\text{O}_2$  in the tissues of the roots of pea seedlings [57]. The participation of  $\text{Ca}^{2+}$  in both processes is obvious, but the mechanism remains to be seen.

### Conflict of Interest

None declared.

### Конфликт интересов

Не указан.

### References

1. Baptista P. Involvement of reactive oxygen species during early stages of ectomycorrhiza establishment between *Castanea sativa* and *Pisolithus tinctorius* / P. Baptista, A. Martins, M.S. Pais et al. // Mycorrhiza. - 2007. – Vol.17. - P. 185-193.
2. Denarie J. Four genes of *Medicago truncatula* controlling components of a Nod factor transduction pathway / J. Denarie // Plant Cell. - 2000. – Vol.12. - P. 647-1666.

3. Andersson C.R. New hemoglobin gene from soybean: a role for hemoglobin in all plants / C.R. Andersson, E.O. Jensen, D.L. Flewellyn et al. // Proc. Natl. Acad. Sci. USA. – 1996. - Vol. 93. – P. 5682-5687.
4. Appleby C.A. The origin and functions of haemoglobin in plants / C.A. Appleby // Science Progress. - 1992. - Vol.76. - P. 365-398.
5. Arrighi J.-F. The *Medicago truncatula* lysine motif–receptor-like kinase gene family includes NFP and new nodule expressed genes / J.-F. Arrighi, A. Barre, B. Ben Amor et al. // Plant Physiology.- 2006. – Vol. 142. - P. 265-279.
6. Batut J. Peptide signaling in the rhizobium-legume symbiosis / J. Batut, P. Mergaert, C. Masson-Boivin // Curr. Opin. Microbiol. – 2011. - Vol. 14. – P. 181-187.
7. Baudouin E. Nitric oxide is formed in *Medicago truncatula* – *Sinorhizobium meliloti* functional nodules / E. Baudouin, L. Pieuchot., G. Engler et al. // Mol. Plant-Microbe Interac. - 2006. – Vol. 19. - P. 970-975.
8. Baxter-Burrell A. Rop GAP4-dependent Rop GTPase rheostat control of *Arabidopsis* oxygen deprivation tolerance / A. Baxter-Burrell, Z. Yang, P.S. Springer et al. // Journal Science. - 2002.- Vol. 296. – P. 2026-2028.
9. Becana M. Reactive oxygen species and antioxidants in legume nodules / M. Becana, D.A. Dalton, J.F. Moran et al. // Physiol. Plant. - 2000. - Vol.109. - P. 372-381.
10. Blilou I. Resistance of pea root to endomycorrhizal fungus or *Rhizobium* correlates with enhanced levels of endogenous salicylic acid / I. Blilou., J. Ocampo, J. Garcia-Garrido // J. Exp. Bot. – 1999. - Vol. 50. – P. 1663- 1668.
11. Blume B. Receptor-mediated increase in cytoplasmic free calcium required for activation of pathogen defense in parsley / B. Blume, T. Nurnberger, N. Nass et al. // Plant Cell. - 2000. – Vol. 12. – P. 1425-1440.
12. Bolwer C. The role calcium and activated oxygen as signals for controlling cross-tolerance / C. Bolwer, R. Fluhr // Trends Plant Science. – 2000. – Vol. 5. - P. 241-246.
13. Bueno P. Time-course of lipoxygenase, antioxidant enzyme activities and H<sub>2</sub>O<sub>2</sub> accumulation during the early stages of *Rhizobium* – legume symbiosis / P. Bueno, M.J. Soto, M.P. Rodriguez-Rosales et al. // New Phytol.- 2001. -Vol. 152. – P. 91-96.
14. Cardenas L. Ion changes in legume root hairs responding to Nod factors / L. Cardenas , T. L. Holdaway-Clarke, F. Sanchez et al. // Plant Physiol. – 2000. - Vol.123. - P 443-452.
15. Catford J.-G. Suppression of arbuscular mycorrhizal colonization and nodulation in split-root systems of alfalfa after preinoculation and treatment with Nod factors/ J.-G. Catford, C. Staehelin, S. Lerat et al. // J. Exp. Bot. – 2003. – Vol. 54. – P. 1481-1487.
16. Catoira R. Fast, transient and specific intracellular ROS changes in root hair cells responding to Nod factors (NFs) / R. Catoira, C. Galera, F. de Billy, R.V. Penmetsa et al. // Plant J. – 2008. – Vol. 56. – P. 802-813.
17. Coelho S.M. A tip-high, Ca<sup>2+</sup>-interdependent, reactive oxygen species gradient is associated with polarized growth in *Fucus serratus* zygotes S.M. Coelho, C. Brownlee, J.H. Bothwell // Planta.- 2008. - Vol. 227. – P. 1037-1046.
18. Courtois C. Nitric oxide signaling in plants: interplays with Ca<sup>2+</sup> and protein kinases / C. Courtois, A. Besson, J. Dahan // J. Exp. Bot. – 2008. – Vol. 59. - P.155-163.
19. Цыганова А.В. Клеточные механизмы развития клубеньков у бобовых растений / А.В. Цыганова, А.Б. Китаева, Н.Ж. Бревин и другие // Сельскохозяйственная биология. – 2011. - № 3. – С. 34-41.
20. D'Haese W. Reactive oxygen species and ethylene play a positive role in lateral root base nodulation of a semiaquatic legume / W. D'Haese, R.R. De Rycke, R. Mathis et al. // Proc. Natl. Acad. Sci. USA. – 2003. – Vol. 100. - P. 11789-11794.
21. Deakin W.J. Symbiotic use of pathogenic strategies: rhizobial protein secretion systems / W.J. Deakin, W.J. Broughton // Nature Rev. Microbiol. – 2009. – Vol. 7. – P. 312-320.
22. Delledonne M. Signal interactions between nitric oxide and reactive oxygen intermediates in the plant hypersensitive disease resistance response / M. Delledonne, J. Zeier, A. Marocco et al. // Proc. Natl. Acad. Sci. USA. – 2001. – Vol. 98. -P. 13454-13459.
23. Doke N. The oxidative burst protects plants against pathogen attack: mechanism and role as an emergency signal for plant biodefense – a Review / N. Doke, Y. Miura., L.M. Sanchez et al. // Gene. - 1996. – Vol.179. – P. 45-51.
24. Ehrhard D.W. Calcium spiking in plant root hairs responding to *Rhizobium* nodulation signals / D.W. Ehrhard, E.M. Atkinson, S.R. Long // Cell. - 1996. – Vol. 85. – P. 673-681.
25. Ehrhard D.W. Depolarization of alfalfa root hair membrane potential by *Rhizobium meliloti* Nod factors / D.W. Ehrhard, E.M. Atkinson, S.R. Long // Science. – 1992. – Vol. 256. – P. 998-1000.
26. Esseling J.J. Nonsymbiotic root hair tip growth phenotype in NORK-mutated legumes: implications for nodulation factor-induced signaling and formation of a multifaceted root hair pocket for bacteria / J.J. Esseling, F.G.P. Lhuissier, A.M.C. Emons // Plant Cell. – 2004.- Vol. 16. – P. 933-944.
27. Etzler M.E. A Nod factor binding with apyrase activity from legume roots / M.E. Etzler, G. Kalsi, N.N. Ewing et al. // Proc. Natl. Acad. Sci. USA. – 1999. – Vol. 96. – P. 5856-5861.
28. Felle H.H. Nod signal – induced plasma membrane potential changes in alfalfa root hairs are differentially sensitive to structural modifications of the lipochitooligosacchride / H.H. Felle, E. Kondorosi, A. Kondorosi et al. // Plant J. – 1995. – Vol. 7. – P. 939-947.
29. Ferguson B.J. Molecular analysis of legume nodule development and autoregulation / B.J. Ferguson, A. Indrasumunar, S. Hayashi et al. // Integr. Plant Biol.- 2010. – Vol.52. – P. 61-76.
30. Ferguson B.J. Signaling interactions during nodule development / B.J. Ferguson, U. Mathesius // J. Plant Growth Regul. - 2003. – Vol. 22. – P. 47-72.
31. Fisher R.F. *Rhizobium*-plant signal exchange / R.F. Fisher, S.R. Long // Nature. – 1992. – Vol. 357. - P. 655-660.
32. Foreman J. Reactive oxygen species produced by NADPH oxidase regulate plant cell growth / J. Foreman, V. Demidchik J.H., Bothwell et al. // Nature. – 2008. – Vol. 422. – P. 442-446.

33. Foreman J. Reactive oxygen species produced by NADPH oxidase regulate plant cell growth / J. Foreman, V. Demidchik, J.H. Bothwell et al. // Nature. - 2003. - Vol.422. - P. 442-446.
34. Foyer C.H. Redox sensing and signaling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria / C.H. Foyer, G. Noctor // Physiol. Plantarum. - 2003. - Vol. 119. - P. 355-364.
35. Gage D.J. Infection and invasion of roots by symbiotic, nitrogen-fixing rhizobia during nodulation of temperate legumes / D.J. Gage // Microbiol. Mol. Biol. Rev. - 2004. - Vol. 68. - P. 280-300.
36. Gamas P. Symbiosis-specific expression of two *Medicago truncatula* nodulin genes, MtN1 and Mt13, incoding products homologous to plant defense proteins / P.Gamas, F. de Billy, G.Truchet // Mol. Plant-Microbe Interac. - 1998. - Vol.11. - P. 393-403.
37. Garcia-Garrido J.M. Regulation of the plant defense response in arbuscular-mycorrhizal symbiosis / J.M. Garcia-Garrido, J.A. Ocampo // Exp. Bot. - 2002. - Vol. 53. - P. 1377-1386.
38. Gilles-Gonzalez M.A. Heme-based sensors, exemplified by the kinase FixL, are a new class of heme protein with distinctive ligand binding and autoxidation / M.A. Gilles-Gonzalez, G. Gonzalez, M.F. Perutz et al. // Biochemistry. - 1994. - Vol. 33. - P. 8067-8073.
39. Glyan'ko A.K. Physiological role of nitric oxide (NO) at vegetative organisms / A.K. Glyan'ko, N.B. Mitanova, A.V. Stepanov // J. Stress Physiol. Biochem. - 2009. - Vol. 5. - P. 33-52.
40. Glyan'ko A.K. The defense and regulatory mechanisms during development of legume-Rhizobium symbiosis / Glyan'ko A.K., G.P. Akimova, M.G. Sokolova et al. // Applied Biochem. Microbiol. - 2007. - Vol. 43. - P. 260-267.
41. Glyan'ko A.K. The NADPH oxidase activity of pea seedling roots in rhizobial infection depending on abiotic factors / A.K. Glyan'ko, G.G. Vasil'eva, A.A. Ischenko et al. // Applied Biochem. Microbiol. - 2010. - Vol. 46. - P. 438-443.
42. Glyan'ko A.K. Influence of environmental factors on the generation of nitric oxide in the roots of etiolated pea seedlings / A.K. Glyan'ko, N.B. Mitanova., A.A. Stepanov // Applied Biochem. Microbiol. - 2012. - V. 48. - P. 83-89.
43. Glyan'ko A.K. Possible involvement of hydrogen peroxide and salicylic acid in the legume-Rhizobium symbiosis / A.K. Glyan'ko, L. E. Makarova, G.G. Vasil'eva et al. // Biology Bulletin. - 2005. - Vol. 32. - P. 245-249.
44. Glyan'ko A.K. Reactive oxygen and nitrogen species in legume-rhizobial symbiosis. A Review / A.K. Glyan'ko, G.G.Vasil'eva // Applied Biochem. Microbiol. - 2010. - Vol. 46. - P. 15-22.
45. Glyan'ko A.K. Structural and functional characteristics of plant NADPH oxidase. A Review / A.K. Glyan'ko, A.A. Ischenko. // Applied Biochem. Microbiol. - 2010. - Vol. 46. - P. 463-471.
46. Goethals K. Conserved motifs in a divergent nod box of *Azorhizobium caulinodans* ORS571 reveals a common structure in promoters regulated by LysR-type proteins / K. Goethals, M. Van Montagu, M. Holsters // Proc. Natl. Acad. Sci. USA. - 1992. - Vol. 89. - P. 1646-1650.
47. Gonzalez-Rizzo S. The *Medicago truncatula* CRE1 cytokinin receptor regulates lateral root development and early symbiotic interaction with *Sinorhizobium meliloti* / S. Gonzalez-Rizzo, M. Crespi, F. Flugier // Plant Cell. - 2006. - Vol.18. - P. 2680-2693.
48. Gough C. Lipochitooligosaccharide signaling in endosymbiotic plant-microbe interactions / C. Gough, J. Cullimore // Mol. Plant-Microbe Interac. - 2011. - Vol.24. - P. 867-878.
49. Hayashi T. A dominant function of CcMK in intracellular accommodation of bacterial and fungal endosymbionts / T. Hayashi, M. Banda., H. Kouchi et al. // Plant J. - 2010. - Vol. 63. - P. 141-154.
50. Heidstra R. Nod factor-induced host responses and mechanisms of Nod factor perception / R. Heidstra, T. Bisseling // New Phytol. - 1996. - Vol.133. - P.25-43.
51. Herouart D. Reactive oxygen species, nitric oxide and glutathione: key role in the establishment of the legume-*Rhizobium* symbiosis / D. Herouart, E.Baudouin, P. Frendo et al. // Plant Physiol. Biochem. - 2002. - Vol. 40. - P. 619-624.
52. Iturbe-Ormaetxe I. The antioxidants of legume nodule mitochondria. / I. Iturbe-Ormaetxe, M.A. Matamoros, M.C. Rubio et al. // Mol. Plant-Microbe Interac. - 2001. - Vol. 14. - P.1189-1196.
53. Jabs T. Elicitor-stimulated ion fluxes and O<sub>2</sub><sup>-</sup> from the oxidative burst are essential components in triggering defense gene activation and phytoalexin synthesis in parsley / T. Jabs, M.Tschope, C. Colling et al. // Proc. Natl. Acad. Sci. USA. - 1997. - Vol. 94. - P. 4800-4805.
54. Jeandroz S. There's more to the picture than meets the eye: nitric oxide cross talk with Ca<sup>2+</sup> signaling / S. Jeandroz, O. Lamotte, J. Astier et al. // Plant Physiol. - 2013. - V. 163. - P. 459-470.
55. Jones K. M. How rhizobial symbionts invade plants: the *Sinorhizobium-Medicago* model / K. M. Jones., H. B. Kobayashi, W. Davies et al. // Nature Rev. Microbiol. - 2007.- Vol. 5. - P. 619-633.
56. Kobayashi M. Subcellular localization of stRboh proteins and NADPH-dependent O<sub>2</sub><sup>-</sup> generating activity potato tuber tissues / M. Kobayashi, K. Kawakita, M. Maeshima et al. // J. Exp. Bot. - 2006. - Vol. 57. - P. 1373-1379.
57. Kolupaev Yu. Ye. Calcium and stress reactions of plants / Yu. Ye. Kolupaev // The Bulletin Kharkiv National Agrarian University. Series Biology. - 2007. - 1(10). - P. 24-41.
58. Космачевская О.В. Влияние физиологических лигандов на функционирование леггемоглобина / Автореферат дис... на соискание ... кандидата наук по спец. «Биохимия»: 03.00.04: защищена 27.05.08.: / Космачевская Ольга Владимировна, М., - 2008. - 24 с.
59. Kotchoni S.O. The reactive oxygen species network pathways: an essential prerequisite for perception of pathogen attack and the acquired disease resistance in plants / S.O. Kotchoni, E.W. Gachomo // J. Biosci. - 2006. - Vol.31. - P. 389-404.
60. Kouchi H. How many peas in a pod? Legume genes responsible for mutualistic symbioses underground / H. Kouchi, H. Imaizumi-Anraku, M. Hayashi et al. // Plant Cell Physiol. - 2010. - Vol. 51. - P. 1381-1397.
61. Kwak J.M. NADPH oxidase *AtrbohD* and *AtrbohF* genes function in ROS-dependent ABA signaling in *Arabidopsis* / J.M. Kwak., I.C. Mori, Z.M. Pei et al. // EMBO J. - 2003.- Vol. 22. - P. 2623-2633.



62. Limpens E. LysM domain receptor kinases regulating rhizobial Nod factor-induced infection / E. Limpens, C.Franken, P. Smit et al. // Science. – 2003. – Vol. 302. – P. 630-633.
63. Lohar D.P. A transient decrease in reactive oxygen species in roots leads to root hair deformation in the legume-rhizobia symbiosis / D.P. Lohar, S. Haridas, J.S. Gantt et al. // New Phytol. - 2007.- Vol.173. – P. 39-49.
64. Lohar D.P. Transcript analysis of early nodulation events in *Medicago truncatula* / D.P. Lohar, N. Sharopova, G. Endre et al. // Plant Physiol. - 2006. – Vol. 140. – P. 221-234.
65. Madsen E.B. A receptor kinase gene of the LysM type is involved in legume perception of rhizobial signals / E.B. Madsen., L.H. Madsen, S. Radutoiu et al. // Nature.- 2003. – Vol. 425. – P. 637-640.
66. Maksimov I.V. Pro-/antioxidant system and resistance of plants to pathogens / I.V.Maksimov, E.A.Cherepanova // Biology Bulletin Reviews. – 2006. – Vol.126. – P. 250-261
67. Marino D. *Medicago truncatula* NADPH oxidase is involved in symbiotic nodule functioning / D.E. Marino, E.Andrio, E.G.J. Danchin et al.// New Phytol. 2011. – Vol.189. – P. 580-592.
68. Martinez-Abarka F. Involvement of salicylic acid in the establishment of the *Rhizobium meliloti*-alfalfa symbiosis / F. Martinez-Abarka, J.A. Herrera-Cervera, P. Bueno et al. // Mol. Plant-Microbe Interac. - 1998. – Vol. 11. 1998. – P. 153-155.
69. Matamoros M.A. Biochemistry and molecular biology of antioxidants in the rhizobia-legume symbiosis / M.A. Matamoros., D.A. Dalton, J. Ramos et al.. // Plant Physiol. - 2003. – Vol.133. – P. 499-509.
70. Mathieu C. Direct detection of radicals in intact soybean nodules: presence of nitric oxide-leghemoglobin complexes / C. Mathieu, S. Moreau, P. Frendo et al. // Free Rad. Biol. Med. – 1998. – Vol. 24. – P. 1242-1249.
71. Медведев С.С. Кальций - сигнальная система в растениях / С.С. Медведев // Сигналинг в клетках. – Казань: Изд. ФЕН. 2010. – С. 26-36.
72. Medvedev S.S. Calcium signaling system in plants / S.S. Medvedev // Russian J. Plant Physiol. -2005. - Vol. 52. – P. 249-270.
73. Meilhoc E. Nitric oxide in legume-rhizobium symbiosis / E. Meilhoc, A. Boscan, C. Bruand et al. // Plant Sci. - 2011. – Vol. 181. – P. 573-581.
74. Мерзляк М.Н. Активированный кислород и окислительные процессы в мембранах растительной клетки / М.Н. Мерзляк. – М: Изд. ВИНТИ, 1989. – 166 с.
75. Miller G. The plant NADPH oxidase RBohD mediates rapid systemic in response to diverse stimuli / G. Miller, K. Schlauch, R. Tam et al. // Sci. Signal. – 2009. – Vol. 2. № 84. ra 45. doi: 10.1126/scisignal.2000448
76. Митанова Н.Б. Влияние минерального азота на начальные этапы формирования бобово-ризобиального симбиоза / Автореферат дис... на соискание... кандидата наук по спец. «Физиология и биохимия растений»: 03.01.05: защищена 02.03.10. / Митанова Наталья Баировна, Иркутск. - 2010. -19 с.
77. Mittler R. ROS signaling: the new wave? / R. Mittler, S. Vanderauwera, N.Suzuki et al. // Trends Plant Sci. - 2011. – Vol.16. - P. 300-309.
78. Miwa H. Analysis of Nod factor - induced calcium signaling in root hairs of symbiotically defective mutants of *Lotus japonicus* / H. Miwa, J. Sun, G.E.D. Oldroyd et al. // Mol. Plant-Microbe Interac. – 2006. – Vol.19. – P. 914-923.
79. Mori I.C. Reactive oxygen species activation of plant Ca<sup>2+</sup> channels. A signaling mechanism in polar growth, hormone transduction, stress signaling, and hypothetically mechanotransduction / I.C.Mori, J.S. Schroeder // Plant Physiol. - 2004. – Vol.135. – P. 702-708.
80. Murray J.D. Invasion by invitation: rhizobial infection in legumes / J.D. Murray // Mol. Plant-Microbe Interac. - 2011. – Vol. 24. – P. 631-639.
81. Okamoto S. Nod factor /nitrate - induced CLE genes that drive HAR1- mediated systemic regulation of nodulation / S. Okamoto, E. Ohnishi, S. Sato et al. // Plant Cell Physiol. – 2009. - Vol. 50. – P. 67-77.
82. Oldroyd G.E.D. Calcium, kinases and nodulation signaling in legumes / G.E.D. Oldroyd, J.A. Downie // Nat. Rev. Mol. Cell Biol. -2004. – Vol. 5. – P. 566-576.
83. Oldroyd G.E.D. Coordinating nodule morphogenesis with rhizobial infection in legumes / G.E.D. Oldroyd, J.A. Downie // Annu. Rev. Plant Biol. – 2008. – Vol. 59. – P. 519-546.
84. Oldroyd G.E.D. The rules of engagement in the legume-rhizobial symbiosis / G.E.D. Oldroyd, J.D. Murray, P.S. Poole et al. // Annu. Rev. Genet. – 2011. – Vol.45. – P. 119-144.
85. Parniske M. Intracellular accommodation of microbes by plants: a common developmental program for symbiosis and disease? / M. Parniske // Curr. Opin. Plant Biol. 2000. 3: 320-328.
86. Pauly N. Reactive oxygen and nitrogen species and glutathione: key players in the legume-*Rhizobium* symbiosis /N. Pauly, C. Pucciariello, K. Mandon et al. // J. Exp. Bot.- 2006. – Vol. 57. – P. 1769-1776.
87. Pei Z.M. Calcium channels activated by hydrogen peroxide mediate abscisic acid signaling in guard cells / Z.M. Pei, Y. Murata, G. Benning et al. // Nature. – 2000. – Vol. 406. – P.731-734.
88. Peleg-Grossman S. Root hair curling and *Rhizobium* infection in *Medicago truncatula* are mediated by phosphatidylinositol – regulated endocytosis and reactive oxygen species / S. Peleg-Grossman, H. Volpin, A.Levine // J. Exp. Bot. - 2007. – Vol. 58. – P. 1637-1649.
89. Perotto S. Cytological evidence for a host defense response that cell and tissue invasion in pea nodules by lipopolysaccharide-defective mutants of *Rhizobium leguminosarum* strain 3841 / S. Perotto, N.J. Brewin, E.I.Kannenbergl // Mol. Plant-Microbe Interac. – 1994. – Vol.7. - P. 99-112.
90. Pieterse C.M.J. Rhizobacteria-mediated induced systemic resistance (ISR) in *Arabidopsis* requires sensitivity to jasmonate and ethylene but is not accompanied by an increase in their production./ C.M.J. Pieterse, J.A. van Pelt, J. Ton et al. // Physiol. Mol. Plant Pathol. – 2000. – Vol. 57. – P. 123-134.
91. Pieterse C.M.J. A novel signaling pathway controlling induced systemic resistance in *Arabidopsis* / C.M.J. Pieterse, S.C.M. van Wees, J.A. van Pelt et al. // Plant Cell. - 1998. – Vol.10. – P. 1571-1580.

92. Полесская О.Г. Растительная клетка и активные формы азота / О.Г. Полесская . – М.: Изд «Университетский Дом Книги», 2007. – 140 с.
93. Popp C. Regulation of signal transduction and bacterial infection during root nodule symbiosis / C. Popp, T. Ott // Curr. Opin. Plant Biol. – 2011. – Vol. 14. – P. 458-467.
94. Potocky M. Reactive oxygen species produced by NADPH oxidase are involved in pollen tube growth / M. Potocky, M.A. Jones, R. Bezvoda et al. // New Phytol. – 2007. – Vol.74. – P. 742-751.
95. Pourrut B. Potential role of NADPH oxidase in early steps of lead-induced oxidative burst in *Vicia faba* roots / B. Pourrut, G. Perchet, J. Silvestre et al. // J. Plant Physiol. – 2008. – Vol. 65. – P. 571-579 .
96. Проворов Н.А. Генетические основы эволюции растительно-микробного симбиоза / Н.А. Проворов, Н.И. Воробьев. – Санкт-Петербург: – Изд. Инфорнавигатор. - 2012. – 400 с.
97. Radutoiu S. Plant recognition of symbiotic bacteria requires two LysM receptor-like kinases / S. Radutoiu, L.H. Madsen, E.B. Madsen et al. // Nature. - 2003. -Vol. 425. – P. 585-592.
98. Ramu K. Nod factor induction of reactive oxygen species production is correlated with expression of the nodulin gene *rip1* in *Medicago truncatula* / K. Ramu, H.M. Peng, D.R. Cook // Mol. Plant-Microbe Interac. – 2002. – Vol.15. – P. 522-528.
99. Reddy A.S.N. Calcium: siler bullet in signaling / A.S.N. Reddy // Plant Sci. - 2001. – Vol.160. - P. 381-404.
100. Ryals J.A. Systemic acquired resistance / J.A. Ryals, U.H. Neuenschwander, M.G. Willits et al. // Plant Cell. – 1996. – Vol. 8. – P. 1809-1819.
101. Sagi M. Production of reactive oxygen species by plant NADPH oxidases / M. Sagi, R. Fluhr // Plant Physiol. – 2006. – Vol. 141. – P 336-340.
102. Sanchez C. Nitric oxide detoxification in the rhizobium-legume symbiosis / C. Sanchez, J.J. Cabrera, A.J. Gates et al. // Biochem. Soc. Transact. - 2011. – Vol.39. – P. 184-186.
103. Santos R. Oxidative burst in alfalfa -*Sinorhizobium meliloti* symbiotic interaction / R. Santos, D. Herouart, S. Sigaud et al. // Mol. Plant-Microbe Interac. – 2001. -Vol.14. – P. 86-89.
104. Shaw S.L. Nod factor elicits two separable calcium responses in *Medicago truncatula* root hair cells / S.L. Shaw, S.R. Long // Plant Physiol. – 2003. – Vol.131. – P. 976-984.
105. Shaw S.L. Nod factor elicits two separable calcium responses in *Medicago truncatula* root hair cells / S.L. Shaw, S.R. Long // Plant Physiol. – 2003. – Vol.131. – P. 976-984.
106. Shaw S.L. Nod factor inhibition of reactive oxygen efflux in a host legume / S.L. Shaw, S.R. Long // Plant Physiol. - 2003a – Vol.132. – P. 2196-2204.
107. Shimoda Y. Symbiotic rhizobium and nitric oxide induce gene expression of non-symbiotic hemoglobin in *Lotus japonicus* / Y. Shimoda, M. Nagata, A. Suzuki et al. // Plant Cell Physiol. – 2005. -Vol. 46. – P. 99-107.
108. Шумный В.К. Биологическая фиксация азота / В.К. Шумный, К.К. Сидорова, И.Л. Клевенская и другие – Новосибирск.: Наука, 1991. – С. 108-110.
109. Soto M.J. Rhizobia and plant-pathogenic bacteria: common infection weapons / M.J. Soto, J. Sanjuan, J. Olivares // Microbiol. - 2006. - Vol.152. - P. 3167-3174.
110. Spaink H.P. A receptor in symbiotic dialogue // H.P. Spaink // Nature. – 2002.- Vol.417. – P. 910-911.
111. Spaink H.P. The molecular basis of infection and nodulation by rhizobia: the ins and outs of sympathogenesis / H.P. Spaink // Annu. Rev. Phytopathol. – 1995. – Vol.33. – P. 345-368.
112. Stacey G. Effect of endogenous salicylic acid on nodulation in the model legumes *Lotus japonicus* and *Medicago truncatula* / G. Stacey, C.B. McAlvin, Sung-Yong Kim et al. // Plant Physiol.- 2006. – Vol. 141. – P.1473-1481.
113. Steinhorst L. Calcium and reactive oxygen species rule the waves of signaling / L. Steinhorst, J. Kudla // Plant Physiol. - 2013. – Vol.163. - P. 471- 485.
114. Suzuki N. Reactive oxygen species and temperature stresses: A delicate balance between signaling and destruction / N. Suzuki, R. Mittler // Physiol. Plant. - 2006. – Vol. 126. – P. 45-51.
115. Тарчевский И.А. Сигнальные системы клеток растений / И.А. Тарчевский. – М.: Наука, 2002. – С. 103-113.
116. Тихонович И.А. Сельскохозяйственная микробиология как основа экологически стабильного сельского хозяйства и прикладные аспекты / И.А. Тихонович, Н.А. Проворов // Сельскохозяйственная биология. – 2011. - № 3. - С.3-9.
117. Trinchant J.C. Nitrite and nitric oxide as inhibitors of nitrogenase from soybean bacteroids / J.C. Trinchant, J. Rigaud // Appl. Environ. Microbiol. - 1982. – Vol. 44. – P. 1385-1388.
118. Van Rhijn P. *Lotus corniculatus* nodulation specificity is changed by the presence of a soybean lectin gene / P. Van Rhijn, R.B. Goldberg, A.M. Hirsch // Plant Cell. - 1998. – Vol.10. – P.1233-1249.
119. Васильева Г.Г. Активные формы кислорода и антиоксидантные ферменты на ранних стадиях взаимодействия гороха и клубеньковых бактерий (*Rhizobium leguminosarum*) / Автореферат дис... на соискание ... кандидата наук по спец. «Физиология и биохимия растений»: 03.01.05: защищена 03.11.04. / Васильева Галина Геннадьевна, Иркутск. – 2004. - 24 с.
120. Васильева Г.Г. Генерация супероксидного аниона в проростках гороха инокулированных азот фиксирующими бактериями разной совместимости / Г.Г. Васильева, Н.В. Миронова, А.К. Глянко и другие // Сельскохозяйственная биология. – 2001. - № 3. – С. 79-83.
121. Vasil'eva G.G. Active oxygen species in pea seedlings during the interactions with symbiotic and pathogenic microorganisms / G.G. Vasil'eva, A.K. Glyan'ko, N.V. Mironova et al. // Applied Biochem. Microbiol. – 2007. – Vol. 43. – P. 217-221.
122. Vasil'eva G.G. Hydrogen peroxide content and catalase activity on inoculation with root nodule bacteria of pea seedlings with different ability for nodulation / G.G. Vasil'eva, A.K. Glyan'ko, N.V. Mironova // Applied Biochem. Microbiol. – 2005. – Vol. 41. – P. 547-550.

123. Vasse J. Abortion of infection during the *Rhizobium meliloti*-alfalfa symbiotic interaction is accompanied by hypersensitive reaction / J. Vasse, F. de Billy, J. Truchet // *Plant J.* - 1993. – Vol. 4. – P. 555-566.
124. Vieweg M.F. Two genes encoding different truncated hemoglobins are regulated during root nodule and arbuscular mycorrhiza symbioses of *Medicago truncatula* / M.F. Vieweg, N. Hohnjec, H. Kuster // *Planta.* – 2005. – Vol. 220. – P. 757-766.
125. Whalley H.J. Calcium signatures are decoded by plants to give specific gene responses / H.J. Whalley, M.R. Knight // *New Phytol.* - 2013. – Vol. 197. – P. 690-693.
126. Yamamoto Y. Inhibition of nitrogen fixation in soybean plants supplied with nitrate / Y. Yamamoto, Y. Kanayama // *Plant Cell Physiol.* – 1990. – Vol. 31. – P. 341-346.
127. Yan Z. mir172 regulates soybean nodulation / Z. Yan, M.S. Hossain, J. Wang // *Mol. Plant-Microbe Interac.* – 2013. – Vol. 26. – P. 1371-1377.
128. Yeriskovskaya N.K. Hereditary hyperproduction of free radicals, induction carcinogenesis / N.K. Yeriskovskaya, A.J.U. Kerkis., N.A. Solov'eva et al. // *Doklady Acad. Sci.* – 1994. – Vol. 338. – P. 255-258.
129. Yun B.W. S-nitrosylation of NADPH oxidase regulates cell death in plant immunity / B.W. Yun, A. Feechan, M. Yin et al. // *Nature.* – 2011. – Vol. 479. – P. 264-268.
130. Zaninotto F. Cross talk between reactive nitrogen and oxygen species during the hypersensitive disease resistance response / F. Zaninotto, S. La Camera, A. Polverari et al. // *Plant Physiol.* 2006 141: 379-383.
131. Zhao J. Reactive oxygen species, nitric oxide, and their interactions play different roles in *Cupressus lusitanica* cell death and phytoalexin biosynthesis / J. Zhao, K. Fujita, K. Sakai // *New Phytol.* 2007. – Vol. 175. – P. 215-229.

### References in English

1. Baptista P. Involvement of reactive oxygen species during early stages of ectomycorrhiza establishment between *Castanea sativa* and *Pisolithus tinctorius* / P. Baptista, A. Martins, M.S. Pais et al. // *Mycorrhiza.* - 2007. – Vol. 17. - P. 185-193.
2. Denarie J. Four genes of *Medicago truncatula* controlling components of a Nod factor transduction pathway / J. Denarie // *Plant Cell.* - 2000. – Vol. 12. - P. 647-1666.
3. Andersson C.R. New hemoglobin gene from soybean: a role for hemoglobin in all plants / C.R. Andersson, E.O. Jensen, D.L. Flewellyn et al. // *Proc. Natl. Acad. Sci. USA.* – 1996. - Vol. 93. – P. 5682-5687.
4. Appleby C.A. The origin and functions of haemoglobin in plants / C.A. Appleby // *Science Progress.* - 1992. - Vol. 76. - P. 365-398.
5. Arrighi J.-F. The *Medicago truncatula* lysine motif–receptor-like kinase gene family includes NFP and new nodule expressed genes / J.-F. Arrighi, A. Barre, B. Ben Amor et al. // *Plant Physiology.* - 2006. – Vol. 142. - P. 265-279.
6. Batut J. Peptide signaling in the rhizobium-legume symbiosis / J. Batut, P. Mergaert, C. Masson-Boivin // *Curr. Opin. Microbiol.* – 2011. - Vol. 14. – P. 181-187.
7. Baudouin E. Nitric oxide is formed in *Medicago truncatula* – *Sinorhizobium meliloti* functional nodules / E. Baudouin, L. Pieuchot., G. Engler et al. // *Mol. Plant-Microbe Interac.* - 2006. – Vol. 19. - P. 970-975.
8. Baxter-Burrell A. Rop GAP4-dependent Rop GTPase rheostat control of *Arabidopsis* oxygen deprivation tolerance / A. Baxter-Burrell, Z. Yang, P.S. Springer et al. // *Journal Science.* - 2002.- Vol. 296. – P. 2026-2028.
9. Becana M. Reactive oxygen species and antioxidants in legume nodules / M. Becana, D.A. Dalton, J.F. Moran et al. // *Physiol. Plant.* - 2000. - Vol. 109. - P. 372-381.
10. Blilou I. Resistance of pea root to endomycorrhizal fungus or *Rhizobium* correlates with enhanced levels of endogenous salicylic acid / I. Blilou., J. Ocampo, J. Garcia-Garrido // *J. Exp. Bot.* – 1999. - Vol. 50. – P. 1663- 1668.
11. Blume B. Receptor-mediated increase in cytoplasmic free calcium required for activation of pathogen defense in parsley / B. Blume, T. Nurnberger, N. Nass et al. // *Plant Cell.* - 2000. – Vol. 12. – P. 1425-1440.
12. Bolwer C. The role calcium and activated oxygen as signals for controlling cross-tolerance / C. Bolwer, R. Fluhr // *Trends Plant Science.* – 2000. – Vol. 5. - P. 241-246.
13. Bueno P. Time-course of lipoxygenase, antioxidant enzyme activities and H<sub>2</sub>O<sub>2</sub> accumulation during the early stages of *Rhizobium* – legume symbiosis / P. Bueno, M.J. Soto, M.P. Rodriguez-Rosales et al. // *New Phytol.* - 2001. - Vol. 152. – P. 91-96.
14. Cardenas L. Ion changes in legume root hairs responding to Nod factors / L. Cardenas, T. L. Holdaway-Clarke, F. Sanchez et al. // *Plant Physiol.* – 2000. - Vol. 123. - P 443-452.
15. Catford J.-G. Suppression of arbuscular mycorrhizal colonization and nodulation in split-root systems of alfalfa after preinoculation and treatment with Nod factors/ J.-G. Catford, C. Staehelin, S. Lerat et al. // *J. Exp. Bot.* – 2003. – Vol. 54. – P. 1481-1487.
16. Catoira R. Fast, transient and specific intracellular ROS changes in root hair cells responding to Nod factors (NFs) / R. Catoira, C. Galera, F. de Billy, R.V. Penmetsa et al. // *Plant J.* – 2008. – Vol. 56. – P. 802-813.
17. Coelho S.M. A tip-high, Ca<sup>2+</sup>-interdependent, reactive oxygen species gradient is associated with polarized growth in *Fucus serratus* zygotes S.M. Coelho, C. Brownlee, J.H. Bothwell // *Planta.* - 2008. - Vol. 227. – P. 1037-1046.
18. Courtois C. Nitric oxide signaling in plants: interplays with Ca<sup>2+</sup> and protein kinases / C. Courtois, A. Besson, J. Dahan // *J. Exp. Bot.* – 2008. – Vol. 59. - P. 155-163.
19. Cyganova A.V. Kletochnye mehanizmy razvitiya kluben'kov u bobovyh rastenij [Cellular mechanisms of nodule development in leguminous plants] / A.V. Cyganova, A.B. Kitaeva, N.Zh. Brevin i drugie // *Sel'skohozjajstvennaja biologija [Agricultural Biology].* – 2011. - № 3. – P. 34-41. [in Russian]
20. D'Haese W. Reactive oxygen species and ethylene play a positive role in lateral root base nodulation of a semiaquatic legume / W. D'Haese, R.R. De Rycke, R. Mathis et al. // *Proc. Natl. Acad. Sci. USA.* – 2003. – Vol. 100. - P. 11789-11794.

21. Deakin W.J. Symbiotic use of pathogenic strategies: rhizobial protein secretion systems / W.J. Deakin, W.J. Broughton // *Nature Rev. Microbiol.* – 2009. – Vol. 7. – P. 312-320.
22. Delledonne M. Signal interactions between nitric oxide and reactive oxygen intermediates in the plant hypersensitive disease resistance response / M. Delledonne, J. Zeier, A. Marocco et al. // *Proc. Natl. Acad. Sci. USA.* – 2001. – Vol. 98. -P. 13454-13459.
23. Doke N. The oxidative burst protects plants against pathogen attack: mechanism and role as an emergency signal for plant biodefense – a Review / N. Doke, Y. Miura., L.M. Sanchez et al. // *Gene.* - 1996. – Vol.179. – P. 45-51.
24. Ehrhard D.W. Calcium spiking in plant root hairs responding to *Rhizobium* nodulation signals / D.W. Ehrhard, E.M. Atkinson, S.R. Long // *Cell.* - 1996. – Vol. 85. – P. 673-681.
25. Ehrhard D.W. Depolarization of alfalfa root hair membrane potential by *Rhizobium meliloti* Nod factors / D.W. Ehrhard, E.M. Atkinson, S.R. Long // *Science.* – 1992. – Vol. 256. – P. 998-1000.
26. Esseling J.J. Nonsymbiotic root hair tip growth phenotype in NORK-mutated legumes: implications for nodulation factor-induced signaling and formation of a multifaceted root hair pocket for bacteria / J.J. Esseling, F.G.P. Lhuissier, A.M.C. Emons // *Plant Cell.* – 2004.- Vol. 16. – P. 933-944.
27. Etzler M.E. A Nod factor binding with apyrase activity from legume roots / M.E. Etzler, G. Kalsi, N.N. Ewing et al. // *Proc. Natl. Acad. Sci. USA.* – 1999. – Vol. 96. – P. 5856-5861.
28. Felle H.H. Nod signal – induced plasma membrane potential changes in alfalfa root hairs are differentially sensitive to structural modifications of the lipochitooligosacchride / H.H. Felle, E. Kondorosi, A. Kondorosi et al. // *Plant J.* – 1995. – Vol. 7. – P. 939-947.
29. Ferguson B.J. Molecular analysis of legume nodule development and autoregulation / B.J. Ferguson, A. Indrasumunar, S. Hayashi et al. // *Integr. Plant Biol.*- 2010. – Vol.52. – P. 61-76.
30. Ferguson B.J. Signaling interactions during nodule development / B.J. Ferguson, U. Mathesius // *J. Plant Growth Regul.* - 2003. – Vol. 22. – P. 47-72.
31. Fisher R.F. *Rhizobium*-plant signal exchange / R.F. Fisher, S.R. Long // *Nature.* – 1992. – Vol. 357. - P. 655-660.
32. Foreman J. Reactive oxygen species produced by NADPH oxidase regulate plant cell growth / J. Foreman, V. Demidchik J.H., Bothwell et al. // *Nature.* – 2008. – Vol. 422. – P. 442-446.
33. Foreman J. Reactive oxygen species produced by NADPH oxidase regulate plant cell growth / J. Foreman, V. Demidchik, J.H. Bothwell et al. // *Nature.*- 2003. – Vol.422. – P. 442-446.
34. Foyer C.H. Redox sensing and signaling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria / C.H. Foyer, G. Noctor // *Physiol. Plantarum.* – 2003. – Vol. 119. – P. 355-364.
35. Gage D.J. Infection and invasion of roots by symbiotic, nitrogen-fixing rhizobia during nodulation of temperate legumes / D.J. Gage // *Microbiol. Mol. Biol. Rev.* - 2004. – Vol. 68. – P. 280-300.
36. Gamas P. Symbiosis-specific expression of two *Medicago truncatula* nodulin genes, MtN1 and Mt13, incoding products homologous to plant defense proteins / P.Gamas, F. de Billy, G.Truchet // *Mol. Plant-Microbe Interac.* - 1998. – Vol.11. - P. 393-403.
37. Garcia-Garrido J.M. Regulation of the plant defense response in arbuscular-mycorrhizal symbiosis / J.M. Garcia-Garrido, J.A. Ocampo // *Exp. Bot.* – 2002. – Vol. 53. – P. 1377-1386.
38. Gilles-Gonzalez M.A. Heme-based sensors, exemplified by the kinase FixL, are a new class of heme protein with distinctive ligand binding and autoxidation / M.A. Gilles-Gonzalez, G. Gonzalez, M.F. Perutz et al. // *Biochemistry.* – 1994. - Vol. 33. – P. 8067-8073.
39. Glyan'ko A.K. Physiological role of nitric oxide (NO) at vegetative organisms / A.K. Glyan'ko, N.B. Mitanova, A.V. Stepanov // *J. Stress Physiol. Biochem.* – 2009. – Vol. 5. – P. 33-52.
40. Glyan'ko A.K. The defense and regulatory mechanisms during development of legume-Rhizobium symbiosis / Glyan'ko A.K., G.P. Akimova, M.G. Sokolova et al. // *Applied Biochem. Microbiol.* – 2007. – Vol. 43. – P. 260-267.
41. Glyan'ko A.K. The NADPH oxidase activity of pea seedling roots in rhizobial infection depending on abiotic factors / A.K. Glyan'ko, G.G. Vasil'eva, A.A. Ischenko et al. // *Applied Biochem. Microbiol.* – 2010. – Vol. 46. – P. 438-443.
42. Glyan'ko A.K. Influence of environmental factors on the generation of nitric oxide in the roots of etiolated pea seedlings / A.K. Glyan'ko, N.B. Mitanova., A.A. Stepanov // *Applied Biochem. Microbiol.* - 2012. – V. 48. – P. 83-89.
43. Glyan'ko A.K. Possible involvement of hydrogen peroxide and salicylic acid in the legume-Rhizobium symbiosis / A.K. Glyan'ko, L. E. Makarova, G.G. Vasil'eva et al. // *Biology Bulletin.* - 2005. – Vol. 32. – P. 245-249.
44. Glyan'ko A.K. Reactive oxygen and nitrogen species in legume-rhizobial symbiosis. A Review / A.K. Glyan'ko, G.G.Vasil'eva // *Applied Biochem. Microbiol.* – 2010. – Vol. 46. – P. 15-22.
45. Glyan'ko A.K. Structural and functional characteristics of plant NADPH oxidase. A Review / A.K. Glyan'ko, A.A. Ischenko. // *Applied Biochem. Microbiol.* - 2010. – Vol. 46. – P. 463-471.
46. Goethals K. Conserved motifs in a divergent nod box of *Azorhizobium caulinodans* ORS571 reveals a common structure in promoters regulated by LysR-type proteins / K. Goethals, M. Van Montagu, M. Holsters // *Proc. Natl. Acad. Sci. USA.* – 1992. – Vol. 89. - P. 1646-1650.
47. Gonzalez-Rizzo S. The *Medicago truncatula* CRE1 cytokinin receptor regulates lateral root development and early symbiotic interaction with *Sinorhizobium meliloti* / S. Gonzalez-Rizzo, M. Crespi, F. Flugier // *Plant Cell.* – 2006. – Vol.18. – P. 2680-2693.
48. Gough C. Lipochitooligosaccharide signaling in endosymbiotic plant-microbe interactions / C. Gough, J. Cullimore // *Mol. Plant-Microbe Interac.* – 2011. – Vol.24. – P. 867-878.
49. Hayashi T. A dominant function of CCaMK in intracellular accommodation of bacterial and fungal endosymbionts / T. Hayashi, M. Banda., H. Kouchi et al. // *Plant J.* – 2010. – Vol. 63. – P. 141-154.

50. Heidstra R. Nod factor-induced host responses and mechanisms of Nod factor perception / R. Heidstra, T. Bisseling // *New Phytol.* - 1996. - Vol.133. - P.25-43.
51. Herouart D. Reactive oxygen species, nitric oxide and glutathione: key role in the establishment of the legume-*Rhizobium* symbiosis / D. Herouart, E.Baudouin, P. Frendo et al. // *Plant Physiol. Biochem.* – 2002. – Vol. 40. – P. 619-624.
52. Iturbe-Ormaetxe I. The antioxidants of legume nodule mitochondria. / I. Iturbe-Ormaetxe, M.A. Matamoros, M.C. Rubio et al. // *Mol. Plant-Microbe Interac.* – 2001. – Vol. 14. – P.1189-1196.
53. Jabs T. Elicitor-stimulated ion fluxes and O<sub>2</sub><sup>•-</sup> from the oxidative burst are essential components in triggering defense gene activation and phytoalexin synthesis in parsley / T. Jabs, M.Tschope, C. Colling et al. // *Proc. Natl. Acad. Sci. USA.* - 1997. - Vol. 94. – P. 4800-4805.
54. Jeandroz S. There's more to the picture than meets the eye: nitric oxide cross talk with Ca<sup>2+</sup> signaling / S. Jeandroz, O. Lamotte, J. Astier et al. // *Plant Physiol.* – 2013. – V. 163. – P. 459-470.
55. Jones K. M. How rhizobial symbionts invade plants: the *Sinorhizobium-Medicago* model / K. M. Jones., H. B. Kobayashi, W. Davies et al. // *Nature Rev. Microbiol.* - 2007.- Vol. 5. – P. 619-633.
56. Kobayashi M. Subcellular localization of stRboh proteins and NADPH-dependent O<sub>2</sub><sup>•-</sup> generating activity potato tuber tissues / M. Kobayashi, K. Kawakita, M. Maeshima et al. // *J. Exp. Bot.* - 2006. – Vol. 57. – P. 1373-1379.
57. Kolupaev Yu. Ye. Calcium and stress reactions of plants / Yu. Ye. Kolupaev // *The Bulletin Kharkiv National Agrarian University. Series Biology.* – 2007. - 1(10). – P. 24-41.
58. Kosmachevskaja O.V. Vlijanie fiziologicheskikh ligandov na funkcionirovanie leggemoglobina [Influence of physiological ligands on the functioning of leghemoglobin] / Abstract of thesis dis... of PhD in Biology : 03.00.04: defense of the thesis 27.05.08. / Kosmachevskaja Ol'ga Vladimirovna, M., - 2008. – 24 p. [in Russian]
59. Kotchoni S.O. The reactive oxygen species network pathways: an essential prerequisite for perception of pathogen attack and the acquired disease resistance in plants / S.O. Kotchoni, E.W. Gachomo // *J. Biosci.* – 2006. – Vol.31. - P. 389-404.
60. Kouchi H. How many peas in a pod? Legume genes responsible for mutualistic symbioses underground / H. Kouchi, H. Imaizumi-Anraku, M. Hayashi et al. // *Plant Cell Physiol.* – 2010. – Vol. 51. – P. 1381-1397.
61. Kwak J.M. NADPH oxidase *AtrbohD* and *AtrbohF* genes function in ROS-dependent ABA signaling in *Arabidopsis* / J.M. Kwak., I.C. Mori, Z.M. Pei et al. // *EMBO J.* - 2003.- Vol. 22. - P. 2623-2633.
62. Limpens E. LysM domain receptor kinases regulating rhizobial Nod factor-induced infection / E. Limpens, C.Franken, P. Smit et al. // *Science.* – 2003. – Vol. 302. – P. 630-633.
63. Lohar D.P. A transient decrease in reactive oxygen species in roots leads to root hair deformation in the legume-rhizobia symbiosis / D.P. Lohar, S. Haridas, J.S. Gantt et al. // *New Phytol.* - 2007.- Vol.173. – P. 39-49.
64. Lohar D.P. Transcript analysis of early nodulation events in *Medicago truncatula* / D.P. Lohar, N. Sharopova, G. Endre et al. // *Plant Physiol.* - 2006. – Vol. 140. – P. 221-234.
65. Madsen E.B. A receptor kinase gene of the LysM type is involved in legume perception of rhizobial signals / E.B. Madsen., L.H. Madsen, S. Radutoiu et al. // *Nature.*- 2003. – Vol. 425. – P. 637-640.
66. Maksimov I.V. Pro-/antioxidant system and resistance of plants to pathogens / I.V.Maksimov, E.A.Cherepanova // *Biology Bulletin Reviews.* – 2006. – Vol.126. – P. 250-261
67. Marino D. *Medicago truncatula* NADPH oxidase is involved in symbiotic nodule functioning / D.E. Marino, E.Andrio, E.G.J. Danchin et al.// *New Phytol.* 2011. – Vol.189. – P. 580-592.
68. Martinez-Abarka F. Involvement of salicylic acid in the establishment of the *Rhizobium meliloti*-alfalfa symbiosis / F. Martinez-Abarka, J.A. Herrera-Cervera, P. Bueno et al. // *Mol. Plant-Microbe Interac.* - 1998. – Vol. 11. 1998. – P. 153-155.
69. Matamoros M.A. Biochemistry and molecular biology of antioxidants in the rhizobia-legume symbiosis / M.A. Matamoros., D.A. Dalton, J. Ramos et al.. // *Plant Physiol.* - 2003. – Vol.133. – P. 499-509.
70. Mathieu C. Direct detection of radicals in intact soybean nodules: presence of nitric oxide-leghemoglobin complexes / C. Mathieu, S. Moreau, P. Frendo et al. // *Free Rad. Biol. Med.* – 1998. – Vol. 24. – P. 1242-1249.
71. Medvedev S.S. [Calcium is a signal system in plants] / S.S. Medvedev // *Signaling v kletkah [Signaling in cells].* – Kazan': Izd. FEN. 2010. – P. 26-36. [in Russian]
72. Medvedev S.S. Calcium signaling system in plants / S.S. Medvedev // *Russian J. Plant Physiol.* -2005. - Vol. 52. – P. 249-270.
73. Meilhoc E. Nitric oxide in legume-rhizobium symbiosis / E. Meilhoc, A. Boscan, C. Bruand et al. // *Plant Sci.* - 2011. – Vol. 181. – P. 573-581.
74. Merzljak M.N. Aktivirovannyj kislород i okislitel'nye processy v membranah rastitel'noj kletki [Activated oxygen and oxidative processes in plant cell membranes] / M.N. Merzljak . – M: Izd. VINITI, 1989. – 166 p. [in Russian]
75. Miller G. The plant NADPH oxidase RBohD mediates rapid systemic in response to diverse stimuli / G. Miller, K. Schlauch, R. Tam et al. // *Sci. Signal.* – 2009. – Vol. 2. № 84. ra 45. doi: 10.1126/scisignal.2000448
76. Mitanova N.B. Vlijanie mineral'nogo azota na nachal'nye jetapy formirovaniya bobovo-rizobial'nogo simbioza [Influence of mineral nitrogen on the initial stages of the formation of legume-rhizobia symbiosis] / Abstract of thesis dis... of PhD in Biology : 03.01.05: defense of the thesis 02.03.10. / Mitanova Natal'ja Bairovna, Irkutsk. - 2010. -19 p. [in Russian]
77. Mittler R. ROS signaling: the new wave? / R. Mittler, S. Vanderauwera, N.Suzuki et al. // *Trends Plant Sci.* - 2011. – Vol.16. - P. 300-309.
78. Miwa H. Analysis of Nod factor - induced calcium signaling in root hairs of symbiotically defective mutants of *Lotus japonicus* / H. Miwa, J. Sun, G.E.D. Oldroyd et al. // *Mol. Plant-Microbe Interac.* – 2006. – Vol.19. – P. 914-923.
79. Mori I.C. Reactive oxygen species activation of plant Ca<sup>2+</sup> channels. A signaling mechanism in polar growth, hormone transduction, stress signaling, and hypothetically mechanotransduction / I.C.Mori, J.S. Schroeder // *Plant Physiol.* - 2004. – Vol.135. – P. 702-708.

80. Murray J.D. Invasion by invitation: rhizobial infection in legumes / J.D. Murray // Mol. Plant-Microbe Interac. - 2011. – Vol. 24. – P. 631-639.
81. Okamoto S. Nod factor /nitrate - induced CLE genes that drive HAR1- mediated systemic regulation of nodulation / S. Okamoto, E. Ohnishi, S. Sato et al. // Plant Cell Physiol. – 2009. – Vol. 50. – P. 67-77.
82. Oldroyd G.E.D. Calcium, kinases and nodulation signaling in legumes / G.E.D. Oldroyd, J.A. Downie // Nat. Rev. Mol. Cell Biol. -2004. – Vol. 5. – P. 566-576.
83. Oldroyd G.E.D. Coordinating nodule morphogenesis with rhizobial infection in legumes / G.E.D. Oldroyd, J.A. Downie // Annu. Rev. Plant Biol. – 2008. – Vol. 59. – P. 519-546.
84. Oldroyd G.E.D. The rules of engagement in the legume-rhizobial symbiosis / G.E.D. Oldroyd, J.D. Murray, P.S. Poole et al. // Annu. Rev. Genet. – 2011. – Vol.45. – P. 119-144.
85. Parniske M. Intracellular accommodation of microbes by plants: a common developmental program for symbiosis and disease? / M. Parniske // Curr. Opin. Plant Biol. 2000. 3: 320-328.
86. Pauly N. Reactive oxygen and nitrogen species and glutathione: key players in the legume-*Rhizobium* symbiosis / N. Pauly, C. Pucciariello, K. Mandon et al. // J. Exp. Bot.- 2006. – Vol. 57. – P. 1769-1776.
87. Pei Z.M. Calcium channels activated by hydrogen peroxide mediate abscisic acid signaling in guard cells / Z.M. Pei, Y. Murata, G. Benning et al. // Nature. – 2000. – Vol. 406. – P.731-734.
88. Peleg-Grossman S. Root hair curling and *Rhizobium* infection in *Medicago truncatula* are mediated by phosphatidylinositol 3-kinase-regulated endocytosis and reactive oxygen species / S. Peleg-Grossman, H. Volpin, A. Levine // J. Exp. Bot. - 2007. – Vol. 58. – P. 1637-1649.
89. Perotto S. Cytological evidence for a host defense response that cell and tissue invasion in pea nodules by lipopolysaccharide-defective mutants of *Rhizobium leguminosarum* strain 3841 / S. Perotto, N.J. Brewin, E.I. Kannenberg // Mol. Plant-Microbe Interac. – 1994. – Vol.7. - P. 99-112.
90. Pieterse C.M.J. Rhizobacteria-mediated induced systemic resistance (ISR) in *Arabidopsis* requires sensitivity to jasmonate and ethylene but is not accompanied by an increase in their production./ C.M.J. Pieterse, J.A. van Pelt, J. Ton et al. // Physiol. Mol. Plant Pathol. – 2000. – Vol. 57. – P. 123-134.
91. Pieterse C.M.J. A novel signaling pathway controlling induced systemic resistance in *Arabidopsis* / C.M.J. Pieterse, S.C.M. van Wees, J.A. van Pelt et al. // Plant Cell. - 1998. – Vol.10. – P. 1571-1580.
92. Pollesskaja O.G. Rastitel'naja kletka i aktivnye formy azota [Plant cell and active forms of nitrogen] / O.G. Pollesskaja . – M.: Izd «Universitetskij Dom Knigi», 2007. – 140 p. [in Russian]
93. Popp C. Regulation of signal transduction and bacterial infection during root nodule symbiosis / C. Popp, T. Ott // Curr. Opin. Plant Biol. – 2011. – Vol. 14. – P. 458-467.
94. Potocky M. Reactive oxygen species produced by NADPH oxidase are involved in pollen tube growth / M. Potocky, M.A. Jones, R. Bezvoda et al. // New Phytol. – 2007. – Vol.74. – P. 742-751.
95. Pourrut B. Potential role of NADPH oxidase in early steps of lead-induced oxidative burst in *Vicia faba* roots / B. Pourrut, G. Perchet, J. Silvestre et al. // J. Plant Physiol. – 2008. – Vol. 65. – P. 571-579.
96. Provorov N.A. Geneticheskie osnovy jevoljucii rastitel'no-mikrobnogo simbioza [Genetic basis of the evolution of plant-microbial symbiosis] / N.A. Provorov, N.I. Vorob'ev. – Sankt-Peterburg: – Izd. Infornavigator. - 2012. – 400 p. [in Russian]
97. Radutoiu S. Plant recognition of symbiotic bacteria requires two LysM receptor-like kinases / S. Radutoiu, L.H. Madsen, E.B. Madsen et al. // Nature. - 2003. -Vol. 425. – P. 585-592.
98. Ramu K. Nod factor induction of reactive oxygen species production is correlated with expression of the nodulin gene *ripl1* in *Medicago truncatula* / K. Ramu, H.M. Peng, D.R. Cook // Mol. Plant-Microbe Interac. – 2002. – Vol.15. – P. 522-528.
99. Reddy A.S.N. Calcium: siler bullet in signaling / A.S.N. Reddy // Plant Sci. - 2001. – Vol.160. - P. 381-404.
100. Ryals J.A. Systemic acquired resistance / J.A. Ryals, U.H. Neuenschwander, M.G. Willits et al. // Plant Cell. – 1996. – Vol. 8. – P. 1809-1819.
101. Sagi M. Production of reactive oxygen species by plant NADPH oxidases / M. Sagi, R. Fluhr // Plant Physiol. – 2006. – Vol. 141. – P 336-340.
102. Sanchez C. Nitric oxide detoxification in the rhizobium-legume symbiosis / C. Sanchez, J.J. Cabrera, A.J. Gates et al. // Biochem. Soc. Transact. - 2011. – Vol.39. – P. 184-186.
103. Santos R. Oxidative burst in alfalfa -*Sinorhizobium meliloti* symbiotic interaction / R. Santos, D. Herouart, S. Sigaud et al. // Mol. Plant-Microbe Interac. – 2001. -Vol.14. – P. 86-89.
104. Shaw S.L. Nod factor elicits two separable calcium responses in *Medicago truncatula* root hair cells / S.L. Shaw, S.R. Long // Plant Physiol. – 2003. – Vol.131. – P. 976-984.
105. Shaw S.L. Nod factor elicits two separable calcium responses in *Medicago truncatula* root hair cells / S.L. Shaw, S.R. Long // Plant Physiol. – 2003. – Vol.131. – P. 976-984.
106. Shaw S.L. Nod factor inhibition of reactive oxygen efflux in a host legume / S.L. Shaw, S.R. Long // Plant Physiol. - 2003a – Vol.132. – P. 2196-2204.
107. Shimoda Y. Symbiotic rhizobium and nitric oxide induce gene expression of non-symbiotic hemoglobin in *Lotus japonicus* / Y. Shimoda, M. Nagata, A. Suzuki et al. // Plant Cell Physiol. – 2005. -Vol. 46. – P. 99-107.
108. Shumnyj V.K. Biologicheskaja fiksacija azota [Biological fixation of nitrogen] / V.K. Shumnyj, K.K. Sidorova, I.L. Klevenskaja et al. – Novosibirsk.: Nauka, 1991. – P. 108-110. [in Russian]
109. Soto M.J. Rhizobia and plant-pathogenic bacteria: common infection weapons / M.J. Soto, J. Sanjuan, J. Olivares // Microbiol. - 2006. - Vol.152. - P. 3167-3174.
110. Spaink H.P. A receptor in symbiotic dialogue // H.P. Spaink // Nature. – 2002.- Vol.417. – P. 910-911.
111. Spaink H.P. The molecular basis of infection and nodulation by rhizobia: the ins and outs of symbiogenesis / H.P. Spaink // Annu. Rev. Phytopathol. – 1995. – Vol.33. – P. 345-368.

112. Stacey G. Effect of endogenous salicylic acid on nodulation in the model legumes *Lotus japonicus* and *Medicago truncatula* / G. Stacey, C.B. McAlvin, Sung-Yong Kim et al. // *Plant Physiol.* - 2006. - Vol. 141. - P. 1473-1481.
113. Steinhorst L. Calcium and reactive oxygen species rule the waves of signaling / L. Steinhorst, J. Kudla // *Plant Physiol.* - 2013. - Vol. 163. - P. 471-485.
114. Suzuki N. Reactive oxygen species and temperature stresses: A delicate balance between signaling and destruction / N. Suzuki, R. Mittler // *Physiol. Plant.* - 2006. - Vol. 126. - P. 45-51.
115. Tarchevskij I.A. Signal'nye sistemy kletok rastenij [Signaling systems of plant cells] / I.A. Tarchevskij. - M.: Nauka, 2002. - P. 103-113. [in Russian]
116. Tihonovich I.A. Sel'skohozjajstvennaja mikrobiologija kak osnova jekologicheski stabil'nogo sel'skogo hozjajstva i prikladnye aspekty [Agricultural microbiology as a basis for environmentally sustainable agriculture and applied aspects] / I.A. Tihonovich, N.A. Provorov // *Sel'skohozjajstvennaja biologija [Agricultural Biology]*. - 2011. - № 3. - P. 3-9. [in Russian]
117. Trinchant J.C. Nitrite and nitric oxide as inhibitors of nitrogenase from soybean bacteroids / J.C. Trinchant, J. Rigaud // *Appl. Environ. Microbiol.* - 1982. - Vol. 44. - P. 1385-1388.
118. Van Rhijn P. *Lotus corniculatus* nodulation specificity is changed by the presence of a soybean lectin gene / P. Van Rhijn, R.B. Goldberg, A.M. Hirsch // *Plant Cell.* - 1998. - Vol. 10. - P. 1233-1249.
119. Vasil'eva G.G. Aktivnye formy kisloroda i antioksidantnye fermenty na rannih stadijah vzaimodejstvija goroha i klubenkovyh bakterij (Rhizobium leguminosarum) [Active forms of oxygen and antioxidant enzymes in the early stages of interaction of peas and nodule bacteria (Rhizobium leguminosarum)] / Abstract of thesis dis... of PhD in Biology : 03.01.05 : defense of the thesis 03.11.04. / Vasil'eva Galina Gennad'evna, Irkutsk. - 2004. - 24 p. [in Russian]
120. Vasil'eva G.G. Generacija superoksidnogo aniona v prorostkah goroha inokulirovannyh azot fiksirujushimi bakterijami raznoj sovmestivosti [Generation of superoxide anion in pea seedlings inoculated with nitrogen by fixing bacteria of different compatibility] / G.G. Vasil'eva, N.V. Mironova, A.K. Gljan'ko i drugie // *Sel'skohozjajstvennaja biologija [Agricultural Biology]*. - 2001. - № 3. - P. 79-83. [in Russian]
121. Vasil'eva G.G. Active oxygen species in pea seedlings during the interactions with symbiotic and pathogenic microorganisms / G.G. Vasil'eva, A.K. Gljan'ko, N.V. Mironova et al. // *Applied Biochem. Microbiol.* - 2007. - Vol. 43. - P. 217-221.
122. Vasil'eva G.G. Hydrogen peroxide content and catalase activity on inoculation with root nodule bacteria of pea seedlings with different ability for nodulation / G.G. Vasil'eva, A.K. Gljan'ko, N.V. Mironova // *Applied Biochem. Microbiol.* - 2005. - Vol. 41. - P. 547-550.
123. Vasse J. Abortion of infection during the *Rhizobium meliloti*-alfalfa symbiotic interaction is accompanied by hypersensitive reaction / J. Vasse, F. de Billy, J. Truchet // *Plant J.* - 1993. - Vol. 4. - P. 555-566.
124. Vieweg M.F. Two genes encoding different truncated hemoglobins are regulated during root nodule and arbuscular mycorrhiza symbioses of *Medicago truncatula* / M.F. Vieweg, N. Hohnjec, H. Kuster // *Planta.* - 2005. - Vol. 220. - P. 757-766.
125. Whalley H.J. Calcium signatures are decoded by plants to give specific gene responses / H.J. Whalley, M.R. Knight // *New Phytol.* - 2013. - Vol. 197. - P. 690-693.
126. Yamamoto Y. Inhibition of nitrogen fixation in soybean plants supplied with nitrate / Y. Yamamoto, Y. Kanayama // *Plant Cell Physiol.* - 1990. - Vol. 31. - P. 341-346.
127. Yan Z. mir172 regulates soybean nodulation / Z. Yan, M.S. Hossain, J. Wang // *Mol. Plant-Microbe Interac.* - 2013. - Vol. 26. - P. 1371-1377.
128. Yeriskovskaya N.K. Hereditary hyperproduction of free radicals, induction carcinogenesis / N.K. Yeriskovskaya, A.J.U. Kerkis., N.A. Solov'eva et al. // *Doklady Acad. Sci.* - 1994. - Vol. 338. - P. 255-258.
129. Yun B.W. S-nitrosylation of NADPH oxidase regulates cell death in plant immunity / B.W. Yun, A. Feechan, M. Yin et al. // *Nature.* - 2011. - Vol. 479. - P. 264-268.
130. Zaninotto F. Cross talk between reactive nitrogen and oxygen species during the hypersensitive disease resistance response / F. Zaninotto, S. La Camera, A. Polverari et al. // *Plant Physiol.* 2006 141: 379-383.
131. Zhao J. Reactive oxygen species, nitric oxide, and their interactions play different roles in *Cupressus lusitanica* cell death and phytoalexin biosynthesis / J. Zhao, K. Fujita, K. Sakai // *New Phytol.* 2007. - Vol. 175. - P. 215-229.