REVIEWS

Interaction between Signal Pathways upon Formation of Plant Defense in Response to Environmental Stress Factors

A. R. Lubyanova^a, *, M. V. Bezrukova^a, and F. M. Shakirova^a

^a Institute of Biochemistry and Genetics, Subdivision of the Ufa Federal Research Centre, Russian Academy of Science, Ufa, Russia

*e-mail: Lubyanova555@mail.ru

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Abstract—In the course of evolution, plants have developed numerous specific regulatory signal pathways, which are hormonal for the most part. Phytohormones comprise not only such generally recognized endogenous growth regulators as abscisic acid, auxins, cytokinins, gibberellins, brassinosteroids (BS), ethylene, salicylic acid (SA), and jasmonates but also recently described derivatives of apocarotenoids—strigolactones (SL). Signal pathways interact at the level of biosynthesis of messengers and their translocation as well as upon activation of target genes. Since abiotic and biotic environmental stressors negatively influence plant productivity, understanding of molecular mechanisms of regulation induced by stress agents may help researchers to produce stress-resistant and high-yielding plants using molecular techniques. This paper is a review of present-day literature dealing with the interaction and interference of nonhormonal and hormonal signals regulating growth and development of plants under ever-changing environmental conditions.

Keywords: stress resistance of plants, phytohormones, interaction between signal pathways, protein kinases, transcription factors, lipid signals, calcium, nitric oxide, reactive oxygen species, strigolactones

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INTRODUCTION

As organisms attached to a certain habitat, plants are often exposed to various and sometimes simultaneous biotic and abiotic stress factors. Drought, salinity, extreme temperatures, chemical toxicants, and sometimes infection cause strong or mild dehydration (osmotic stress), which is reflected in a decrease in turgor pressure and water loss by plants and is a point of convergence for many abiotic stress [1]. Upon prolonged exposure to salinity or heavy metals and in the case of irrational application of fertilizers, in addition to osmotic stress, we observe a toxic effect of excess ions on plant cells and induction of oxidative stress caused by imbalance between production and elimination of reactive oxygen species (ROS) and reactive nitrogen species in different cell compartments leading to the excess of these molecules [2]. Generation of ROS and activation of the system of their detoxification are typical plant responses to adverse environmental effects, which comprises manifestation of their damaging action on the cells and simultaneous development of the systems of defense. An important role in the stress-induced activation of antioxidant enzymes

belongs to ABA [3]. Moreover, ROS and phytohormones are believed to be key points of convergence of abiotic and biotic stress interactions.

Owing to overlapping signal pathways, stress factors of different nature cause similar plant responses: injury of cell components, disturbance of metabolism, reduction in energy supply via suppression or obstruction of photosynthesis and increase in the proportion of catabolic reactions, and retardation of growth [4]. Under stress conditions, plants try to maintain cell turgor, photosynthesis, and transpiration at a level necessary for survival; they try to regulate accumulation of osmolytes and equilibrium of the redox system using various pathways of signaling. This review deals with promising components of plant signaling pathways, which may be modified by the methods of genetic engineering with the purpose of production of resistant and high-yielding cultivars in the near future.

NONHORMONAL PATHWAYS OF SIGNALING

Calcium. In the course of evolution, positively charged calcium ions have become the main signal element of the cells. Calcium is one of the key messengers for operation as a central site of the common signal network; it plays an important role in ensuring stress resistance in plants [5, 6]. Transient (within seconds) arrival of Ca^{2+} from apoplast in cytosol is a com-

Abbreviations: ACC—1-aminocyclopropane-1-carboxylic acid; BS—brassinosteroids; JA—jasmonic acid; MAPK—mitogen-activated protein kinase; MeJA—methyl jasmonate; SA—salicylic acid; SL—strigolactones.

ponent of primary response to different stress conditions; in addition, Ca^{2+} released from intracellular stores also participates in the formation of a calcium signal [7]. Cells can distinguish among stimulus-induced rises, different in nature and intensity, in the concentration of free calcium in the cytosol [5, 6]. Specificity and/or crosstalk in Ca^{2+} signaling may depend on the value, duration, and subcellular location of Ca^{2+} oscillations as well as on diversity of calcium sensors. These differences may allow plant cells to distinguish one type of stress from another and induce expression of the gene responsible for adaptation to a specific stress.

Stress-induced accumulation of Ca^{2+} in the cytoplasm subsequently activates NADPH-oxidase and signaling of reactive oxygen species showing a synergism between signal mechanisms of calcium and ROS [8]. Calcium-permeable channels and NADPH-oxidase produce a self-amplifying hub where elevation of Ca^{2+} results in the production of more ROS and vice versa [6]. Moreover, the level of calcium in plant cells is also controlled by signal molecules, for instance, by lipid signals. For instance, inositol triphosphate causes stress-induced Ca^{2+} release in the cytoplasm of guard cells and stomatal closure [9]. Changes in the level of cytosolic Ca^{2+} are recognized by calcium-binding proteins that interact with the next signal components kinases and/or phosphatases, transmit the signal to the proteins of cytoskeleton, enzymes, and ion channels and trigger expression of the main stress-induced genes responsible for physiological response or transcription of factors that control these genes [5, 6]. The main calcium sensors are calmodulins (CaMs), calcineurin B-like proteins (CBLs), calcium-dependent protein kinases (CPK/CDPK), etc. Together with other components, these Ca^{2+} sensors convert Ca^{2+} signals to subsequent signaling events, such as phosphorylation, transcription reprogramming, activation of MAPK cascade, and accumulation of ROS or nitric oxide (NO); Ca^{2+} signaling is assumed to play a key role in mediation of plant response to stress [8].

A large number of promising stress sensor proteins may be used for production of resistant and high-yielding cultivars. In *Arabidopsis*, OSCA1 is a putative sensor of osmotic stress [10], COLD1/RGA1 is a sensor of low temperature [11], and CNGC2 is a sensor of high temperature [12]; they are protein carriers of calcium in the plasma membrane. Activation of sodium ions' sensor MOCA1 causes a gradual depolarization of plasma membrane potential, inactivation of the channels of Ca^{2+} influx, and activation of Na^+/H^+ -antiporter [13]. Moreover, accumulation of ROS and ABA induces an increase in the free calcium concentration in the cytosol of plant cells. For instance, hydrogen peroxide (H_2O_2) activates sensor HPCA1 located on the plasma membrane, which leads to autophosphorylation of HPCA1, activation by this protein of calcium channels in guard cells, and stomatal clo-

sure [14]. Calcium-dependent activation of these sensor proteins subsequently leads to interaction with CIPKs (a specific group of protein kinases) and activation of the pumps removing sodium ions from cytoplasm of plants under salinity [15]. In rice, drought-induced expression of genes *OsDSM2* and *OsCam1-1* encoding *b*-carotene hydrolase and Ca^{2+} -binding calmodulin, respectively, triggers Ca^{2+} signaling followed by accumulation of ABA and formation of stress resistance [16]. In *A. thaliana* plants, the overexpression of calcium-binding membrane protein *PcaP2* induces resistance to drought; it is interesting that this protein is common for stress-induced signaling of three pathways: not only calcium but also ABA and salicylate since expression of gene *PcaP2* is induced by both ABA and salicylic acid (SA) [15]. Calcium also regulates signaling of auxins as even a brief rise in calcium content in the cytosol modifies polarity of auxin transporter [17].

Reactive oxygen species. Under stress, the rigorous system of regulation of reactive oxygen species homeostasis is impaired and reversible accumulation of ROS acts as a signal triggering stress-induced cell processes and causes oxidation of molecules including phytohormones [18]. NADPH-oxidase catalyzes the generation of superoxide anion; however, the most stable and probably most efficient signal molecule among ROS is H_2O_2 . The genes responsive to H_2O_2 are involved in metabolism and energy exchange, transport of protein, homeostasis of auxins, gene transcription, and stress defense of cells. Elevated content of ROS may affect auxin gradient and/or plant sensitivity to this phytohormone via oxidative degradation or conjugation, modification of auxin transport within plants, and location of auxin exporters PINFORMED (PIN) proteins [19]. Equilibrium between the levels of ROS and auxins partially determines stress-induced morphological changes in plants, and the main points of interaction between ROS and auxin signaling are probably ROS-dependent MAPK cascade and calcium signaling. Rho-guanosine triphosphates in *Arabidopsis* are another point of interaction between auxin and ROS. One of the subclasses of these diverse monomeric GTP-binding proteins encoded by genes *RAC/ROP* regulates such processes as hormonal and stress responses, growth, development, reproduction, and transduction of calcium signals. *RAC/ROP* proteins are activated by auxin and, via induction of operation of NADPH-oxidases, subsequently cause the production of ROS in the apoplast [19]. Auxin receptors TIR1/AFB participate in the activation of expression of the genes responsible for resistance to oxidative stress via regulation of the level of ROS by antioxidant enzymes and chlorophyll content in plants. Together with auxin, ROS actively influence important stages of plant growth and development, such as adaptation to stress, cell cycle and plasticity of the cell wall, shoot branching, and blossom time. For instance, auxin-

induced accumulation of H_2O_2 regulates gravitropism of roots, size of the stomatal aperture, and rigidity of the cell wall.

Upon stress-induced stomatal closure, ROS-mediated accumulation of NO is followed by the production of ABA [20]. Together with salicylic acid, ROS participate in the induction of defense responses in soybean [21]. ROS and ethylene signal pathways also interact during of programmed cell death, acclimatization, development of defense responses to biotrophic pathogens, and organogenesis [19], with activation of signaling cascades involving ROS and Ca^{2+} occurring synergistically [4, 9]. ROS and gibberellins jointly regulate the germination of barley seeds. ROS produced by NADPH-oxidase participate in biosynthesis of gibberellins via regulating expression of the genes encoding the enzymes of their biosynthesis (*HvKAO1* and *HvGA3ox1*) in barley embryos [22].

Nitric oxide. NO is an endogenous signal molecule that plays a key role in plant adaptation to stress influences. NO is produced in all plant cells in oxidation reactions catalyzed by unidentified NOS-like enzyme, from polyamines, and in reduction reactions catalyzed by nitrate reductase, nitrite-NO-reductase, peroxisome xanthine oxidoreductase, and mitochondrial cytochrome *c* oxidase [23]. Accumulation of NO in plants is dynamically regulated by phytohormones, such as ABA, auxin, cytokinin, SA, jasmonic acid (JA), and ethylene, as well as by abiotic and biotic stress agents [20]. Elevated content of NO in plant tissues leads to the same after-effects as the influence of the stress factor, which shows itself in suppression of primary root growth, activity of cell divisions, and, accordingly, in the size of the root system, probably due to interaction between nitric oxide and Ca^{2+} signaling, ROS, and protein kinases. Moreover, excess accumulation of NO in mutant *nox1* causes reduction in *PIN1* expression and decreases the accumulation of auxin in plant root [24]. In addition to auxins, NO affects signaling cascades of gibberellins, cytokinins, ethylene, ABA, SA, JA, brassinosteroids (BS), and strigolactones (SL) at the level of biosynthesis, transport, degradation, and conjugation of all the signaling elements [20]. NO exerts influence on nitrosylation of transition metals (Fe, Zn, and Cu) within proteins, covalent modification of amino acid residues of cysteine (*S*-nitrosylation), and nitration of amino acid residues of tyrosine. These posttranslational modifications change the activity of the proteins, their stability, intracellular location, and interaction with partner proteins as well as protein phosphorylation [23]. Many physiological processes in plants are regulated by phytohormones with the participation of nitric oxide. For instance, NO and SA coordinate photosynthesis and generation of ROS; under salinity, they act synergistically and normalize the arrival of sodium in plants. Together with ROS and phytohormones ABA, SA, and JA, NO participates in stress-induced stomatal closure [20].

Lipid signals. Membranes are a source of components of lipid signaling, such as phosphatidic acid, phosphoinositides, sphingolipids, lysophospholipids, oxylipins, N-acyl ethanolamines, free fatty acids, and others generated by phospholipases, lipid kinases, and phosphatases. Upon exposure to abiotic and biotic stressors and under the influence of phytohormones, signal molecules of a lipid nature accumulate rapidly and transiently; they can quickly draw protein targets to membranes and thus exert influence on conformation and activity of intracellular proteins and metabolites. Interaction with such lipid signal as phosphatidic acid may induce translocation of proteins attracted to the membrane and, thus, block their activity. Moreover, phosphatidic acid promotes stomatal closure via binding and inhibiting protein phosphatase ABI1—a negative regulator of the ABA signal pathway. Phosphatidic acid interacts with a negative regulator of ethylene signal pathway—constitutive triple response kinase (CTR1) from *Arabidopsis*—and inhibits its activity, whereas binding with sphingosine kinase results in its activation. A pool of phosphoinositides and lipid kinases was found in the nucleus, with their activity rising under stress. Consensus motif of binding phosphatidic acid was not identified, and such a sequence may be nonexistent. This fact suggests the existence of an electrostatic/hydrogen bond that accounts for the molecular basis of binding phosphatidic acid by unique properties of its molecule. Moreover, inositol-5-phosphate is a structural cofactor of coronatine-insensitive JA receptor (COI1), and inositol-6-phosphate is an inhibitor of auxin receptor (TIR1), which integrates lipid and hormonal signaling [9].

HORMONAL PATHWAYS OF SIGNALING

Phytohormones are key regulators of physiological processes in plants over their whole life cycle in normal growing conditions and under stress exposures. Metabolic processes and hormonal signaling cascades are appropriate targets for manipulations aiming to improve plants' stress resistance. In this case, it is crucial to maintain such a hormonal balance that would reduce the possible negative effects on plant growth and development. It is also necessary to take into consideration numerous external and internal signal factors of both hormonal and nonhormonal nature; at the same time, it is important to take into account the spatial arrangement of their targets and the time necessary for accumulating signal factors and activating defense mechanisms as well the stage of plant development.

ABA. Environmental stressors stimulate in plastids the synthesis of isoprenoid phytohormone ABA that induces in plants a great number of adaptive responses, including stomatal closure and expression of defense genes. ABA-mediated plant response to stress starts from the interaction of ABA with soluble receptors PYR/PYL/RCAR and PP2C and numerous

ABA transporters, for instance, with NPF4.6 involved in intercellular translocation of this hormone [25]. Central regulators of ABA-dependent signaling are SnRK2 kinases that subsequently phosphorylate ARE/ARF and trigger gene transcription.

ABA also regulates expression of the genes encoding transcription factors that, in turn, interact with ABA-responsive elements (*ABRE*) of ABA-regulated genes [26]. Sensitive to ABA transcription factors, such as ABF, MYC, and MYB, participate in the expression of ABA-dependent stress genes via interaction with *ABRE* (ACGTGGC), *MYCRS* (CAnnTG), and *MYBRS* (YAACR), respectively; moreover the expression requires interaction with more than one ABA-responsive element [27]. Activation of ABA-responsive transcription factors occurs by phosphorylation performed by ABA-induced kinases [28]. Overexpression of AREB/ABF transcription factors regulating both ABA signals transduction and expression of ABA-dependent genes improves the stress tolerance of plants [27].

It is interesting that, under stress conditions, ABA-dependent and ABA-independent pathways of signal transduction interact with each other [29]. Regulation of plant growth and development occurs upon joint action of ABA and other signals; for instance, ripening of grape berries involves ABA, ethylene, and H₂O₂ [30]. Sulfurase regulates the import of two chloroplast aldehyde oxidases that catalyze the final stages of IAA and ABA biosynthesis and govern xanthine dehydrogenases XHD1 and XHD2 participating in the degradation of purine and generation of ROS under environmental stress conditions. Thus, this enzyme acts as a sensor of redox potential and affects the production of hormones IAA and ABA [31]. Together with ABA, drought-induced accumulation of JA in plants regulates stomatal closure via stimulation of influx of extracellular Ca²⁺ and/or by means of activation of H₂O₂/NO signaling. Subsequently, there occurs a rise in Ca²⁺-dependent activity of protein kinase CDPK followed by a cascade of defense responses, including a reduction in stomatal aperture in the leaves of *Arabidopsis* [28]. The interplay between methyl jasmonate (MeJA) and ABA signal pathways under stress conditions probably depends on the interaction between their signal proteins and receptors [29]. Plant treatment with exogenous ABA negatively regulates the key gene of cytokinin biosynthesis encoding isopentenyl transferase and activates genes of cytokinin oxidases and dehydrogenases [32].

Auxins are produced in one tryptophan-independent and four tryptophan-dependent ways. The most common form of auxin in the plant cell is IAA, an important regulator of cell division, elongation, and differentiation. The remaining auxins—indole-3-butyric acid, 4-chloroindole-3-acetic acid, and phenylacetic acid—also show a hormonal activity and occur in plants in appreciable quantities. Such a

redundancy of active auxins and the pathways of their synthesis points to an extraordinary importance of these phytohormones for plants, including their adaptation to stress conditions. Many internal and external signals induce a differential distribution of auxin in *Arabidopsis* plants by means of modification of polarity and localization of PIN proteins responsible for auxin transport. In addition, active participation of auxins in plant adaptation to changing environmental conditions is confirmed by the existence of several auxin-dependent genes that respond to biotic and abiotic stress.

Interaction between auxin and cytoplasmic receptor AUXIN-BINDING PROTEIN1 (ABP1) triggers a nontranscriptional auxin signaling by which clathrin-mediated endocytosis acts as an important feedback of auxin on its own transport [19]. Influence of auxin on plants also activates transcription by means of a down-regulation when binding of auxin with its receptor proteins TRANSPORT INHIBITOR RESPONSE1 (TIR1) and AUXIN SIGNALING F-BOX (AFB) triggers ubiquitination and subsequent proteasome degradation of transcriptional suppressors Aux/IAA and release of auxin response transcription factors (ARF). These ARF either activate or suppress expression of auxin-sensitive genes.

Under stress exposure, plant growth is inhibited in order to release resources necessary for survival; in other words, synthesis and translocation of auxin are suppressed. Auxin transport is performed by carriers located in cell membranes whose activity and/or quantity may be modified in order to produce resistant cultivars. For instance, carrier OsPIN3t participated in polar auxin transport in rice exposed to drought; knockdown of its gene caused root abnormalities in an early stage and its overexpression led to improved drought resistance [33]. Low acid protonated auxin indoleacetic acid hydrolase (IAAH) can freely diffuse through the lipid plasma membrane and actively interact with carriers AUXIN RESISTANT1/LIKE AUX1 (AUX/LAX), and IAAH dissociates into its deprotonated form in the cytosol of target cells. Regulation of IAA content in the cells of projected resistant plants will probably need active efflux of this phytohormone by means of PIN and P-glycoproteins (PGP) of the ATP-binding cassette family B efflux carriers [19].

Transgenic plants with overexpression of *Arabidopsis* gene *YUCCA6* participating in tryptophan-dependent pathway of IAA biosynthesis contained more free IAA and transcripts of early gene response to auxin than control plants. Such transgenic plants are resistant to drought probably due to a lower level of ROS [34].

Cytokinins. Plant 6-aminopurine hormones stimulate cell division, regulate apical dominance, biogenesis of chloroplasts, mobilization of nutrients, leaf senescence, vascular differentiation, and maturation. Under stress conditions, cytokinins prevent cell injury by ROS, reduce the activity of chlorophyllases and dechelatases

that destroy chlorophyll during senescence, elevate the activity of antioxidant enzymes, and induce accumulation of antioxidant molecules and xanthophylls. As a rule, expression of cytokinin-sensitive genes is suppressed in response to stress exposures [35].

Active cytokinins are identified by the plasma membrane or intracellular membranes by means of membrane-bound histidine kinase proteins (AHK2, AHK3, and AHK4/CRE1 in *Arabidopsis*) that subsequently become autophosphorylated and pass the phosphoryl group to histidine phosphotransfer proteins (AHP). AHP proteins subsequently migrate to the nucleus and phosphorylate a response regulator (ARR). There are two types of ARR: phosphorylation of type B response regulators activates target genes by binding with their promoters; expression of type A ARR rises under the effect of type B regulators, and they consume much activated phosphates themselves, which reduces cytokinin-dependent transcription and leads to a suppression of cytokinin response [36]. At the same time, NO inhibits some stages of phosphorylation and ethylene receptor protein ETR1 receives signals from ethylene receptors integrating signaling of ethylene and cytokinins [37].

When stress responses develop, signal pathways of cytokinins and ABA become antagonistically interacting processes [38]. Three cytokinin receptors—AHK2, AHK3, and AHK4/CRE1—act as negative regulators in ABA-dependent and ABA-independent signaling [39]. In addition, key regulatory components of cytokinin signaling are the enzymes responsible for inactivation of cytokinins, cytokinin oxidase and dehydrogenase (CKX), which are positively regulated by ABA [40]. Under stress, the majority of plant tissues accumulate less cytokinins (the same as auxins) and elevate plant sensitivity to ABA for mediation of stress response. In resistant wheat cultivars exposed to stress, cytokinins are suppressed almost immediately, while it is a little later and to a lesser extent in sensitive plants [40]. In the early stages of stress, the quantity of cytokinins in plants may transiently increase. Upon exposure to strong abiotic stress, the quantity of cytokinins may be maintained at a high level [35].

The same as with auxin, the disturbance of cytokinin synthesis and signaling leads to a negative pleiotropic effect. For instance, deficient in cytokinins *Arabidopsis* overexpressing CKX or knockout in four genes *ipt1*, 3, 5, 7 was very sensitive to ABA upon seed germination and expression of genes related to ABA [32]. However, targeted and clever regulation of enzymes responsible for biosynthesis of cytokinins or disconnection of some components of their signaling in certain tissues may improve productivity and preserve drought resistance.

Gibberellins. Gibberellic acids (GA), a group of 130 diterpenoids of tetracyclic carboxylic acids, are key growth regulators in different stages of plant development, which control division and elongation of the

cells as well as reproductive development [26]. Their biosynthesis is regulated by dioxygenases—GA3-oxidase (GA3oxs) and GA20-oxidase (GA20oxs)—and inactivation depends on GA2-oxidase (GA2oxs). Mutant genes *GA2ox6* moderately reduce the accumulation of GA, which leads to a shortening of plants, formation of more developed root system, intensification of photosynthesis, a rise in productivity by 10–30%, and improvement of stress resistance in transgenic rice [41]. Soluble protein GIBBERELLIN INSENSITIVE DWARF1 (GID1) is a receptor of active GA (GA1, GA3, GA4, and GA7); it interacts with DELLA proteins (negative regulators of plant response to GA) triggering a targeted degradation of DELLA transcription factors by 26S proteasome complex and development of plant response to GA [42].

Environmental stressors inhibit plant growth reducing endogenous levels of GA via suppression of their biosynthesis or acceleration of degradation [43]. Mutant plants with a reduced content of GA show dwarf phenotype and are drought-resistant. Such important agricultural crops as rice and barley are famous for their dwarf cultivars. Application of GA inhibitors under drought simultaneously improves stress resistance and increases biomass accumulation and plant productivity [44]. Complete elimination of GA from plants will inevitably lead to a reduction in yield; therefore, the creation of productive and resistant cultivars should be based on the enzymes controlling the content of GA. For instance, ectopic expression of several *GA2ox* genes in rice leads to a moderate reduction in GA content in plants of dwarfish phenotype; however, plants more efficiently used water and showed higher productivity and improved resistance to abiotic stress [41].

JUNGBRUNNEN1 (JUB1) is a transcriptional regulator of gibberellin and brassinosteroid signaling in *A. thaliana*; via repression of the genes *GA3ox1* and *DWARF4* (*DWF4*) encoding hormone biosynthesis it reduces the levels of GA and BS and promotes the production of typical GA/BS deficiency phenotypes. JUB1 also inhibits PIF4, an important transcription factor that connects hormonal signals and environmental stimuli. On the other hand, JUB1 activates genes *DELLA GA INSENSITIVE* (*GAI*) and *RGA-LIKE1* (*RGL1*). In addition, BZR1 (BRASSINAZOLE-RESISTANT1) and PIF4 act as direct transcriptional repressors establishing a negative feedback loop. Thus, JUB1 forms the core of a regulatory module that triggers DELLA accumulation, thereby restricting cell elongation and simultaneously enhancing stress tolerance [45].

Brassinosteroids. This group of polyhydroxylated steroid hormones plays an important role in regulation of growth, development and defense reactions in plants. A wide range of regulatory functions of BS covers cell division and elongation, termination of cell elongation, vascular differentiation, response to biotic

and abiotic stimuli, and senescence. Treatment with exogenous brassinosteroids alleviates stress-induced retardation of growth and photosynthetic activity, improves the plant membranes status, and enhances activity of antioxidant enzymes and content of proline [46, 47]. Thus, manipulations with BS signaling aiming to improve stress resistance and elevate plant productivity are promising.

Membrane-located kinase BRI1 and its homologs BRL1 and BRL3 are receptors of BS. Binding of BS with the receptors triggers the formation of heterodimer SERK3 (SOMATIC EMBRYOGENESIS RECEPTOR KINASE3) that, in turn, initiates intracellular phosphorylation cascade. Plant transcription factors BZR1 and BES1 (BRI1-EMS-SUPPRESSOR1) control the transcription of brassinosteroid-specific genes. In the absence of BS, special GSK3-like kinase BIN2 (BRASSINOSTEROID-INSENSITIVE2) phosphorylates proteins BZR1/BES1 and inactivates them promoting their degradation, which inhibits the ability of BZR1/BES1 to bind DNA [48]. BIN2 kinases also phosphorylate SnRK2, which is a common feature of ABA and BS signaling [49].

In transgenic plants of *A. thaliana* overexpressing *TaBRI1*, kinase BRI1 interacts with five members of the wheat somatic embryogenesis receptor kinase family (TaSERKs) located at the plasma membrane and increases yield, improves thermotolerance, and stimulates early flowering [50]. Since BRI1 is followed in the BS signaling cascade by a negative BS regulator glycogen synthase kinase (BIN2), elucidation of the mechanisms controlling activation of BIN2 under stress conditions may promote molecular selection of resistant plant cultivars [1].

BS may actively participate in the formation of plant resistance to stress not only by themselves but also in cooperation with signaling cascades of other hormones and due to common targets. Together with auxins, brassinosteroids participate in the formation of vessels in *Arabidopsis* and activate expression of transcription factor ERF115 (ETHYLENE RESPONSE FACTOR115) that plays a leading role in growth and development of roots [48]. The pathways of auxin and BS signal transduction have common key components, such as BZR1 and ARF (AUXIN-RESPONSE FACTORS). For normal growth and development, plants must have a specific ratio between auxins and BS, and recovery of the upset balance occurs with regulatory participation of brassinosteroids on a feedback principle [51, 52].

ABA and BS act as antagonists in such processes as seed germination, root growth, and stomatal closure, but this does not prevent them from jointly regulating expression of approximately 100 different genes [53]. Brassinosteroids reduce accumulation of ABA in plants [47], whereas ABA inhibits BS signaling via components of ABA signaling, including its receptors and ABI2. ABA and GSK3 proteins of brassinosteroid

signaling (in particular, BIN2, BIL1, and BIL2) antagonistically and jointly regulate the expression of common stress genes [49]. In *Arabidopsis* and rice plants, direct BZR1/BES1 interaction makes it possible to bind with promoters of numerous metabolic genes of GA and then control their expression [51, 52]. For instance, BZR1/BES1 controls expression of the gene of GA biosynthesis *GA20ox1* (*GA 20-oxidase 1*) in *Arabidopsis* [54] and physically interacts with the principal negative regulator of GA signal transduction: DELLA proteins [53]. Simultaneous emergence of BS-activated BZR1 and GA-inactivated regulators of transcription DELLA allows these two classes of phytohormones to act synergistically.

Salicylic acid is an endogenous phenolic compound regulating plant growth and development, the state of the antioxidant system, germination, photosynthesis, and ripening. SA is synthesized via isochlorismate and phenylalanine ammonia lyase. Upon exogenous application, low concentrations of SA are preferable, whereas high concentrations of salicylic acid intensify oxidative stress in plants [55]. The majority of genes that respond to SA treatment are associated with stress and signal pathways that lead to cell death in the end. Genes activated by SA encode chaperones, heat shock proteins, dehydrins, antioxidants, and secondary metabolites. Treatment of wheat plants with SA somewhat reduces stress-induced retardation of growth, prevents membrane injury, and normalizes water exchange stimulating accumulation of osmolytes. Treatment with exogenous SA reduces stress-induced injury of plants via regulation of ROS level affecting the generation of H_2O_2 by NADPH-oxidase, which, in turn, stimulates the production and activity of antioxidant enzymes.

Signal pathways of SA and IAA interact, and pretreatment of plants with salicylic acid elevates accumulation of auxin in plants and has a beneficial effect on plant growth under stress [55]. The process involves Gretchen Hagen3 (GH3) acyl acid amido synthetases, for instance, AtGH3.5 capable of conjugating both IAA and SA [56]. Operation of these enzymes in plants also affects jasmonates: group I GH3 are amido synthetases not only for salicylic but also for jasmonic acid, group II GH3 participate in regulation of IAA concentration on a negative feedback principle, and group III GH3 are involved in salicylic acid signal transduction [57].

SA acts jointly with BS in the processes of growth stimulation, elevation of the content of photosynthetic pigments, and activation of antioxidant defense of brown mustard plants exposed to stress. At the same time, protein NPR1 sensitive to ROS is an important component in formation of stress resistance mediated by BS and SA [58]. Transcription factors WRKY46, WRKY54, and WRKY70 involved in signaling cascade of BS participate together with BES1 in realization of plant defense programs under biotic and abi-

otic stress conditions, in particular, regulating stomatal closure [59]. In addition, transcription factor WRKY70 operating somewhat later than NPR1 participates in expression of SA-induced PR gene [60]. Thus, WRKY and NPR1 may be potential points of convergence of SA and BS signal pathways.

Influence of SA on plants reduces stress-induced accumulation of ethylene by inhibiting aminocyclopropane-carboxylate synthase (ACC synthase) of wheat, thus reducing the inhibitory effect of stress, which suggests that SA and ethylene are antagonists [61].

Jasmonates. Jasmonic acid, methyl jasmonate (MeJA), (3R,7S)-jasmonyl-L-isoleucine (JA-Ile), *cis*-jasmonate, and jasmonyl-1-aminocyclopropane-1-carboxylic acid (JA-ACC) are cyclopentanone phytohormones produced during metabolism of fatty acids. Jasmonates regulate plant development (in particular, flowering, fruit-bearing, and senescence) under normal conditions and plant response to biotic stress and pathogen invasion; they also play an important role in plant resistance to abiotic stress [62]. Treatment with exogenous jasmonates produces a beneficial effect on growth and productivity of plants exposed to abiotic stress [63] owing probably to enhancement of expression and activity of antioxidant enzymes, activation of ascorbate-glutathione cycle, and reduction in oxidative injury induced by ROS via accumulation of JA-induced nitric oxide. JA treatment of wheat seedlings exposed to drought after pretreatment with NO scavenger did not improve drought resistance, which demonstrates NO participation in signal transduction from JA to the ascorbate-glutathione cycle [64].

JA-Ile is the only known active biomolecule. The remaining jasmonates form conjugates with isoleucine; subsequently this promotes interaction of jasmonate with ZIM domains of JAZ transcription factors and with F-box motifs of JA-receptors of ubiquitin ligase COI1, which initiate degradation of JAZ proteins. Since JAZ proteins are transcriptional repressors, their degradation causes the transcription of numerous JA-dependent genes. Active hormone jasmonate mediates protein-protein interaction that leads to polyubiquitination and degradation of JAZ proteins by proteasome 26S. Transcription factors MYC2 may subsequently activate expression of the genes involved in the JA signal pathway. There is a TPL corepressor that represses not only jasmonates but also ethylene signaling [62].

Promoter sequence of *TaMYB33* contains four motifs potentially responsive to MeJA, which points to its participation in a cascade of jasmonate signal transduction. Overexpression of *TaMYB33* in *Arabidopsis* caused activation of defense gene *PDF1.2A*, which suggests that *TaMYB33* may be a link integrating signaling cascades of biotic and abiotic stress [65]. Expression of gene *TaEXPB23* of wheat expansin is induced by drought and exogenous MeJA. Promoter

region of *TaEXPB23* contains a MeJA-sensitive repeat, and overexpression of *TaEXPB23* in tobacco improves plant resistance to salinity [66].

Wheat oxide cyclase gene *TaAOC1* also integrates responses to JA, ABA and resistance to abiotic stress. In wheat plants, expression of gene *TaAOC1* is induced by salinity, drought, and treatment with ABA and MeJA. Overexpression of *TaAOC1* in wheat and *Arabidopsis* plants boosted stress resistance owing to intensification of JA biosynthesis and accumulation of MYC2. In the *myc2-2* mutant, overexpression of *TaAOC1* improves weak salinity tolerance, which suggests that MYC2 is an important component in JA signaling. It is possible that MYC2 is a point of convergence for ABA and JA signaling cascades under salinity. Cross interaction of JA and ABA signal pathways integrates plant responses to environmental stress conditions [67].

Signal pathways of jasmonates and cytokinins also interact since pretreatment with MeJA causes a transient accumulation of cytokinins in wheat seedlings [68], which should be taken into consideration when stress resistance of plants is analyzed. JA and BS differently affect plants exposed to biotic stress. For instance, brassinosteroids promote rice susceptibility to pest insects via jasmonate signaling. Invasion of pest insects inhibits the pathway of BS signaling and activates the JA signal pathway [69]. However, under abiotic stress JA and BS act synergistically and jointly enhance plant resistance [53].

Ethylene. The precursor to gaseous ethylene, polyamines, methionine, and other amino acids produced from aspartate is S-adenosyl methionine (SAM). Water deficit induces the accumulation of SAM that participates in lignification of plant cell walls via methylation of lignin monomers, which prevents water loss. ACC synthase transforms SAM into cyclic nonprotein amino acid ACC, and then ACC oxidase converts ACC into ethylene. Usually ethylene operates as a negative growth regulator. In response to environmental stress factors, ethylene stops growth, stimulates plant senescence, interrupts the development of the embryo, reduces grain filling, and affects distribution of nutrients in plants [70, 71].

The same as cytokinin, ethylene is perceived by cell receptors with histidine kinase activity located on membranes of endoplasmic reticulum, which subsequently undergo autophosphorylation and trigger the histidine/aspartate phosphotransferase system. Within this system, phosphates are sent to histidine-phosphotransferase proteins that subsequently activate transcription factors known as ERF [72]. ERF regulate the expression of ethylene-dependent genes via direct binding with numerous *cis*-elements in promoter regions of ERF target genes. Some of these proteins can integrate ethylene signaling with the transduction of other signals. For instance, SI-ERF.B3 perceives

ethylene and auxin signals via regulation of expression of auxin signal component *SI-IAA27* [73].

Ethylene and ABA act as antagonists to each other, which makes it possible to temporarily desensitize plant tissues to ABA and maintain stomatal conductance and photosynthesis [71]; they also jointly activate expression of some ERF proteins (including *TaERF1* and *TaERF3*) that enhance stress resistance [72]. Drought and heat stress greatly stimulate the activity of ACC-synthase inducing accumulation of ACC in the grains; severe water deficit considerably inhibited enzymes necessary for synthesis and accumulation of starch (sucrose synthase, ADP-glucose pyrophosphorylase, and soluble starch synthase); accordingly, grain filling deteriorated, maturation and desiccation of seeds accelerated, and early senescence of flag leaf was initiated. The inhibitor of ACC-synthase aminoethoxyvinylglycine mitigated processes induced by this enzyme [74]. Some ERF were shown to play an important role in signal transduction under environmental stress exposure, for instance, upon salinity. Increased expression of these factors preserved photosynthetic potential, induced accumulation of osmolytes, and reduced production of H_2O_2 enhancing resistance to salinity, drought, and low temperature [72], whereas application of inhibitors of ethylene synthesis reduced plant tolerance to environmental stress conditions [70]. Thus, application of inhibitors of perception and/or biosynthesis of ethylene under environmental stress exposure may contribute to the reduction of stress-induced plant responses to ethylene, including maintenance of growth and elevation of productivity. In addition, regulation and overexpression of certain *ERF* genes (for instance, *TaERF1* and *TaERF3*) may improve the total tolerance to environmental stress agents [72].

Ethylene and auxin regulate plant growth and development via ubiquitin-mediated proteolysis of transcriptional repressors; ubiquitin ligase $SCF^{TIR1/AFB}$ hydrolyzes Aux/IAA and triggers transcriptional signaling of auxins, whereas ubiquitin ligase SOR1 controls ethylene-dependent root responses modifying the stability of the Aux/IAA protein. Enzyme SOR1 interacts with OsIAA26 (atypical Aux/IAA protein) and OsIAA9 (canonical Aux/IAA protein) targeting OsIAA26 for ubiquitin/26S-mediated proteasome degradation, whereas OsIAA9 protects protein OsIAA26 from degradation by inhibiting the activity of ubiquitin ligase SOR1. Probably, SOR1-OsIAA26 module acts downstream of the $OsTIR1/AFB2$ -auxin-OsIAA9 signaling to regulate ethylene inhibition of root growth in rice [75].

Ethylene and polyamines (putrescine, spermine, and spermidine) have a common precursor; therefore, elevation of their production along with improvement of plant resistance to a stressor reduces stress-induced accumulation of ethylene. Ethylene often acts together with SA and JA in the regulation of plant defense

against pests and pathogens. Upon regulation of gravitropism and activity of antioxidant enzymes, pathways of BS and ethylene signaling behave antagonistically [60]. Interaction between ethylene and BS mediated by H_2O_2 occurs in tomato plants under salinity. The activity of ACC synthase responsible for ethylene synthesis rises after pretreatment of plants with BS, and reduction in ethylene generation or suppression of activity of ethylene signaling components diminishes BS-induced salt resistance [76].

Strigolactones. These recently described plant hormones are derivatives of apocarotenoids; they participate in the programs of plant development and symbiotic relationships in the rhizosphere of all the examined plants by means of independent pathways of reception and signaling cascades. To date, we know 20 SL that are terpenoid molecules of lactone with a tricyclic ABC ring covalently bound with ring D via an enol-ether bridge that is considered to be a bioactive part of all the molecules from the strigolactones family [77]. SL can regulate stress-induced formation of shoot and root systems, which is important for realization of plant resistance programs. For instance, upon exposure to environmental stress factors, SL suppress activity of axillary meristem, forward resources to the main stem and root, and stimulate growth of root hairs.

SL are predominantly synthesized in the roots and translocated in both directions probably by means of PDR1 transporter asymmetrically localized on the plasma membrane depending on the type of root cells; this determines the direction of SL transfer. Moreover, strigolactones may be quickly translocated along the xylem. In plants, SL receptors are specific α/β -hydroxylases; after interaction with them, the repressor protein becomes degraded [77]. Some proteins involved in strigolactone signaling have amino acid sequence identical with receptors of auxins and jasmonic acids and the mechanism of SL signal transduction resembles signaling of gibberellins.

Exogenous treatment of *Brassica napus* with a synthetic SL analog (GR24) improves plant growth under salinity, elevates the activity of antioxidant enzymes superoxide dismutase and peroxidase [78], and considerably diminishes stress-induced reduction in the weight of one thousand grain and productivity of winter wheat [79]; therefore, modification of SL signaling cascade by means of genetic engineering is promising.

PROTEIN KINASES AND TRANSCRIPTION FACTORS

Protein kinases (mediators of stress responses) and transcription factors (the targets sensitive to phytohormones and nonhormonal signals) represent universal mechanisms of signaling in living organisms. The application of molecular genetics techniques to these proteins and the proteins of heat shock capable of regulating phytohormone signaling is promising in

respect to production of high-yielding and stress resistant plant cultivars.

Protein kinases. Plant SnRK1 protein kinases are activated in response to stress-induced reduction in energy supply inducing intensification of catabolism and suppression of energy-consuming anabolic processes and growth. Under stress exposure, SnRK1 signaling is blocked by sugars [80]. Subclass III SnRK2 participate in ABA signaling cascade, whereas subclass I and II SnRK2 are in responses to abiotic agents (including osmotic stress) without participation of ABA [81]; SnRK3 are important regulators of ionic homeostasis necessary for survival under salinity or adverse changes in the content of nutrients in the soil [4]. When one modifies the quantity or activity of SnRK, it is possible to produce high-yielding and stress-resistant plants. For instance, tobacco plants overexpressing gene *SoSnRK2.1* showed an improved resistance to drought [82]. In *Arabidopsis* plants exposed to salinity, it was shown that ABA-nonactivated SnRK2.4 and SnRK2.10 elevate stress resistance regulating the ROS balance and modifying activity of antioxidant enzymes and expression of their genes [83].

TOR protein kinases play an important role antagonistic to SnRK1 in regulation of metabolism and gene expression [80]. TOR protein kinases promote the activation of growth and biosynthetic processes in response to the availability of energy in the form of glucose [84]. SnRK1-TOR signaling is crucial for plant adaptation to environmental conditions and is closely interlaced with hormonal signal pathways. TOR activity is regulated by auxins and they also regulate the expression of the components of auxin signaling [85]. In addition, TOR stabilizes transcription factor BZR1, a component of BS signaling [86], and induces expression of the genes participating in ABA, ethylene, SA, and JA signaling simultaneously suppressing genes participating in signal pathways of BS, GA, auxins, and cytokinins [87]. High expression of TOR genes in *Arabidopsis* plants improves their resistance to abiotic stress [88].

All stress pathways also comprise mitogen-activated protein kinases (MAPK) that perform a conservative function of the stress signal in living organisms. A large number of MAPK proteins were found in plants and quick activation of some of them was recorded not only in response to environmental stress exposures but also under normal growing conditions upon the influence of growth and development signals [89]. For instance, low temperature in *Arabidopsis* activated the MAPK cascade that, in turn, controlled the expression of *COR* genes and plant tolerance to freezing [90]. For realization of resistance to stress agents, the MAPK cascade is a connecting link in signal transduction from ROS to phytohormones [18]. The reverse was also shown: interaction between BS and the elements of the MAPK cascade induced resistance of tobacco plants to tobacco mosaic virus [91].

A large family of receptor-like kinases (RLK) participates in defense responses of plants to abiotic stress integrating responses to ABA treatment, effect of calcium, and ROS. In rice, overexpression of gene *OsSIK1* improves drought resistance via reduction in the number of stomata. RLK participate in stress-induced activation of the antioxidant system, regulation of activity of water channels and ion transporters, and stimulation of expression of ABA-induced genes. Upon stress exposures, receptor-like kinase CRLK1 may integrate accumulation of calcium with MAPK cascade since CRLK1 binds to calcium and calmodulin, interacts with MEKK1, and is necessary for the activation of MAPK at a low temperature [92].

Transcription factors. ABA-independent pathway of stress responses is mediated by several families of regulatory transcription factors. Abiotic stressors may induce transcription factors from NAC and DREB families via *NACRS* (*CACG*) and *DRE* (*G/ACCGAC*)-binding DNA sequences in promoter regions and expression of stress genes independent of ABA. Apart from DREB and NAC domain proteins, zinc finger homeodomain ZFHD (except for ZFHD1) may independently of ABA regulate the expression of stress genes. Overexpression of transcription factors DREB1/CBF, DREB2, and SNAC controlled by appropriate promoters improves plant stress tolerance [27].

One of the largest families of proteins capable of interacting with DNA and regulating expression of genes responsible for growth, development, and defense responses to stress consists of WRKY transcription factors. Quick, transient, and tissue-specific WRKY expression starts right after plant exposure to stress or regulatory molecules. For instance, transcription of *TaWRKY70* is increased in wheat plants by invasion of pathogens, exposure to low temperature, and treatment with SA or ethylene and decreases at high temperature or in the presence of MeJA [93]. WRKY transcription factors can directly interact with components of the MAPK pathway of signal transduction [94] and participate in ABA-mediated signaling [95]. Stress-induced defense responses with participation of WRKY are realized via transcription of stress genes and regulation of osmotic and oxidative balance [94].

Heat shock proteins. Abiotic stressors and invasion of pathogens induce accumulation of heat shock proteins (HSP). *Arabidopsis* encodes seven isoforms of HSP90, out of which four are cytoplasmic and the rest are located in the chloroplasts, mitochondria, and in the lumen of endoplasmic reticulum, whereas maize has 15 isoforms of HSP90 [96]. Many HSP operate as conserved pleiotropic molecular chaperones for prevention of protein denaturation and maintenance of protein homeostasis. Moreover, HSP70, HSP90, and their cochaperones SGT1 and RAR1 are related to target-oriented transport and degradation of proteins as

well as signaling. For instance, in the case of pathogen attack on tobacco plants the SGT1-HSP90 complex participates in formation of hypersensitive response induced by MEK2DD [97]. HSP90 can interact with BES1 and affect BS signaling [98]. The HSP90-SGT1 complex also participates in transduction of JA, auxin, and GA signals [96, 98], which suggests that the chaperone system of HSP90 is interrelated with other plant hormones.

CONCLUSIONS

This review deals with different signal pathways in plants exposed to abiotic and biotic environmental stress agents with an emphasis on an interplay among signaling cascades of the most thoroughly investigated signal molecules: phytohormones. We briefly described pathways of biosynthesis of phytohormones and known points of interaction of signaling of various phytohormones and nonhormonal signal molecules; modification of their regulation may result in the production of high-yielding and stress-resistant plants. Interaction of plant signal pathways is complex; it may be species- and tissue-specific, synergistic and antagonistic, and depend on the concentration of the examined substances. Numerous signal pathways have common points of convergence. It should be stressed that complex knowledge about regulation of plant growth and development under normal- and stress-growing conditions may help genetic engineers and selectionists to choose promising avenues to produce resistant and high-yielding cultivars of agricultural crops. The most important present-day goal for researchers is to indicate genetic markers for crop breeders to work on.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of humans or animals. This article does not contain any studies involving animals performed by any of the authors.

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