
CROP PRODUCTION

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DEFENSIVE MECHANISMS OF A RHIZOBIA - INFECTED LEGUME

Review

Abstract

The data on the defensive mechanisms of a legume plant infected with nodule bacteria (rhizobia) have been summarized. The participation of plant defensive systems MTI (MAMP-triggered immunity) and ETI (effector-triggered immunity) in counteracting rhizobia invasion as probable pathogens into root tissues at the initial stages of organisms interaction, and later on as a regulating mechanism of root rhizobial infection is asserted. The plant ability to block rhizobia invasion into plant's other organs (for instance, pea epicotyls) is stated. A notion of legume local and systemic resistance to rhizobial infection is proposed. In the first case rhizobia suppress immune response of plant root cells; in the second – enhance plant resistance to rhizobia. The role of Nod-factors of rhizobia (NFs) and interacting plant receptors in blocking root defensive reactions and triggering signal cascade within nodule organogenesis is considered. It is concluded that innate legume cell immunity actively participates in formation and functioning of legume-rhizobial symbiosis.

Keywords: Rhizobium, legumes, legume-rhizobial symbiosis, Nod-factors, plant MTI/ETI-defensive mechanisms, bacterial T3/4SS-secretion mechanisms, LysM/LRR-domain RLKs – plant receptors.

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ЗАЩИТНЫЕ МЕХАНИЗМЫ БОБОВОГО РАСТЕНИЯ, ИНФИЦИРОВАННОГО РИЗОБИЯМИ

Обзор

Аннотация

Обобщены данные о защитных механизмах бобового растения, инфицированного клубеньковыми бактериями (ризобиями). Доказывается тезис об участии защитных систем растения MTI (MAMP-triggered immunity) и ETI (effector-triggered immunity) в противодействии инвазии ризобий как возможных патогенов в ткани корня на начальных этапах взаимодействия организмов, а также в дальнейшем, как регулирующий механизм ризобияльного инфицирования корней. Отмечается возможность блокирования растением инвазии ризобий в другие органы растения (например, эпикотили), не подвергающихся инфицированию ризобиями. Предлагается ввести понятие локальной и системной устойчивости бобового растения к ризобияльной инфекции. В первом случае ризобии подавляют иммунный ответ клеток корня растения, во втором – усиливают устойчивость растения к ризобиям. Рассматривается роль Nod-факторов ризобий (NFs) и взаимодействующих с ними растительных рецепторов в блокировании защитных реакций корня и запуске сигнального каскада по органогенезу клубеньков. Делается вывод, что врожденный иммунитет клеток бобового растения активно участвует в формировании и функционировании бобово-ризобияльного симбиоза.

Ключевые слова: Rhizobium, бобовые растения, бобово-ризобияльный симбиоз, Nod-факторы, MTI/ETI-защитные системы растения, T3/4SS-секреторные системы бактерий, LysM/LRR-домен RLKs – растительные рецепторы.

1. Introduction

Pathogenic and mutualistic plant-microbial interactions are widespread in nature. In the first case, pathogenic bacteria during invasion into plant cells receive a unilateral benefit by consuming plant nutrients for their reproduction and “poisoning” the plant body with products of their vital activity. That leads to plant life processes depression, decrease in their productivity and, in the worst case, to death. In mutual associations, the waste products of organisms are used by both partners. For instance, a symbiosis between nodule bacteria (Rhizobiaceae family) and plants of the legume family (Fabaceae) is characterized by the exchange of vital compounds: root nodule bacteria (rhizobia) supply reduced nitrogen (ammonium) to the legume plant, and the plant supplies the bacteria with carbohydrates (dicarboxylic acids).

Understanding the mechanisms of legume-rhizobial interactions is associated with the overcoming of the host plant defensive systems by bacteria and the “legitimate” existence of rhizobia in root tissues of legume plants. How do “enemies” (rhizobia) turn into plant “friends”? These issues require a detailed study in connection with the prospect of creating an N₂-fixing apparatus in other plants that could capture atmospheric nitrogen in cooperation with bacteria [10], [19].

The review attempts to reveal the physiological features of a rhizobia-infected legume’s defensive systems functioning in comparison with pathogenic and other virulent bacteria. It was also taken into account, that in the very early stages of invasion, rhizobia (as well as other bacteria) encounter resistance to introduction on the part of legumes by activating their defensive mechanisms [31]. Further, rhizobia bypass or suppress defensive reactions, but they apparently “leave” the host plant the ability to regulate the infection process often using the same immunity mechanisms that are used against other microorganisms [56], [64].

2. Plant-microorganism interactions

The main feature of the plant-bacterial interaction is that the introduction of any bacteria into the plant body tissue is accompanied by the activation of its defensive reactions, the suppression or overcoming of which leads to bacterial colonization of plant cells. Currently, there are two branches of the plant immune system of cells [12], [52], [88]. One branch uses transmembrane pattern recognition receptors (PRRs), which perceive microbial- or pathogen-associated molecular patterns MAMPs or PAMPs. These microbial molecular structures – “patterns” (elicitors) are found in virtually all microorganisms including rhizobia. Bacterial flagellin (flg) and fungal chitin can be named as the example of these “patterns”. As a result, during the initial stages of invasion, any bacteria are recognized as alien; that leads to the initiation of a nonspecific immune response of plant cells [52]. This type of immunity is called PTI (pattern-triggered immunity) or MTI (MAMP-triggered immunity). It should be noted that plant PRRs are receptor kinases (RKs) superficially located on membranes or receptor-like proteins (RLPs) containing various extracellular ligand-related domains (ectodomains) that perceive MAMPs or PAMPs [42]. The binding of MAMPs to the extracellular domains of receptor kinases (for example, LysM RLK) activates the intracellular kinase domains (for example, LRR RLK), which, in turn, cause the activation of the complex signaling cascade leading to the initiation of various defensive reactions.

The second branch of the plant's innate immunity is called ETI (effector-triggered immunity). It acts intracellularly and is characterized by the interaction of effectors – products of avirulent (Avr) genes of plant pathogens and receptor proteins (products of R-genes); that leads to the development of hypersensitivity reactions (HSR) resulting in the death of a plant cell or inhibition of a bacterial infection [54]. During this interaction, plants use polymorphic NB-LRR-protein products encoded by R-genes. Pathogenic compounds (Avr proteins) are recognized by NB-LRR-proteins and activate defense genes [91].

T3SS or T4SS secretion systems of pathogenic microbes deliver effector proteins and nucleic acids to plant cells. These systems are used by gram-negative pathogenic bacteria. Pathogens use secretion systems in the early stages of the infection to establish cell-to-cell contact. When the contact is made, T3/4SS perform the direct secretion and translocation of various groups of bacterial proteins, nucleic acids, toxins, known as secretion effectors, into host plant cells [49], [100].

Consequently, the PTI (MTI)-immune system bound with plant membrane receptors provides the primary resistance to most non-pathogenic and pathogenic microbes and contributes to the plant's basic resistance during infection. However, a more significant role in plant immunity belongs to ETI, which uses intracellular immune receptors (NBS-LRR) interacting with many effector proteins of pathogenic microbes. During ETI activity, the “gene-for-gene” principle works [36]. It means that the bacterial protein effector corresponds to a plant compound – R-gene product (for example, complementary NB-LRR). The possible functioning of these mechanisms of mutual recognition in rhizobia and legumes will be analyzed below.

3. Legume-rhizobial symbiosis formation

Rhizobia colonize the roots along the pathway used by pathogenic microorganisms, but the defensive reactions of the host plant are not initiated during successful symbiosis. However, legumes seem to regulate the invasion of bacteria: failures in efficient nodule formation or infection with mutant rhizobia often cause defensive reactions of the host plant, which are also observed during pathogens invasion.

The plant's innate immunity plays a significant role during the early stages of legume-rhizobial interaction [71], [51], [43], [58], [66], [79], [67], [89]. On the one hand, the main participants in the partner recognition process in rhizobia and legumes are rhizobial lipochitooligosaccharides (Nod-factors); on the other hand – receptor-like kinases (RLKs) of legumes. Nod-factors

(NFs) are synthesized by rhizobial bacteria as a result of the nod-genes expression initiated by phenolic compounds, which are secreted by the plant into the rhizosphere. Nod-factors are perceived by plant epidermal cells, on the plasma membrane of which the receptor-like kinases complex (RLK), for example, NFR or NFP, is localized. Chemical recognition of partners at the initial stages of LRS leads to the activation of symbiotic pathways in the host plant, associated with infection and nodulation [74] and, apparently, with defensive systems suppression [42]. This is the first branch of the host plant's response to rhizobia invasion: the bacterial component in the form of the Nod-factor (MAMP-pattern) and the plant component – the PRR receptor in the form of receptor-like kinases localized on the cell plasma membrane (LysM RLK) and intracellularly (LRR RLK) [33].

The interaction of rhizobia and a legume at the initial stages is accompanied by root hairs deformation and the formation of specific structures – infectious threads (ITs), in which rhizobia reproduce and transport to the root cortical cells, where meristematic activity and nodule organogenesis are initiated [4], [41]. Upon reaching the cortex, rhizobia penetrate into the cells of the host plant and, in the nodules formed, differentiate into bacteroids, in which the atmospheric nitrogen fixation takes place with the participation of the bacterial nitrogenase enzyme complex.

Thus, the relatively free colonization of root cells with rhizobia indicates a decrease in plant resistance to these bacteria, probably by blocking or “bypassing” the host plant defensive systems. This is confirmed by a significant inhibition of the defensive genes expression in infected nodule cells as compared to uninfected ones [56], [60]. According to Sokolova [11], rhizobial infection activates the pectolytic enzyme polygalacturonase pea roots, which leads to a decrease in the level of pectins, softening of the cell wall and contributes to the easier penetration of rhizobia into the root. Here one can talk about the activation of virulence factors in the reducing the resistance of a legume during rhizobial infection is also discussed in the article by Gourion et al. [42], devoted to the analysis of factors involved in the suppression of plant immunity in LRS. However, it should be noted that not the whole root is equally susceptible to rhizobial infection [40]. There are root zones (infectious sites, foci of infection) that are sensitive to rhizobia. They are assumed to be determined by periods of meristematic activity in cortical cells, where the nodule meristem is later formed [78], [11]. According to Vasileva et al. [2], [85], the content of superoxide anion radical ($O_2^{\bullet-}$), H_2O_2 , as well as the activity of superoxide dismutase and catalase in the root of etiolated pea seedlings and in the epicotyl changed after rhizobial inoculation (after 24 and 48 h). These facts may indicate a systemic regulation that prevents epicotyl and, apparently, the whole plant from infecting by rhizobia. This system is possibly induced due to the formation of the so-called “anxiety factors” at the initial stage of rhizobia invasion by means of signal molecules (ROS, Ca^{2+} , NO) initiation and their wave propagation throughout the plant body [8], [37]. This phenomenon is discussed in relation to pathogens and is probably associated with MTI (PTI) - the plant's immune system, which includes defensive reactions: increased stress hormone biosynthesis, ROS, NO, phytoalexins and other compounds [88]. However, ETI-system is possible to be also involved in the formation of anxiety factors [42].

This assumption is quite acceptable if to take into account that rhizobia behave as pathogenic microorganisms at the initial stages of infection. But, on the other hand, legumes are able to induce defensive reactions during rhizobial infection, which, in particular, is indicated by the results of experiments with the death of infectious threads in alfalfa roots as a result of a hypersensitive reaction [96] and by blocking of defensive reactions in functioning alfalfa nodules by the rhizobial BacA protein, which is also associated with animal pathogens [21].

Are rhizobia a virulent pathogen or not? At first thought, there are no conditions for the plant to initiate defense mechanisms during rhizobial infection. However, at the earliest stage of invasion and at some other stages, rhizobia seem to be perceived as enemies, so that the plant activates its defensive mechanisms to counteract their penetration into the root cells [28], [17]. Therefore, the presence of certain rhizobial compounds that counteract the defensive reactions of the host plant allows rhizobia to infect plant cells. It can be concluded that rhizobia, on the one hand, exhibit phytopathogens properties at the early stages of interaction, and on the other, they have their own unique metabolic pathways that allow regulating the effectiveness of infection and the functional activity of symbiosis [13], [86].

In particular, these compounds include rhizobial polysaccharides, MAMP-compounds (for example, rhizobial flagellin and fungal chitin), T3/4SS-systems, Nop L (nodulation protein L) and others.

4. Defensive reactions observed during rhizobial infection

The initial stage of LRS includes the mutual recognition of symbiotic partners, the penetration and spread of the microsymbiont within plant cells with the simultaneous initiation of the formation of a nodule primordium [33], [80]. Signal exchange between the two organisms induces cell division in the internal root cortex with forming a nodule primordium [62], [41]. In parallel, the root undergoes rhizobial infection through infectious threads (ITs) that form in the root hairs [50]. Rhizobia are then moved along ITs to the host plant cells by endocytosis and form organelle-like structures – symbiosomes – that are then differentiated into nitrogen-fixing bacteroids. Legumes should be noted to be capable of finely regulating the infection process and nodulation, determining the localization of rhizobia penetration, their number and the number of nodules [9], [46]. However, a successful infection, resulting in the nodulation, does not occur as often as one would expect. The experiments of Vasse et al. [96] showed the accumulation of phenolic compounds, PR-proteins, phytoalexins, and other compounds in ITs that are characteristic of the hypersensitive reaction (HSR) during the phytopathogenic attack. One of these PR-proteins, the acidic chitinase of necrotic cells, hydrolyzes the Nod-factor in ITs [96].

HSR occurrence during rhizobial infection is assumed to be a part of the mechanism for regulating the number of successful infections and the resulting nodules by the feedback type. Plant ROS and other signal molecules (ions) ($O_2^{\bullet-}$, NO, Ca^{2+}), which play an important role in pathogenesis, can be another factor of regulating rhizobial infection [29], [1], [40], [41], [72]. Under

normal conditions, the plant does not seek to completely block the rhizobia invasion into the root (Vasse et al., 1993). [96]. That can be explained by the fact that with an increase in the infectious load on the plant, the rhizobia can strongly suppress the development of the defensive-regulatory functions of the host plant; it leads to the excessive formation of ineffective nodules [9].

At the initial stages of rhizobial infection, plant defense reactions are activated but then rapidly suppressed. Thus, in soybean, inoculation of *Bradyrhizobium japonicum* at an exposure of 12 hours caused a strong induction of defensive genes in the plant. However, after 24 hours, the activation of these genes was replaced by the suppression [59]. A similar pattern was found in other studies [64], [56], [66].

The growth of ROS generation is one of the main mechanisms of plant defense against infection. This mechanism is well studied in pathogenesis [7], [15], [27], [37]. When legumes are infected with symbiotic bacteria, a similar mechanism also functions [3], [87], [30], [40] and may be activated at the initial stages and during infection [96], [70]. In the experiments of Vasilieva et al. [2] after 24 h and 48 h after inoculation of pea seedlings with rhizobia, the H₂O₂ content decreased by 43 and 48% in the roots and increased by 170 and 221% in the epicotyl, respectively. The same patterns were also found when studying the content of superoxide radical (O₂^{•-}) in peas roots and epicotyls [3]. These data mean that rhizobia have a different effect on ROS synthesis in organs, perceiving nodule bacteria (root) and not perceiving them (epicotyl).

There are results that prove the necessity of hydrogen peroxide for rhizobial infection. Thus, alfalfa mutant in symbiosis with *S. meliloti* is characterized by severe H₂O₂ degradation due to the overexpression of the catalase gene, as a result of which infection properties change and a decrease in the number of nodules is observed [48]. But at the same time, rhizobial infection contributes to the reduction of H₂O₂ and salicylic acid in the roots of etiolated pea seedlings [39]. According to Lohar et al. [65], a transient ROS decrease in alfalfa roots contributes to the deformation of the root hair when inoculated with *Sinorhizobium meliloti*. A number of studies have shown a positive role in the formation of legume-rhizobial symbiosis of NADPH-oxidase involved in H₂O₂ generation [69], [73], [14]. ROS and other antimicrobial compounds of the host plant are not inconceivable to be involved in the autoregulation of nodulation by blocking the processes of rhizobial infection at certain time stages [86]. Thus, these results indicate that the genetically incorporated resistance functions of the legume are activated during the earliest stages of rhizobial infection and subsequently during the formation of symbiosis. In other words, bacterial symbiotic nitrogen fixers at the early stages of interaction exhibit the properties of pathogens; that allows them to enter the plant by suppressing its immunity [53], [55], [79].

Consequently, legumes in some cases soften the defensive reaction, while in others – strengthen them. It can be concluded that during rhizobial infection, the system of bacterial defense is weakened only in the root zone (most sensitive to rhizobia) and does not lose its effectiveness in other organs. In this case, it can be said about the local and systemic regulation of the host plant resistance to rhizobial infection. In the case of a local infection (for example, in the root zone which is the most sensible to infection), rhizobial bacteria suppress the defensive reactions of the host plant through various mechanisms, including those characteristic of pathogens, for example, using surface exopolysaccharides or Nod-factors [71], [61], [57]. In the second case, some rhizobia, like phytopathogenic bacteria, use T3SS or T4SS secretion systems to deliver effector proteins into plant cells that can be recognized by the intracellular domains of RLK membrane causing ETI defense system initiation, which is transmitted from cell to cell and increases cells resistance to invasion.

NopL (nodulation outer protein L) is one of such proteins, which is delivered to the plant cell by the T3SS secretion system and blocks defensive reactions, in particular, PR genes transcription, modifying the activity of plant kinases [18], [79]. The involvement of MTI (PTI) in symbiosis suppression was proven in experiments using bacterial MAMP-flagellin (flg22) [34], [66]. It was shown that treatment with flg22 – an active epitope of MAMR – reduces the response of *Lotus japonicus* to Nod-factors and significantly reduces nodulation relative to the control. These results may indicate a reduction in the ability of rhizobia to withstand resistance associated with flg22. Additionally, expression of the flagellin-sensitive receptor FLS2 in a plant sharply reduces the nodules number in *Lotus japonicus* [66], that indicates a decrease in defensive reactions during nodulation. Similar to flg22 effect, hormones of the plant defensive system (salicylic acid ([90], [81]), jasmonic acid and ethylene ([83], [94]) affect LRS.

Thus, it can be concluded that the immune system of legumes cells can prevent rhizobia invasion at the earliest stages of symbiotic interaction, as well as under certain conditions during the formation and functioning of LRS; that confirms the hypothesis of the existence of multiple stages of plant immunity suppression during the symbiotic process [86], [21]. According to Gourion et al. [42], rhizobial infection, accompanied by the suppression of defensive reactions and the “invasion” of a compatible rhizobial strain into plant cells, was the driving force that led to rhizobial host specificity.

5. The role of rhizobial polysaccharides in blocking defensive reactions of a legume plant

The role of rhizobial polysaccharides as antagonists in the negative induction regulation of defensive reactions has been proven [47], [71], [61]. Oligopolysaccharides – components of the bacterial cell surface – are signal molecules in the relationship of microbes with the host, including animals [63], [20], [82]. Exopolysaccharides (EPS), lipopolysaccharides (LPS) and cyclic β- glucans have been shown to function during LRS formation. Experiments with various associations of rhizobia and legumes have shown that mutants defective in the synthesis of any of these carbohydrates are not capable of sufficiently infecting the host or forming effective nitrogen-fixing nodules. In this case, violations in symbiotic interaction are accompanied by plant defensive reactions [35], [77], [32], [26], [76], [6]. These results suggest an essential role of rhizobial polysaccharides in the nodulation process. Apparently, they can play the role of signal molecules and suppressors of the host plant defensive reactions.

6. Suppression of plant defensive systems involving the Nod-factor

NFs initiate an infection process and induce nodule morphogenesis. The rhizobial genes responsible for NFs synthesis are not only actively transcribed after infection, but also remain active in the nitrogen fixation zone in *Medicago truncatula* nodules [84]. This suggests that NFs can function after nodule organogenesis.

The Nod factors representing a lipochitooligosaccharide with 3-6 residues of N-acetyl-D-glucosamine is obviously a bacterial MAMP compound. In free-living soil rhizobia, NFs are not present, and their synthesis is initiated by the phenolic compounds of a legume released into the rhizosphere [5]. The oligosaccharide base (skeleton) of Nod-factors is similar to fungal chitin – an elicitor (MAMP), which initiates plant defensive mechanisms. Legumes have been established to recognize lipochitooligosaccharides (LCO) and chitooligosaccharides due to the fact that the basic skeleton of NFs has modifications that vary in different rhizobia species by the length and degree of saturation of lateral fatty acid residues and by the presence of radicals such as acetyl, sulfate, carbomoyl, etc. [44]. NFs lateral chains specifically interact with the plant receptor, and this molecular complex of two organisms transduces the signal along the mutualistic interaction pathway [44]. NFs complex structure determines the specificity of rhizobia for leguminous host plants [93]. At the same time, the polyspecificity of rhizobia for the host plant is due to the diversity of their NFs synthesis. An example of the broad specificity of Nod factors is the rhizobial strain NGR234, which is able to infect and nodulate more than 112 species of legumes, as well as a non-legume *Parasponia andersonii* [92]. Plant receptors (LysM RLKs) “recognize” rhizobial Nod-factors, inhibiting the MTI-defense system with an unknown mechanism and initiating a cascade of reactions to form LRS [58]. This basic condition in certain circumstances may be violated; that leads to defensive mechanisms activation. Unexpectedly, Nod-factors can be “recognized” by non-legumes (*Arabidopsis*, wheat, tomatoes) through a mechanism, which leads to a strong inhibition of the plant defense system associated with MAMP and initiated by *flg22* [58].

NFs are necessary compounds for LRS. However, as recent studies have shown, not all rhizobia are able to produce NFs. Thus, sequestering the genome of two rhizobial symbionts of the legume *Aeschynomene afraspera* showed that these rhizobial strains (of the genus *Bradyrhizobium*) lack the canonical NFs nod genes [38]. This is coherent with the fact that soybean and *L. japonicus* mutant can both become infected and nodulated in the absence of either NFs or their receptors, respectively [68], [79]. Moreover, some rhizobia do not require NFs for LRS; others use T3SS or T4SS. Some rhizobia appear to use both NFs and T3 / 4SS. These data confirm the coevolution of the symbiont and the host plant. Pathogenic interactions with plants during evolution are possible to be characterized by the loss of some pathogenesis features, and the response of the host plant to rhizobia invasion became less aggressive [42], [95].

It was shown that T3SS effector from *Bradyrhizobium elkanii* could replace the NF-receptor in the corresponding soy mutants [79]. Since T3SS-effector and NFs can suppress the innate resistance, Rhizobium effector proteins (for example, NopL) can perform this function in the absence of NF-signaling in this particular case [18].

MTI activity was shown to be suppressed using high NFs concentrations [58]. Initiation of plant defensive mechanisms with high doses of Nod-factors (10⁻⁶ – 10⁻⁹ M) in Rhizobium-infected roots can be a part of the mechanism by which nodulation is regulated according to the feedback type, namely, according to activating or deactivating plant defenses with different NFs concentrations [25]. Rhizobia can affect MTI through NF-related suppression of MTI by inhibiting defensive reactions with extracellular calcium chelation of bacterial exopolysaccharides or by inhibiting ROS products using bacterial lipopolysaccharides [16].

A large number of symbiosis-specific plant peptides are known to function in LRS. These peptides are similar to antimicrobial ones – effectors of the innate resistance. For instance, the bacterial BacA protein, which causes intracellular infectious diseases in animals, also functions in bacteroids and provides the normal N₂-fixing ability of rhizobia by suppressing nodules defensive system [22]. This suggests that the virulent pathogenesis factor and effectors of the innate resistance are used in symbiosis in favor of the macrosymbiont.

Thus, the results of recent studies indicate different functions of rhizobial Nod-factors. In addition to the main function, as the MAMP-pattern, to interact with the plant receptor and trigger a cascade of symbiotic reactions, NFs can participate in blocking or activating the defense system of plant cells, regulating symbiotic signaling and, possibly, in other as yet unknown reactions associated with nodule organogenesis and its functioning.

7. Conclusion

Analyzing the data on the defense system of a rhizobia-infected legume, we should first of all note the particularity of LRS formation – the biochemical complementarity of Nod-factors to the host plant receptors (LysM receptor or LRR-receptor kinase). The interaction of these compounds causes a cascade of reactions leading to LRS formation and blocking of defensive reactions. However, according to Nakagawa et al. [75]), NFs not only activate symbiotic genes in *Lotus japonicus*, but also can transiently activate defense genes through Nod-factors receptors. It should be noted that chitin-oligosaccharides – structural analogs of Nod-factors – can also induce the symbiotic genes expression in *Lotus japonicus* through an unidentified chitin receptor [75].

The second particularity is the activation of defense mechanisms by the host plant for the regulation of rhizobial infection using two branches of the plant immune system – MTI and ETI – which can act against rhizobia, but are blocked by rhizobia upon successful infection. Rhizobia can come out as pathogens at the earliest stages of invasion. They can probably act to prevent infection of other plant organs (for example, pea epicotyls) when plant defense systems are activated. In these cases, one should

apparently distinguish between local and systemic resistance of the legume against rhizobial infection. In addition, the defensive reactions of legumes are activated by rejecting the pathways of rhizobial infection and nodulation under the influence of various factors.

Rhizobial Nod-factors are generally recognized to be necessary compounds for triggering a signaling cascade during LRS formation [38]. However, it has been found that some rhizobia (*Bradyrhizobium*, strains ORS278, BTAi1) do not have the canonical nodABC-genes that are required for NFs synthesis. However, the inoculation of legumes from the genus *Aeschynomene* did not reveal differences in the nodulation processes in nod-independent and nod-dependent plants of this genus [24]. Unexpectedly, Nod-factors can be perceived by non-legumes (*Arabidopsis*, wheat, tomatoes) [58]. It was shown that in this case, suppression of the plant MAMP-associated immunity is observed. Soybean mutants according to the Nod-factor receptor NFR1 or NFR5 were not able to induce symbiotic functions (for example, gene expression) in response to the addition of the Nod-factor, but they (the mutants) remain able to suppress the MAMP-defensive system [58], [99]. Nod-factors, necessary for LRS, were optional in some other cases. For example, chitin oligosaccharides – structural analogs of NFs -factors – can activate symbiotic genes in *Lotus japonicus* without the participation of NFs receptors, but, probably, with the participation of other receptors [75]. Similarly, the NF-receptor involved in the early-stage symbiosis was found to function during pathogen infection [55]. Therefore, there is a sufficient reason to believe that plant innate immunity against pathogens is a decisive condition in establishing and maintaining LRS.

Consequently, the available results indicate that genetically incorporated resistance functions in legumes are activated during the very early stages of rhizobial infection, as well as during the intracellular stages of symbiosis formation. Therefore, the innate resistance of legumes is actively involved in the formation and functioning of LRS [97]. The main counteracting factor here is rhizobial NFs. They trigger a cascade of symbiotic reactions and inhibit the activity of host plant defense systems, which could interfere with successful rhizobia invasion. Solving the physiological, genetic, biochemical, molecular, and other mechanisms of the mutualistic relationship of rhizobia and legumes is the way to create new cultivated plants with the unique ability to fix atmospheric nitrogen.

Conflict of Interest

None declared.

Конфликт интересов

Не указан.

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