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ACYL-HOMOSERINE LACTONES FOR CROP PRODUCTION AND STRESS TOLERANCE OF AGRICULTURAL PLANTS

(review)

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Abstract

Acyl homoserine lactones (AHL) are a class of mediator molecules coordinating cell activity in the gram-negative bacteria population. AHLs synchronize individual genomes due to which bacterial populations function as multicellular organisms. AHLs provide remote signaling between bacteria colonizing the phytosphere that enables the bacterial population to respond to external influences and establish symbiotic or antagonistic relationships with the host plant (A.R. Stacy et al., 2018; A. Shrestha et al., 2020). Autoreception of quantitative parameters of the bacterial population is called "quorum sensing" (QS) (R.G. Abisado et al., 2018). QS systems form autoinducer signaling molecules that easily penetrate from cells into the environment and back into the cell (M.B. Miller et al., 2001; B. Bassler, 2002). QS systems play a key role in the regulation of metabolic and physiological processes in a bacterial cell (M. Frederix et al., 2011; M. Whiteley et al., 2017). Bacterial signaling is perceived by eukaryotes, which form a symbiosis with microbial communities (A. Schenk et al., 2015; L.M. Babenko et al., 2016, 2017). Plant growth and development, nutrients assimilation, and stress resistance are largely determined by the pattern of this interaction (H.P. Bais et al., 2006; R. Ortнz-Castro et al., 2009; S. Basu et al., 2017). Within the plant, bacterial signaling is controlled by the quorum quenching (QQ) system (N. Calatrava-Morales et al., 2018), whose mechanism of action is to suppress AHL synthesis by plant metabolites, compete with AHL for binding to receptor proteins, and repression of QS-controlled genes (H. Zhu et al., 2008; R. Sarkar et al., 2015). However, to date, the molecular mechanisms by which plants respond to bacterial signaling are not fully understood. Individual metabolites of AHL signaling have been characterized, but their role in the chemical interaction of partners in most cases requires further study. It has been shown that the QS phenomenon and its participants are involved in the regulation of prokaryotic-eukaryotic interactions, including biofilm formation, phytohormones synthesis, plasmids transfer, virulence factors production, bioluminescence, sporulation, and the formation of nodules (L.M. Babenko et al., 2017). Differences in the structure of molecules ensure that bacteria recognize their own AHL and separate foreign ones. The transfer of AHL from bacteria to a host plant is carried out through membrane vesicles (M. Toyofuku, 2019). In recent years, there has been an active study of genetics, genomics, biochemistry, and signaling diversity of QS molecules. Rhizosphere is the most dynamic site of interaction between the plant and the associated microflora with the participation of AHL. The regulation of rhizosphere functions is the task of particular importance in the development of new biotechnological approaches aimed at increasing the yield and stress resistance of crops. One of the effective technologies for increasing resistance to biotic and abiotic stresses is pre-sowing treatment (priming) of seeds (A. Shrestha et al., 2020). Both direct

(on plants) and indirect (on rhizosphere microflora) effects of AHL priming were established (O.V. Moshynets et al., 2019). AHL induce an increase of growth, of photosynthetic pigments content, as well as cause changes in the ratio of phytohormones in organs and tissues, affect the formation of defense mechanisms, which increases the productivity of crops (A. Schikora, S.T. Schenk, 2016; A. Shrestha et al., 2020). AHL meets the requirements of intensive organic farming, they are considered as promising ecological phytostimulants and phytomodulators capable of safely increasing the quantity and quality of agricultural products.

Keywords: acyl-homoserine lactones (AHL), quorum sensing (QS), quorum quenching (QQ), plant-microbial signaling, AHL-priming, AHL-mimicry, phytostimulants, phytomodulators, stress resistance

In recent decades, the study of the mechanisms of plant resistance to unfavorable environmental factors has become one of the most urgent problems of plant molecular physiology in connection with global climatic changes and anthropogenic load on the biosphere. Extreme temperatures are one of the most common abiotic stressors. Global warming threatens not only agriculture but also biodiversity conservation. The predicted increase in average temperature by 1 °C can lead to a reduction in plant species diversity by one-third [1]. At the same time, the cold and frost resistance of plants should not be ignored. Winter thaws, alternating with frosts, cause serious damage to plants and reduce yields. The earlier onset of a meteorological spring increases the likelihood of damage from spring frosts. Another unfavorable climatic factor, the effect of which is increasing, is a lack of moisture and redistribution of the annual precipitation [2]. An increase in temperature and changes in the precipitation pattern lead to a hydrological regime violation and a decrease in water resources. So, within the Ukraine territory in the last quarter of the twentieth century, there was a steady trend towards a decrease in the annual precipitation [3]. At the same time, the frequency of rainfalls increased, which also negatively affects plant productivity. Acid rain and heavy metal pollution are serious threats. The ecological balance is disturbed due to the irrational use of chemical crop protection products. About 2 million tons of pesticides are used annually in world agricultural production. In 2020, an increase in the global use of pesticides was predicted to reach 3.5 million tons [4], but this did not solve the problem of effectively increasing crop yields.

To meet the growing demand for food, safe agrobiotechnologies are needed, which will increase the agricultural product quantity and quality [5-8]. The use of bacterial inoculates that improve plant growth, as well as bacterial growth regulators for presowing seed priming and foliar treatment of plants is considered a promising biotechnological approach [5, 9, 10]. This “green” technology is becoming more and more popular. In some cases, natural phytostimulants can improve the stress tolerance of crops and increase yields without undesirable effects on the environment [11].

In recent years, attention has been focused on a phenomenon called “quorum sensing” (QS). This is a system of bacterial intercellular communication which depends on the cell population density and coordinates the response to changes in environmental conditions [12, 13]. QS systems form autoinducer signaling molecules that easily diffuse from cells into the environment and back [14, 15]. QS regulation has been established for more than 500 species of bacteria. QS systems play a key role in the regulation of metabolic and physiological processes in a bacterial cell [16, 17]. Bacterial signaling is perceived by eukaryotic organisms that form a symbiosis with microbial communities and provide bacteria and plant interaction [7, 18-21]. Plant growth and development, assimilation of nutrients, stress resistance are largely determined by the nature of such interaction [22-24]. Signaling compounds of the acyl-homoserine lactones (AHLs) class [25] are involved in the QS regulation of gram-negative bacteria [25], which have been shown

as effective plant growth stimulators and phytomodulators of resistance to biotic and abiotic stressors [8, 26].

The purpose of this review was to analyze and summarize the latest literature data on the role of bacterial QS and AHLs in the formation and functioning of plant-microbial signaling, the participation of AHLs in the regulation of plant growth and development, the resistance formation, as well as the prospects for using these compounds to create environmentally friendly preparations that can increase the yield of crops.

The influence of PGPR-group microorganisms on plant growth, development, and resistance. Plant growth and development depend on environmental conditions, primarily the soil in which various living organism forms are concentrated. Edaphic microbiota significantly affects mineral nutrition and soil-forming processes in general. For its part, the root system is actively involved in plant habitat formation. The main ecological niche occupied by rhizospheric bacteria is the zone of root exometabolite active release. A root system is a peculiar form of communication between plants and soil microflora, the main source of physiologically active substances, which during the growing season play the role of a link in the donor-acceptor interaction between plants and microbial communities in the soil [22, 27, 28]. The rhizosphere microbiota affects plant immunity and soil suppression [29]. Due to the high root secretory activity, soil microorganisms are provided with a nutrient substrate and form strong associative bonds both in the rhizoplane and in the rhizosphere. At the same time, root exometabolites can be one of the factors determining soil fungistasis. The reaction of pathogens such as stimulation or suppression of development depends on their composition and concentration [30]. Each plant has a protection system against pathogens; however, the method for detecting and distinguishing beneficial microorganisms from pathogens is not fully understood. It is believed that the plant has receptors responding to microbial molecules [31]. This process involves both various signaling mechanisms (chemoattraction, nodulation) and direct chemicals (organic acids, sugars, flavonoids, volatile organic substances) [32]. The presence of a certain connection becomes a signal for the beginning of root colonization or nodulation. After root colonization, bacteria correct the plant metabolism [33].

Bacteria colonizing the surface of roots and rhizosphere and having properties useful for plants are defined as the PGPR group (plant growth-promoting rhizobacteria) [22]. The PGPR group representatives can overcome the endodermal barrier. They enter the plant mainly through the root cortex, infect the vascular system, and form endophytic populations in roots, stems, leaves, and other organs [22]. The PGPR effect on plant growth and development is direct and indirect. Thus, under the PGPR direct influence, an active synthesis of phytohormones that stimulate growth (auxins, cytokinins, and gibberellins) occurs, as well as inhibition of the synthesis of stress phytohormones (ethylene, salicylic, and abscisic acids), the absorption of nutrients and water is enhanced (using N_2 fixatives, phosphate solubilizers, producers of siderophores). The PGPR indirect effects are in the defense mechanism induction, namely, the activation of the antibiotic synthesis and cell wall lytic enzymes (chitinases), which exhibit phytostimulating and biopesticidal effects [34]. Due to these properties, PGPRs are used as a component of microbiological fertilizers to increase agricultural crop productivity in an environmentally friendly way [5].

PGPRs of *Rhizobium*, *Klebsiella*, *Clostridium*, *Nostoc*, *Anabaena*, *Bacillus* genera have a phytostimulating effect. They have a positive effect on phosphorus solubilization and nitrogen fixation, stimulate phytohormone synthesis, induce

mechanisms against pathogens, and accelerate reversibility after stress [5, 35]. By inducing solubilization and chelation, as well as redox reactions, PGPRs facilitate the soil micronutrient availability and through the biofortification of nitrogen, iron, zinc, and selenium provide the necessary content of these microelements in plants. PGPRs mitigate the negative effects of high temperatures, drought, salinity, and other abiotic stressors which makes it possible to use them in the creation of resistant microbiological preparations [36].

One of the most important tasks of biotechnology is phytoremediation of contaminated soils, the revival of areas of little use for farming agriculture. PGPRs as growth stimulators and modulators of plant resistance are positioned as promising detoxicants [37, 38].

Microbiological fertilizers are an environmentally friendly alternative to chemical fertilizers and agrochemicals which are detrimental to the environment [5]. Four groups of microbiological preparations that increase soil fertility and provide plant protection are currently presented on the market. These are nitrogen fixators (associative and symbiotic), phosphate-mobilizing bacteria, phytostimulants, as well as bacterial preparations decomposing plant residues [39]. However, the low quality of microbiological fertilizers causes distrust among farmers and complicates commercialization. To increase production and their widespread introduction, it is necessary to stabilize the final product.

Intercellular communication of microorganisms. Biofilm formation is an ancient and integral component of the life cycle of prokaryotes, as well as a key factor ensuring survival in various ecological niches [20, 40, 41]. A biofilm is a highly organized bacterial formation, a kind of ecological niche with stable conditions of existence, in which complex trophic links are formed [14, 17]. Within biofilms, bacteria coordinate and synchronize the work of individual genomes, which allows the population to function like a multicellular organism [42]. The interaction of individual cells in a bacterial population is necessary for its survival in changing environmental conditions and the establishment of symbiotic or parasitic relationships with multicellular organisms [17, 43]. The coordinated activity of bacterial cells within the biofilm is carried out due to the QS interaction of specialized chemical molecules — communicative mediators, or autoinducers (AI), named because of their ability to stimulate their biosynthesis [12, 44].

Signaling AI molecules serve as gene expression regulators. They freely diffuse through cell membranes creating conditions under which the bacterial cell acquires the ability to respond to any changes in their intracellular concentration and thus determine the population size [45]. Intercellular QS signaling coordinates the bacterial population behavior. With an increase in the bacteria number, the AI content increases, and after reaching the AI threshold concentration, they bind and activate receptor proteins [42]. The ligand-receptor complex initiates the transcription of QS-regulated genes and determines the population phenotype which depends on the bacterial cell density.

Bacterial QS systems (with some approximation) can be considered a prototype of complex regulatory systems (hormonal and immune) of higher organisms that use mediators to coordinate various cell functions and form an adaptive response at the level of tissues, organs, and the body as a whole [46]. Among the mediators of bacterial QS, the most studied lactones are low molecular weight chemical compounds of the L-homoserine lactone acyl derivative class. Signaling systems, which include N-AHLs and their receptors, are most common in most gram-negative bacteria [25, 47]. AHLs contain a homoserine lactone five-membered ring and a variable acyl side chain attached to it by an amide bond (Fig. 1). Homoserine lactones were discovered by Nealson et al. [48] in the study of the

bioluminescent symbiont bacterium *Vibrio fischeri*, living in the photophores of Hawaiian calamari and causing the luminescence of these organs at a cell concentration of 10^{11}.

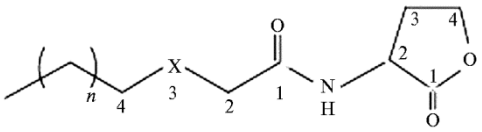

Fig. 1. Molecular structure of acyl-homoserine lactone: X — possible substituents of radicals in the third carbon atom of the side chain (H, OH, O), *n* — the number of carbon atoms of the acyl side chain.

AHL molecules synthesized by bacteria of different species differ in chain length and the radical presence or absence in the third carbon atom side chain. Differences in the molecular structure ensure bacteria recognizing their own and foreign AHLs [17]. Bacteria synthesize both short-chain AHLs (3-6 carbon atoms in the acyl group), which freely diffuse through the cell membrane, and long-chain AHLs (10-16 carbon atoms), which can be incorporated into the cell membrane [7]. In addition to participating in the QS system functioning, AHLs can directly affect the eukaryotic organism's cells, in particular, plant cells [49]. AHL biosynthesis is carried out by AHL synthases of the LuxI type. As the bacterial population grows, AHLs accumulate up to a certain threshold value and bind to the corresponding receptor proteins, forming complexes that regulate certain bacterial gene expression [50] (Fig. 2). Recent studies have shown that bacterial signaling molecules are transferred by membrane vesicles. Previously, it was believed that vesicles are formed as a result of the cell membrane blebbing, but later it was found that they also appear after explosive lysis or cell death, which expands the understanding of the intercellular interaction between microorganisms [51].

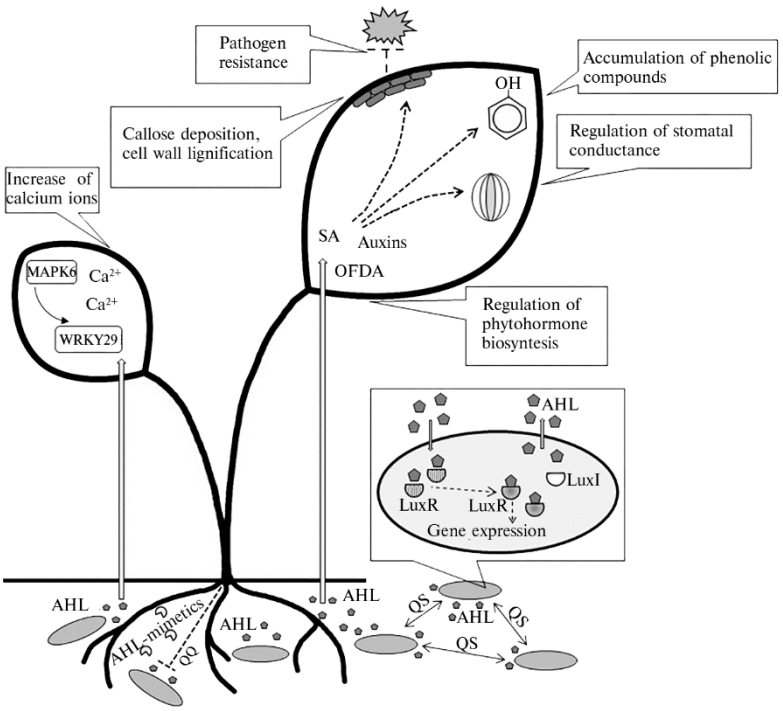

Fig. 2. Physiological and biochemical processes induced by acyl homoserine lactones (AHL). In the quorum sensing (QS) system, bacterial cells produce AHL molecules. The synthesis of these molecules involves two types of AHL synthases — LuxI and LuxR. The LuxI protein is directly involved in the synthesis of AHL. LuxR acts as a binding promoter protein. The concentration of AHL increases with the increasing density of the bacterial population. After the threshold level is reached, AHL penetrate into the cell, bind to proteins of the LuxR type, and activate the expression of target genes. AHL

molecules, penetrating into root cells, cause various plant responses. Among them are triggering a signaling cascade with the participation of mitogen-activated protein kinase (MAPK), expression of WRKY-type transcription factors, an increase in the concentration of Ca^{2+} ions in the cytosol, activation of the oxophytodienic acid cascade (OFDA), synthesis of phytohormones – salicylic acid (SA), auxins. Various protective reactions are formed, including callose deposition, accumulation of phenolic compounds, regulation of stomatal conductance. The quorum quenching (QQ) system of plant intervention allows manipulating QS signaling, selectively inhibiting AHL synthesis, competing with AHL for binding to receptor proteins, and inhibiting the activity of QS-controlled genes. AHL mimetics, plant metabolites produced by root cells and regulating bacterial QS, are considered as one of the components of QQ. The information presented was adapted from A. Schikora et al., 2016 (19).

QS regulates a variety of physiological processes in gram-negative bacteria. Many plant and animal pathogens use QS to manage virulence, which is very promising for practical purposes [52]. Recently, biotechnological developments have appeared aimed at obtaining AHL antagonists [53]. Such substances are used to protect crops from phytopathogens, and in medicine and veterinary medicine, they are used as antimicrobial drugs. With the help of QS, the synthesis of antibiotics is regulated, which makes it possible to activate bacterial culture growth in a production environment. However, the use of QS and AHLs as specific regulators of the bacterial processes is limited by insufficient knowledge of their action mechanism and autoinducer effects. Some literature reports that the study of intercellular communication in vitro does not provide a complete understanding of the mechanisms of the QS system and AHL functioning and effects and that further investigation of this phenomenon requires new approaches in the *in situ* system [54].

Role of the host plant in the regulation of bacterial QS. Since bacteria and eukaryotic organisms have co-evolved over millions of years, eukaryotes have developed mechanisms that allow them to perceive QS signaling, manipulate and respond to bacterial interactions [55]. The molecular mechanisms of these processes are not fully understood [13]. In contrast to the QS system, which regulates the behavior of bacterial cells when interacting with the host, the "quorum quenching" (QQ) intervention system functions in plants to manipulate bacterial signaling [56]. The QQ molecular mechanisms of plant metabolites include suppression of AHL synthesis, competition with AHLs for binding to receptor proteins, and a decrease in the QS-controlled gene expression [57-60]. Plant metabolites interacting with AHL receptors and activating transcription of target bacterial genes are of particular interest (see Fig. 2). The ability of such compounds to replace AHLs when interacting with receptor proteins is called AHL mimicry [61].

AHL mimicry is one of the mechanism affected bacterial QS. Plant root exudates contain low molecular weight signaling compounds (so-called AHL mimetics) which regulate bacterial QS and act as antagonists or synergists [63, 63]. It is assumed that AHL mimetics can regulate the functions and composition of the rhizosphere bacterial population, forming the plant rhizomicrobiome [64]. The root exudate of *Medicago truncatula* contains up to 20 signal-mimic compounds which can affect bacterial QS. The secretion intensity and such compound composition changed with the plant age, as well as after the seedling treatment with AHL solutions [62]. Notably, the synthesis of AHL mimetics is activated in plants under the rhizobacteria QS signal influence. The chemical structure of plant molecules affecting AHL-mediated bacterial QS is not understood. It would seem logical that AHL mimetics should have a structure close to AHL; however, the studies performed indicate differences in the structure of these compounds [65, 66].

The first identified eukaryotic AHL mimetic structurally different from AHLs but capable of activating the bacterial QS system was luminochrome [67].

It probably directly interacts with the AHL-binding pocket of the receptor LasRy protein of *Pseudomonas aeruginosa* (AHL receptor LuxR type) [68]. L-canavanine, an analog of arginine found in alfalfa seed exudates, suppressed QS regulation in *Sinorhizobium meliloti* [69]. Rosmarinic acid stimulated the activity of the RhlR transcription regulator in *Pseudomonas aeruginosa* [66]. Coumaric acid secreted by plant roots forms a special QS signal, coumaroyl homoserine lactone, which is perceived by some bacteria [44]. The catechin and naringenin flavonoids of many plants exhibited the QS mimetic activity [70, 71]. AHL-mimetics of rice and bean root exudates regulated the bacterial biofilm formation which indicates the role of these compounds in the plant-bacteria symbiosis formation [65]. *Arachis hypogaea* forms a rhizobial symbiosis with *Bradyrhizobium* spp. synthesizing long-chain AHLs. *A. hypogaea* seed and root exudates containing QS mimetics similar to long-chain AHLs stimulated the growth of bacteria with long-chain ALH-mediated QS-signaling and suppressed the growth and germination of bacteria with short-chain QS AHL-signaling [72].

Another action on bacterial QS is based on the availability and stability of AHL molecules in the rhizosphere. Thus, during the joint cultivation of *Sinorhizobium meliloti* and *Arabidopsis thaliana*, the AHLs synthesized by bacteria decreased, which could be due to both inhibition of the synthesis of these compounds by the host plant and changes in their quantity and availability [73]. The AHL concentration in the rhizosphere depends on soil particle adsorption, the lactone ring hydrolysis, as well as environmental temperature and pH. Another factor in the rhizosphere AHL degradation is their hydrolysis by plant QQ enzymes. Some plants can synthesize enzymes that destroy bacterial AHLs [74, 75]. The degradation of AHLs by plant enzymes is a species-specific process. Thus, AHL destruction within the rhizosphere of dicotyledonous plants proceeded rapidly, while within the monocotyledon rhizosphere, it was slow or absent altogether [74, 76]. The AHL destruction mechanism within the plant rhizosphere is also under-researched. It is thought that by analogy with bacterial degradation, two enzymes can participate in it such as AHL lactonases hydrolyzing the lactone ring or AHL-acylase hydrolyzing the amide bond between the acyl side chain and homoserine lactone, resulting in fatty acid separation from the homoserine lactone. However, the existence of such a mechanism in plants has not yet been established [74, 76]. It is assumed that in the coevolution process, plants have developed specific mechanisms for detecting AHLs in the extracellular environment and strategies for manipulating the bacterial QS systems. Thus, in response to the QQ system of intervention, the host plant can influence AHL-mediated bacterial signaling and determine the nature of relationships between partners in the rhizosphere.

Molecular action of AHLs. AHL priming activates the signaling mechanisms of the plant defense response, resulting in the modulation of salicylate-dependent and oxylipin-induced stress responses, the MAP kinase cascade, stomatal closure, cell wall thickening, and synthesis of phenolic metabolites [18, 20, 77]. PGPR group bacteria induce the surface-active metabolite secretion and the volatile compound synthesis that activate protective signaling pathways and help plants resist the attack of pathogens [78]. Thus, the treatment of tomato roots with AHLs produced by the *Serratia liquefaciens* MG1 rhizobacterium induced resistance to *Alternaria alternata*. The signaling pathway activated by salicylic acid (SA) was involved in the formation of resistance to the pathogen action. Treatment of tomato roots with butanoyl homoserine lactone (C_4-AHL) and hexanoyl homoserine lactone (C_6-AHL) caused the expression of the pathogen-associated protein 1a (PR1a) gene and the genes of two chitinases – components of the SA/ethylene-dependent pathway in tomato leaves. The results obtained showed that

short-chain AHLs in tomato plants acted as a trigger for the SA-dependent signaling pathway [77]. After treatment of Arabidopsis roots with tetradecanoyl homoserine lactone (C_{14}-AHL), the pathogen-associated molecular pattern increased the activity of AtMPK3 and AtMPK6, which expressed WRKY22 and WRKR29 transcription factors involved in PR1 synthesis [18, 79]. It is in response to the action of a pathogen that plants actively synthesize the pathogen-dependent PR1 protein [80, 81]. AHLs stimulated the synthesis of oxophytodienic acid (OFDA) and SAs which are involved in the defense reaction forming. Arabidopsis plants treated with C_{14}-AHL accumulated SA and oxophytodienic acid in leaves, which increased the expression of *HSP70*, *HSP17*, and *CYP81D11* genes which synthesize heat shock proteins and cytochrome P450 [49].

Abscisic acid (ABA) and SA induce stomatal closure, playing a key role in adaptation to stress [82]. Priming of C14-AHL Arabidopsis plants infected with *Pseudomonas syringae* activated stomatal closure; however, priming did not affect the activity of the RD22, RD29, and RAB18 genes involved in ABA synthesis [49, 83]. The mechanism of movement of stomatal guard cells under stress is associated with the ABA accumulation and the specific ion channel activation [84]. Open Stomata 1 (OST1) Ca^{2+}-independent protein kinase and Ca^{2+}-dependent protein kinases (CPKs) are key enzymes for ABA-induced activation of the SLAC1 slow-type anion channel and stomata closure [82, 85, 86]. It is thought that SA signaling is integrated with ABA signaling [82]. Blocking of SA-induced closure of the stomatal apparatus and SA-activation of the slow-type anion channel was found in the *cpk3* and *cpk6* Arabidopsis mutants with impaired CPK synthesis, and was not found in the *ost1-3* mutant with impaired OST_1 synthesis [87]. The SLAC1 phosphorylation sites in ABA signaling, serine-59, and serine-120 are key for SA signaling [88]. Superoxide anion chemiluminescent identification showed that SA signaling did not require activation of *cpk3* and *cpk6* for the reactive oxygen species (ROS) formation. SA activates the peroxidase-mediated ROS signal induced in the Ca^{2+}/CPK-dependent branch of ABA signaling, rather than the OST1-dependent signaling branch in stomatal guard cells [82]. After treatment with AHL, stomatal conductance and leaf transpiration increased, which increased the nutrient supply to the bean root colonizing bacteria [89].

In genetically modified tobacco plants with bacterial genes for AHL synthesis and degradation, effective protection against pathogens was formed in AHL-synthesizing plants, while plants with AHL-degrading genes could not protect against pathogen damage. Exogenous treatment with C_{14}-AHL enhanced the systemic resistance of Arabidopsis to the *Golovinomyces orontii* and *P. syringae* pathogens and barley — to *Blumeria graminis* f. sp. *hordei* [18]. After treatment with a C_{14}-AHL solution, callose deposition, phenolic compound accumulation, cell wall lignification, changes in oxylipins, and closure of plant stomata were recorded [7, 49]. The primary root elongation in the *Arabidopsis thaliana* wild genotype, induced by treatment with solutions of C_6-AHL and octanoyl homoserine lactone (C_8-AHL), was not observed in AHL-insensitive mutants [90]. Treatment of Arabidopsis plants with C_4-AHL led to a temporary increase in Ca^{2+} in the cytosol, while treatment with C_6-AHL induced an increase in calcium-binding protein (calmodulin). These results indicate the involvement of calcium ions in the perception of bacterial AHL signaling [32, 91]. It is thought that Cand2 and Cand7 G-proteins (G-protein coupled receptors) are involved in the perception of AHL signals, which are known as the trigger of cell proliferation, formation of defense reactions, light perception, stomatal conductance, regulation of ion channels, seed germination, and synthesis of gibberellin, brassinosteroids, abscisic and jasmonic acids, auxins and ethylene (see Fig. 2). This assumption was based on the

polymerase chain reaction analysis of plants primed with C_6-AHL and C_8-AHL, in which the expression of genes synthesizing Cand2 and Cand7 was observed [92].

Phytostimulating and phytoprotective effects of priming and foliar treatment with AHL solutions. Climatic conditions significantly affect the crop quality and unfavorable changes in temperature and water regime reduce plant resistance to bacterial and fungal invasions. One of the effective technologies for increasing resistance to biotic and abiotic stressors is seed pre-sowing priming, which improves germination and activates defense mechanisms [6-8]. Plant growth and development are also stimulated by bacterial inoculants. They improve mineral nutrition and reduce the pathogen influence in response to competition and stimulation of defense systems [19, 78]. For example, the *Serratia marcescens* bacterium induces systemic resistance of *Solanum lycopersicum* to the *Alternaria alternata* fungal pathogen [93], and root treatment with solutions of synthetic AHLs enhances the expression of genes involved in the defense mechanism formation in tomato leaves [77]. After the presowing priming of C_6-AHL, the number of germinated grains increased by 1.2 times, and the size of the winter wheat coleoptile and root increased by 1.4 times [8]. Field studies have shown an increase in plant biomass at the tillering stage by 1.4 times, productivity by 1.5 times, and grain quality by 1.3 times. In the F_1 generation grown from seeds from primed parental plants, an increase in yield indicating the priming effect preservation was also recorded [8]

Rhizosphere and phylosphere associated microbial communities have a positive effect on plant growth and resistance to pathogens [94, 95]. AHLs in the soil with primed seeds stimulate the growth of PGPR of bacteria of the genera *Bacillus* and *Pseudomonas*, which colonize the root surface and inhibit the pathogen activity [96]. Under the action of AHLs in the rhizosphere zone, the amylolytic bacteria involved in the degradation of dead root cells increase, the growth of roots increases, and the supply of sugars necessary for other rhizosphere bacteria increases. AHLs affect the formation of a plant defense reaction, initiate systemic resistance, and improve the recognition of pathogenic microorganisms [97]. The priming of *Cicer arietinum* seeds with C_4-AHL enhanced plant growth and increased stress resistance [26]. The primed seeds germinated well under simulated oxidative (5 mM H_2O_2) and salt (200 mM NaCl) stresses. In seedlings, the biomass, chlorophyll, and proteins, and the resistance to damage by *Fusarium oxysporum* f. sp. *ciceri* increased [26]. C_6-AHL can stimulate growth and root formation processes [90, 98, 99] and induce systemic resistance to a wide range of pathogens in many plant species [100]. Thus, various studies have demonstrated that bacterial AHLs can be used to improve plant growth and productivity, reduce dependence on fungicides and fertilizers, and fight pathogens and stressors [101].

So, in the remote transduction of signals in the phytospheric bacterial biocenosis—plant system, AHLs, mediator molecules of bacterial origin, are involved. Among the AHL molecules synthesized by bacteria of different species, there are short-chain ones with 3-6 carbon atoms in the acyl group and long-chain ones with 10-18 carbon atoms. Differences in the structure of molecules ensure that bacteria recognize their own AHLs and separate foreign ones. AHL molecules play a key role in the cooperative activity of bacterial populations, their colonization of new ecological niches, and the regulation of partner interactions within the rhizosphere. AHLs, synthesized by bacteria associated with plants, affect the composition of microbial communities and plant life processes. Plants receive and respond to bacterial AHL signals by adapting to changing conditions and releasing their own AHL mimetics. The AHL transfer from a bacterium to a

host plant is carried out by membrane vesicles. Most phytopathogenic bacteria use QS systems that are directly related to virulence. The expression of virulence factors regulated by QS becomes one of the causes of infection. Phytopathogenic bacteria signaling molecules and QS systems have been studied in sufficient detail. The study of gene expression of QS-regulated virulence functions has led to the development of a QS intervention strategy to fight bacterial plant diseases. A well-known example is the QQ system of bacteria of the genus *Bacillus*, which synthesize lactonase and acylase that break down N-AHLs. Bacteria use volatile organic compounds to interfere with the QS systems of competitive species. In turn, plants synthesize compounds like AHLs (chemical mimicry) that can inhibit or stimulate bacterial QS systems. In recent years, genetics, genomics, biochemistry, and signaling diversity of QS molecules have been actively studied. Rhizosphere is the most dynamic site of the plant and the associated microflora interaction with the AHL participation. The regulation of its functions is the task of particular importance in the development of new biotechnological approaches aimed at increasing the agricultural crop yield and stress resistance. AHLs induce an increased growth, and elevation of photosynthetic pigments causes changes in the ratio of phytohormones in organs and tissues affects the formation of defense mechanisms, which increases the yield of crops. Since AHLs meet the requirements of intensive organic farming, they are considered as promising ecological phytostimulants and phytomodulators.

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