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PROSPECTS FOR THE APPLICATION OF JASMONATES, SALICYLATES, AND ABSCISIC ACID IN AGRICULTURE TO INCREASE PLANT STRESS RESISTANCE

(review)

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Abstract

Nowadays, the search for new effective methods and approaches based on using natural bioactive compounds that control plant growth, development, and plant productivity with minimal impact to the environment and human health is still in great demand. One of the directions developing during the last decades contributing to the "greening" of agricultural production is the application agrochemicals based on phytohormones with protective functions, such as abscisic acid, salicylic acid, and jasmonates. The use of these phytohormones is very promising since it can significantly increase plant tolerance to unfavorable factors of biotic and abiotic nature. This review summarizes the current information on the biological functions of abscisic acid, jasmonates, and salicylates, presents the examples demonstrating crop species treatment with the agrochemicals based on these phytohormones, and discusses the promising directions for the phytohormones application in agriculture. Abscisic acid, jasmonates, and salicylates are often referred to as stress hormones because they regulate the plant adaptive responses to adverse environmental conditions. Abscisic acid is a regulator of plant growth and development throughout ontogenesis, as well as tolerance to abiotic and biotic stress factors (J. Li et al., 2017), plays a role in the stomata closure, regulating the ion flow in the guard cells, controls all stages of seed maturation (K. Chen et al., 2020). Abscisic acid can play positive and negative roles in plant protection against pathogens (L. Lievens et al., 2017; K. Xie et al., 2018) and influence the symbiotic relationships with fungi and bacteria (A. Tsyganova, V. Tsyganov, 2015). Salicylic acid controls plant tolerance to pathogens (A. Vlot et al., 2009; P. Ding, Y. Ding, 2020), plays a role in the development of hypersensitive response, death of infected cells (D. Klessig and J. Malamy, 1994; M. Alvarez, 2000), and formation of tolerance in unaffected plant parts (systemic acquired resistance) (M. Bürger, J. Chory, 2019). Salicylic acid may also be involved in the enhancement of plant tolerance to salt and low temperature stress (E. Horvath et al., 2015; Yu. Kolupaev, Yu. Karpets, 2021; W. Wang et al., 2018) and maintenance of the root zone microbiome (S. Lebeis et al., 2015). The range of regulatory effects of jasmonates is broad, but their functions are primarily associated with the regulation of mechanisms that determine plant tolerance to necrotrophic pathogens and insects, including root pests (C. Rohwer, J. Erwin, 2008; S. Johnson et al., 2018). Jasmonates also control plant tolerance to low temperature, salt stress, flooding, drought, ozone, heavy metals, and ultraviolet radiation (T. Savchenko et al., 2014; D. Pandita, 2022; T. Savchenko et al., 2019; K. Kazan, 2015; H. Kim et al., 2021). The high biological activity of abscisic acid, salicylates and jasmonates determines the significant potential of their application in agriculture to increase plant stress tolerance. At the same time, according to published data, the increase in plant tolerance mediated by the mentioned phytohormones is often accompanied by the suppression of growth-related processes, which can adversely affect crop yields and product quality. To assess the prospects for the practical use of agrochemicals based on abscisic acid, jasmonates, and salicylic acid, a comprehensive analysis of the available data on the physiological effects caused by these substances is necessary due to their spectrum of actions, dependent on species/variety specificity, phase of plant development,-susceptibility of the target tissue, chemicals concentration, duration of treatment and conditions of application.

Keywords: phytohormones, abscisic acid, jasmonic acid, salicylic acid, physiological effects, plant tolerance, abiotic stress, biotic stressors, exogenous treatment, adaptive response

Phytohormones regulate plant growth, ontogeny, metabolism and adaptive responses to changing environmental conditions. Since the beginning of the 21st century, researchers have made significant progress in understanding the biological functions of plant hormones, identifying regulatory mechanisms and signal transduction pathways that they control to form a background for their use in agricultural practice. Auxins, ethylene, gibberellins, abscisic acid, cytokinins, the so-called classical plant hormones have been well known since the mid-20th century. The potential of jasmonates, salicylic acid, brassinosteroids and strigolactones, the compounds with regulatory functions proven relatively recently is currently being actively studied. The number of new regulatory molecules is growing, and, in addition to the classes of compounds mentioned, hormone-like properties have been discovered in polyamines, karrikins, triacontanol, turgorins, and peptide hormones [1-3].

The prospects for using phytohormones in agriculture as plant growth regulators and inducers of protective responses are beyond doubt [4-6). Preparations based on cytokinins, auxins, gibberellins, brassinosteroids and their functional analogues for the treatment of fruits during the post-harvest period [7], seeds and vegetative tissues [8-10], have successfully entered into practice. The potential of phytohormones with pronounced protective properties, such as abscisic acid, jasmonates and salicylates, has not yet been discovered. In Russia, preparations based on these phytohormones have not yet been used. Wider application is hampered not only by the difficulties of industrial scale roduction of these compounds but also by the lack of necessary approaches and practical recommendations for various crops.

Here, we analyze current data on the effect of abscisic acid, jasmonates and salicylates on various crops, and also to outline possible prospects for the practical use of each of the phytohormones under consideration in widespread agricultural practice.

Abscisic acid. Abscisic acid (ABA) is involved in the regulation of plant growth and development throughout ontogenesis and determines resistance to abiotic and biotic stress factors [11]. ABA regulates ion fluxes in stomatal guard cells. ABA-mediated stomatal closure can occur in response to drought, low humidity, high CO_2 concentrations, pathogen attack, darkness, etc. Stomata allow gas exchange and transpiration, and can also allow pathogens to enter, so regulating the opening and closing of stomata is important in ensuring plant resistance to adverse environmental influences [12].

ABA is involved in the regulation of seed maturation [12]. Early on, ABA slows down the cell cycle at the G1/S transition stage [13, 14], which inhibits embryonic growth through cell division and activates growth through cell elongation. During the early stages of seed development, ABA accumulates through transport from the mother plant [15]. Later, ABA is synthesized in the cells of the embryo itself and regulates the activity of the network of LAFL transcription factors LEC1/ABSCISIC ACID (ABA)-INSENSITIVE3 (ABI3), FUSCA3 (FUS3) and LEAFY COTYLEDON2 (LEC2) which control seed maturation. Seed desiccation and nutrient accumulation are also controlled by ABA [12]. ABA is a key regulator of seed dormancy, since in mutants with reduced ABA content, seeds germinate prematurely while still on the mother plant [15].

During evolution, plants have acquired complex mechanisms that ensure seed germination only under optimal environmental conditions. The ratio of ABA and gibberellic acid (GA) is crucial in maintaining seed dormancy which is regulated by both endogenous factors associated with plant development and external influences. During germination, ABA catabolism and gibberellin synthesis are enhanced, and GC signaling is activated [11]. A change in the ABA:GA ratio is achieved primarily through changes in the expression of the *RGL2* gene, which encodes RGA-like 2 protein (Repressor of GA). Exogenous ABA is able to activate the expression of *RGL2,* and in the seeds of mutant plants carrying a nonfunctional *rgl2* variant, the ABA content is reduced after imbibition, which leads to accelerated dormancy release and germination. With a high content of gibberellins, DELLA proteins, key negative regulators of the gibberellin signal, are destroyed. This leads to a decrease in the activity of the regulatory module, which, in addition to DELLA, includes the ABI3 and ABI5 proteins (ABA-dependent transcription factors, the main negative regulators of seed germination). As a result, the expression of gibberellin-dependent genes is induced and accelerated germination occurs. It has been shown that during cold stratification, the expression of genes of the *CYP707A* family, involved in ABA catabolism, and the *AtGA3OX1* gene, involved in the biosynthesis of gibberellins, increases [12]. When exposed to high temperature, increased activity of a regulatory module including DELLA, ABI3, and ABI5 inhibits germination [12]. ABA, produced in the tissues of the mother plant, plays an important role in the development of the embryo and affects plant yield [16]. When unfavorable conditions occur, ABA causes growth arrest to protect the seedling [12].

The action of ABA inhibits cell division and elongation, regulates the transition from cell proliferation to differentiation, the development of lateral roots, and the formation of the suberin barrier in roots subject to water stress, providing control of water and nutrient flows [17]. Under normal conditions, ABA suppresses the emergence of new leaves [18] and plays a critical role in accelerating leaf senescence. This is necessary for the efficient distribution of resources from senescent leaves to the floral meristem and seeds. ABA serves as an inhibitor in the regulation of floral meristem activity and flowering time [12]. The participation of ABA in the development of male and female gametophytes and the flower as a whole is discussed in detail in the work of Y. Zhao et al. [19].

With transgenic *Arabidopsis* plants in the mesophilic leaves of which ABA signaling is constitutively suppressed, it was shown that ABA does not directly affect photosynthesis, but the presence of ABA is necessary to achieve maximum plant productivity. Under optimal conditions, transgenic plants with impaired ABA signaling were characterized by more vigorous growth at the initial stages of development, earlier flowering, smaller flowers, delayed chlorophyll degradation and fewer seeds compared to wild-type plants, but no such differences were observed under drought conditions [20].

ABA accumulates rapidly in plants in response to a variety of stress factors. When favorable conditions return, the ABA content decreases due to glycosylation or oxidation to phaseic acid, which is further converted into dihydrophaseic acid. When a plant is exposed to a stress factor with the participation of ABA, the stomata close, the expression of aquaporin genes is inhibited, but the expression of genes encoding chaperone proteins, hydrophilic LEA proteins (late embryogenesis abundant, dehydrins) and antifreeze proteins, enzymes for the synthesis of wax and suberin are activated, and accumulate sugars and proline, the antioxidant system is activated, and other protective changes occur [11]. The prevailing view in the scientific community is that ABA is a growth inhibitory hormone, but recent studies show that nanomolar concentrations of exogenous ABA can stimulate growth, including a positive effect on hypocotyl growth in the dark [21].

The functions of ABA in protecting plants from pathogens are carried out in interaction with other hormones: salicylic acid (SA), jasmonic acid (JA) and ethylene. ABA can cause stomatal closure to block pathogen entry and stimulate callose deposition in plant cells, limiting pathogen spread. Virulence factors of some pathogens are aimed at suppressing ABA signaling in plants, although in other cases, on the contrary, ABA produced by the pathogen acts as an effector that suppresses defense responses [22]. Interestingly, ABA can play both positive and negative roles in plant resistance to viruses [23]. The positive effect of ABA on the symbiotic relationships of plants with fungi and bacteria is the formation of arbuscular mycorrhiza, while the negative effect is the establishment of rhizobial symbiosis [24].

The use of exogenous ABA for pre-sowing seed treatment and foliar treatment of plants increases the stress resistance of grain crops, which leads to an increase in yield [9]. Based on ABA, Valent BioSciences (USA) has developed the BioNik™ drug which is used to delay the development of plants of inbred lines of pollen donors in order to synchronize and extend the period of cross-pollination when growing corn for grain (https://www.valentbiosciences.com).

Exogenous treatment of soybean plants with abscisic acid over several seasons of field and greenhouse trials increased dry mass of aerial parts, root length density, leaf area, number of seeds per pod, and seed oil content [25]. Due to this and due to the distribution of metabolic flows from the vegetative parts of the plant to the seeds, ABA promotes an increase in soybean yields [25].

The use of ABA on sunflower under conditions of sufficient water supply negatively affects plants, while spraying under drought conditions can mitigate the negative effects of stress by increasing the leaf blade area, flowerhead diameter, number of seeds per head, yield, 1000-seed weight and oil yield [26, 27]. Spraying ABA during the budding stage is more effective than spraying during the flowering stage, while the treatment efficiency was different for different hybrids.

The use of the drug ProTone™ (20% ABA, Valent BioSciences) contributed to 100% leaf fall from apple trees in early autumn, without affecting the shoots of axillary buds [28], which indicates the possibility of using this drug to prepare the plant for harvesting and wintering. Exogenous ABA protected apple trees during drought by stimulating stomatal closure [29). Spraying the crown of cherry trees or directly treating fruits enhanced the color of drupes in various varieties [30]. The use of ABA on citrus trees improved the color of fruits, increased resistance to cold, and reduced the content of organic acids in fruits. It was noted that the observed effect was achieved only by foliar treatment while root treatment did not have any effect [31, 32].

The use of ABA on grapes has been well studied. ABA stimulates the ripening of berries, enhances their color by increasing the content of anthocyanins and phenolic compounds, and reduces the content of organic acids [33]. This is due to the fact that ABA controls the biosynthesis of phenolic compounds and anthocyanins [34-36]. The ability of ABA to control the timing of grape berry ripening depends on the concentration of the sprayed solution and also on the target organ, since different tissues demonstrate unequal absorption rates due to the permeability of the cuticle. Cabernet Sauvignon berries absorbed ABA less readily than leaves, but in both cases, ABA treatment accelerated the onset of berry coloring. A cool and wet growing season enhances the effect of exogenous ABA on fruit quality. The bunches treated with ABA had a lower berry weight and a higher dry skin weight which is acceptable for winemaking. Exogenous application of ABA can be an alternative agronomic technique to accelerate berry ripening and improve their quality in cool years, in humid climates and in regions where the likelihood of early frosts is high [33].

In a recent study, J. Li et al. [37] showed a relationship between exogenous exposure to ABA and the content of endogenous phytohormones and metabolites that determine the quality of Ruidu Hongyu grape berries. Treatment with ABA significantly improved the appearance of berries and the content of a number of metabolites (sugars, anthocyanins, polyphenols, soluble sugars, ascorbic acid) by increasing the expression of genes involved in the biosynthesis of these substances. In addition, an increase occurred in the content of endogenous ABA, auxin and cytokinin and the transcription of genes associated with ABA biosynthesis and signaling in fruits.

ABA-based ProTone™ (200 to 400 g/ha) is used in many countries to improve the color of red table grapes. The action of the drug is based on increasing the activity of UDP-glucose flavonoid 3-0-glucosyltransferase (UFGT). The effect of ProTone™ is similar to that of 2-chloroethylphosphonic acid (Ethephon), a precursor of ethylene, but ProTone™ does not lead to softening of fruit tissue and is more technologically advanced because it is not volatile, unlike ethylene (https://www.valentbiosciences.com). The mechanisms by which ABA regulates fruit ripening are discussed in detail in a review article by X. Kou et al. [38).

ABA can find application in vegetable growing. It was shown that exogenous ABA treatment of red and green leaf lettuce significantly reduced yield, but induced the accumulation of chlorophyll b and an increase in the content of total carotenoids in the leaves, while the content of phenols and anthocyanins in red leaf lettuce significantly increased [39]. Exogenous ABA treatment increased carotenoid accumulation in tomatoes [40].

Salicylic acid. Salicylic acid (SA) provides plant resistance to pathogens [41, 42]. During infection, SA synthesis plays a key role in the development of a hypersensitivity reaction, local death of plant cells together with the pathogen [43, 44], as well as the formation of resistance (systemic acquired resistance) in unaffected parts of the plant [45].

The most compelling evidence of the protective role of SA was obtained by analyzing *Arabidopsis thaliana* (L.) Heynh. plants which are unable to accumulate it due to the expression of the bacterial gene *NahG*, which encodes the enzyme salicylate hydroxylase which converts SA into catechol. After infection, these plants could not develop systemic acquired resistance because they did not express PR (pathogenesis-related) genes and were vulnerable to attack by the pathogen. Treatment with a synthetic analogue of SA restored plant resistance and expression of PR genes [46, 47].

The main molecules through which the SA signal is transmitted are the NPR1 and NPR3/NPR4 proteins (non-expressor of PR proteins) and the SABP group of proteins (salicylic acid-binding proteins) [48]. Signal transmission into the nucleus occurs through NPR proteins which, after the action of SA, enter the nucleus and activate the expression of a large group of genes encoding PR proteins, among which are genes encoding chitinases (PR-3) and β-1,3-glucanases (PR-2), proteinase inhibitors (PR-6), cysteine-rich proteins, similar thaumatin (PR-5), as well as a group of proteins grouped in the PR-1 family, which inhibit fungal growth in an in vitro system [49]. The role of other SA-regulated proteins is not yet entirely clear, but their expression is associated with increased resistance to a large number of bacterial, fungal and viral infections. It should be noted that while NPR1 positively regulates the expression of PR genes, NPR3 and NPR4 (paralogues of NPR1) function more as transcriptional repressors of salicylate-activated genes at low SA content in the cell [50]. SABP proteins do not transmit a signal to the nucleus, but change their activity upon SA binding. Among the SABP proteins, in particular, catalases (SABP1, CAT2) and phosphatase 2A are distinguished, which negatively regulate the PIN2 protein associated with auxin transport [51, 52].

Treatment with salicylates is often used to make plants resistant to various infections [53]. For example, treatment with SA increased resistance to *Fusarium oxysporum* [54] and yellow leaf curl virus [55] in tomatoes, to *Magnaporthe grisea* and *Xanthomonas oryzae* [56, 57] in rice, and to *Xanthomonas axonopodis* [58] in citrus plants. However, it should be taken into account that SA has an antagonistic relationship with jasmonates and often inhibits jasmonate-regulated responses to necrotrophic pathogens [59-61]. Thus, exogenous treatment with SA suppresses plant resistance to necrotrophic infections for which jasmonates are responsible. SA is important for the resistance to *Botrytis cinerea*. S. Ferrari et al. [62] showed that, along with ethylene and FA, the activity of SA signaling pathways is required for the formation of local resistance to *B. cinerea* in *Arabidopsis*. Treatment of tomatoes with SA resulted in the accumulation of reactive oxygen species in tissues and increased resistance to pathogens of the genus *Botrytis* [63].

SA may be involved in the formation of plant resistance to abiotic stresses. Treatment with SA contributed to an increase in the resistance of tomatoes to salt stress [64, 65] and frost resistance of wheat [66]. There are known examples of the participation of SA in the regulation of plant growth and development [67] and in the process of microbiome formation in the root zone [68].

One of the effects associated with the use of SA is inhibition of plant growth. Like other protective hormones, SA regulates the distribution of resources between processes that ensure plant growth and protection. Exogenous SA can have different effects on plant growth depending on the dose, duration of treatment, species, and stage of plant development [67]. If the use of small doses stimulates seed germination, then in high concentrations SA almost always has a negative effect. For example, treatment with a 1 mM SA solution significantly inhibited the growth and development of Arabidopsis seedlings [69]. Disruption in SA hydroxylation resulted in a pronounced dwarf phenotype in *A. thaliana* [48, 70, 71].

A special physiological effect of SA was discovered when studying thermogenesis in aroids. During flowering of *Sauromatum guttatum* (Wall.) Schott, two periods of thermogenesis are noted (increase in temperature in the flower by 10-12 °C), and shortly before this there is an almost 100-fold increase in the endogenous content of SA [72]. Exogenous treatment with SA or its analogues is capable of stimulating thermogenesis, while only two substances (aspirin and 2,6-dihydrobenzoic acid) which are most similar to SA, increased the temperature in flowers, while other analyzed SA analogues (31 compounds) did not have such an effect possessed. The observed increase in temperature is associated with activation of mitochondrial alternative oxidase [73].

In the 1970s, it was suggested that SA might be a flowering inducer because exogenous treatments stimulated flowering in both short- and long-day plants [74]. The participation of SA in the regulation of flowering is confirmed by the following facts: mutant Arabidopsis plants with SA deficiency and transgenic *NahG* forms expressing the salicylate hydroxylase gene are significantly delayed in flowering under short-day conditions [75]; SA synthesis and accumulation are required for the transition to far-ultraviolet (UV-C, wavelength 200-290 nm)-activated flowering [75]; plants accumulating SA are characterized by an early flowering phenotype [48, 76].

There is evidence of the involvement of SA in the regulation of the aging process of plants. Thus, during *Arabidopsis* aging, the amount of SC in tissues increased. In addition, in plants with reduced SA content (*npr1* mutant and plants overexpressing *NahG*), and the number of transcripts of a number of genes associated with aging decreased [77].

SA treatment can improve crop yields. For example, treatment of tomato leaves with SA solution (> 0.125 mM) for 2 weeks increased yield (number and size of fruits) and improved consumer qualities (increased density of fruit pulp, increased content of phenols, lycopene and vitamin C) [78]. An effective way to increase stress resistance of agricultural crops is treatment with SA at the stage of seeds and early seedlings. Soaking tomato and bean seeds in SA solution or watering the soil during sowing increased the survival of seedlings under drought conditions and during high and low temperature stress [79]. Pretreatment of lupine seedlings with SA increased plant resistance to high temperatures [80]. Treatment of leaves of adult tomato plants with SA stimulated growth under salinity conditions, increased root mass, proline content and soluble carbohydrates in leaves, significantly increasing salt tolerance [81]. Salicylic acid helps keep cut flowers fresh [82].

Jasmonates. Modern scientific literature has accumulated a significant amount of experimental data on the physiological effects caused by endogenously produced and exogenously applied jasmonates to plants [83-86]. In higher plants, jasmonates are represented by 12-oxo-phytodienoic acid (12-OPDA), jasmonic acid (JA) and its derivatives, including methyl jasmonate (MeJA) and a conjugate of jasmonate with isoleucine which is responsible for the regulation of most jasmonate-dependent processes. It was found that 12-OPDC which serves as the final product of the plastid stage of biosynthesis, FA and its derivatives exhibit biological activity, while their functions overlap only partially [87, 88). The question of the functional specificity of certain jasmonates is of particular interest. Thus, there are known genes whose expression is regulated by 12-OPDK, but not by FA or MeFA, and the 12-OPDK signal can be transmitted through components of the FA signaling pathway or through other signaling pathways [89-92].

The regulatory effects of jasmonates are varied, but primarily the functions of jasmonates are associated with the regulation of mechanisms that determine plant resistance to necrotrophic pathogens and insects, including root pests [93, 94]. Plants lacking jasmonates are very sensitive to the action of these biotic environmental factors. Extensive evidence suggests a role for these substances in regulating resistance to biotrophic pathogens [95]. In response to mechanical damage and disruption of tissue integrity, jasmonates activate a complex of responses, the so-called wound responses, associated with changes in the expression of many genes [96, 97]. The protective responses induced by jasmonates include the biosynthesis of secondary metabolites, toxic compounds, as well as substances or enzymes that reduce the nutritional value of plant tissues, such as inhibitors of proteinases, deaminases and polyphenol oxidases [98-101]. An important aspect of FA participation in plant defense responses to insect attacks is the regulation of circadian genes, which allows synchronizing the rhythms of defense processes with insect behavior [102]. In response to the presence of pathogens, it is with the participation of jasmonates that the biosynthesis of protective secondary metabolites with antimicrobial and antioxidant properties (phytoalexins, phenylpropanoids, terpenoids, polyamines, and alkaloids) is initiated [103]. Jasmonates regulate the accumulation of free amino acids, which have protective properties (104). There is evidence that these hormones have a direct effect on the pathogens themselves [93]. Jasmonates help the plant fight competitors. For example, MeFA activates the biosynthesis of sorghum, a compound with pronounced herbicidal activity, in sorghum roots [105].

Jasmonates are involved in the regulation of indirect defense responses associated with the release of volatile compounds that can attract natural enemies that attack insects [106-108]. The response of plants to insect pest attacks depends largely on the type of the damage, the insect feeding, and the type of pest mouthparts [103, 109, 110]. Volatile compounds released may also serve as an alarm signal to neighboring plants, allowing coordination of defense responses at the population level [111, 112].

Regulation of adaptive responses under conditions of biotic stress occurs as a result of the coordinated action of jasmonates and other phytohormones, including salicylic acid, ethylene, and ABA.

The role of jasmonates in regulating plant adaptation to abiotic stresses is also well known [113-118]. Jasmonates control resistance to low temperature and salt stress, flooding, drought, ozone, heavy metals and ultraviolet radiation. They serve as the main regulators of the most important signaling pathway that controls plant frost resistance — (ICE)-C-repeat Binding Factor/DRE Binding factor1 (CBF/DREB1) [119]. Data on the role of jasmonates in the formation of plant resistance to elevated temperatures are very contradictory. Most likely, jasmonates play a negative role under high temperature conditions, and increased catabolism of active forms of jasmonates under these conditions is an important adaptive mechanism [120]. The importance of FA and MeFA in plant protection under drought conditions has been demonstrated for many crops [117, 118, 121, 122]. The participation of 12-OPDC in the formation of drought resistance in *Arabidopsis* plants was also determined [121, 124]. Numerous studies indicate the protective effects of jasmonates under salinity conditions [116, 117, 125, 126]. Coronatine, a phytotoxin from *Pseudomonas syringae* (a functional analogue of jasmonates), significantly increases the resistance of maize to water deficiency and osmotic stress caused by polyethylene glycol by stimulating the formation of ROS and activating the antioxidant system [127].

The signaling and protective functions of jasmonates under biotic and abiotic stress conditions are in many cases associated with both oxidative stress and the antioxidant system [128]. Jasmonates regulate the formation of ROS, primarily $O_2^{\bullet-}$ (superoxide anion radical) and $HO^{\bullet}$ (hydroxyl radical). At the same time, treatment with jasmonates stimulates the activity of antioxidant enzymes [129].

In addition to adaptive processes under stress conditions, jasmonates regulate plant growth, development [95, 130-132] and flower formation [133], control fertility [87, 134] and flowering time [135], influence photosynthesis [136 and seed germination [137]. They inhibit root and shoot growth [96], but very low concentrations of these phytohormones can enhance stem growth, as it has been shown in grapes and morning glory (*Pharbitis nil*) [138, 139].

The high biological activity of jasmonates certainly determines the significant potential for their use in agriculture [140]. Not only jasmonates are used, but also their functional analogues, such as coronatine [83] and prohydrojasmone [141]. MeFA can be used as a volatile compound in closed containers/rooms, as well as in aerosols, in the form of diluted solutions. There are examples of the use of jasmonates to regulate flowering time, slow down plant growth, change their morphology, accumulate secondary metabolites and, of course, protect against insects and pathogens [140, 142]. Stimulation of the formation of storage organs, tubers, and bulbs has been demonstrated in many crops, including potatoes, *Dioscorea polystachya*, and orchids [143-146]. Exogenous treatment with jasmonate has been shown to inhibit unwanted sprouting of potato tubers and also prevent color change during processing or cooking [147]. Recent studies indicate that jasmonates regulate the distribution of metabolic and energy resources between processes leading to growth and biomass accumulation and processes associated with the synthesis of protective metabolites [148]. That is, by influencing the activity of the jasmonate system, it is possible to control central metabolism, stability, and, consequently, plant productivity and crop quality. It is important that the effects of growth suppression are short-lived. This means that correct short-term use of these hormones should not affect plant growth and productivity, making their widespread use possible in practice [149].

Jasmonates can be used in fields to protect plants from abiotic and biotic stress factors during growth, crop ripening and after harvest without additional use of chemicals. In addition, jasmonates can improve the quality and phytochemical composition of food crops, make fruits more vibrant, aromatic, sweet, tasty, resistant to cracking, accelerate their ripening and increase their content of secondary metabolites (especially phenolic compounds), antioxidants and vitamins [93, 141, 150-152], slow down the deterioration and softening of tissues of berries and fruits [153-155], increase the ability to trap free radicals [153, 154], preserve the bright color of cut flowers [156]. Unlike many chemicals used in crop production, jasmonates are considered completely safe compounds, and there are no restrictions on their use as plant growth regulators [150].

Effects from treating various crops with jasmonates, salicylates and abscisic acid

Crop	Concentration	Stage of ontogenesis/organs	Effects	References
		Abscisic acid		
Triticum aestivum L., *Oryza sativa* L., *Sorghum bicolor* (L.) Moench, *Zea mays* L.	1 μM-1 mM	Seeds, seed germination, flowering	Regulation of growth and metabolic processes; stimulation of antioxidant protection, biosynthesis of stress proteins and secondary metabolites; increasing stress resistance and productivity	[9]
Glycine max (L.) Merr.	300 mg/l	7 leaves	Improving the distribution of metabolic flows; an increase in the dry mass of the above-ground parts, root density, leaf area, number of seeds in the bean and oil concentration, but not protein in the seeds; increase in soybean yield	[25]
Helianthus annuus L.	0.5-10 μM	Budding (preferred), flowering	Mitigation of the negative consequences of stress; increase in leaf area, basket diameter, number of achenes per basket, yield, weight of 1000 achenes, oil yield. Under sufficient moisture, negative effects occure	[26, 27]
Malus domestica Borkh.	20% ProTone™ (Valent BioSciences, USA)	Crown	Fall of leaves (without affecting the shoots of axillary buds)	[28]
Prunus avium (L.) L.	400 mg/l	Crown, fruits	Enhanced coloration of drupes	[30]
Citrus × *paradise* Macfad, *Citrus reticulate* Blanco	500 μM and 1 mM (crown), 1 nM-1 mM (roots)	Crown, roots (no effect)	Increased cold resistance; improving the color of fruits and reducing the content of organic acids in them	[31, 32]
Vitis vinifera L.	300 and 500 mg/l, 10 or 20% ProTone™ (Valent BioSciences, USA) at 200-400 g/ha	Vines, leaves only or bunches only	Acceleration of the beginning of berry ripening and increased color intensity; a decrease in the weight of berries with an increase in the dry weight of the skin; increased content of sugar, phenols, anthocyanins; decrease in transpiration rate	[33, 37, 157]
Lactuca sativa L.	150 and 300 μM	Leaves	Decrease in yield; an increase in the content of phenolic compounds and anthocyanins in red leaf lettuce, but not in green; inducing the accumulation of chlorophyll b and total carotenoids	[39]

Continued Table

Solanum lycopersicum L.	500 mg/l (foliar treatment) and 50 mg/l (root treatment)	Leaves, roots	Foliar application increases the content of carotenoids and chlorophylls in leaves and fruits, and root application reduces it; foliar and root treatment increases the sugar content in fruits and reduces the content of organic acids in them	[40]
Zea mays L.	25% BioNik™ (Valent BioSciences, USA)	Seeds	Delay in germination of male inbred lines to synchronize the pollination period with female flowers	[157]
		Salicylates		
Solanum lycopersicum L.	0.2 mM	Root feeding and leaf treatment	Resistance to *Fusarium oxysporum*	[54]
Solanum lycopersicum L.	2 mM	Spraying leaves	Resistance to tomato yellow leaf curl virus	[55]
Oryza sativa L.	0.05-8 mM	In a hydroponic solution and spraying leaves	Resistance to *Magnaporthe grisea* and *Xanthomonas oryzae*	[56, 57]
Solanum lycopersicum L.	0.1 μM and 0.1 mM	In nutritional solution	Salt stress tolerance	[64]
Triticum aestivum L.	10-1000 μM (100 μM is optimal concentration)	Leaves	Increased frost resistance	[66]
Solanum lycopersicum L.	0,.025 mM-0.125 mM	Leaves	Increased yield (number of fruits and their size) and consumer qualities (increased density, increased content of phenols, lycopene and vitamin C)	[78]
Phaseolus vulgaris L., *Lycopersicon esculentum* L.	0.1-0.5 mM	Seeds	Increased survival under drought, high and low temperature stress	[79]
Lupinus angustifolius L.	0.5 mM	Sprouts	Resistance to elevated temperatures	[80]
Solanum lycopersicum L.	100 mg/l	Roots and leaves	Stimulation of plant growth under salinity conditions	[81]
Rosa hybrida E.H.L. Krause, *Lilium asiaticum*, *Gerbera jamesonii* Bolus ex Hooker f.	100-300 mg/l	Cut flowers in a vase	Cut flowers stay fresh longer	[82]
		Jasmonic acid and jasmonates		
Garden and vegetable crops, cereals, legumes	Jasmonates, 10^{-7}-10^{-3} M	Various	Formation of storage organs, degradation of chlorophyll and leaf fall, reduction of transpiration, synthesis of secondary metabolites, protection from pests and pathogens	[93]
Microlaena stipoides (Labill.) R.Br.	MeJA, 10 μg/ml	Leaves	Protection from the root pest *Dermolepida albohirtum*	[94]
Larix olgensis A. Henry	Cis-jasmone, MeJA, JA, 0.01-1 mM	Sprouts	Induction of defense mechanisms due to the accumulation of free amino acids	[104]
Sorghum bicolor L.	MeJA, 0.5-500 μM	Seed soaking and sprout treatment	Biosynthesis of the natural herbicide sorgaleon	[105]
Oryza sativa L.	JA, 30 μM	Hydroponics	Increased salt tolerance	[126]
Zea mays L.	Coronatine, 0.0001-0.1 μM	Immerse the stems in the solution for 12 hours	Increased resistance to drought and osmotic stress	[127]
Solanum tuberosum L.	MeJA, JA, 0.1-0 μM	Stem segments	Stimulation of tuber formation	[144]
Solanum tuberosum L.	MeJA, 0,001 mM-0.1 mM	Potato tubers	Suppression of tuber germination and darkening	[147]
Prunus mume Sieb.	Prohydrojasmone, 0.4 mM	Fruit dipping in the solution	Increased aroma and resistance to *Colletotrichum gloeosporioides*	[152]
Malus domestica Borkh, *Vitis vinifera* L.	Prohydrojasmone, ~ 1 l/ha	Treating fruits on the plant	Enhance color, synthesis of anthocyanins, increase resistance to low temperatures, protection from pests	[158]

Note. MeJA — methyl jasmonate, JA — jasmonic acid.

The phytohormones that regulate plant stress responses can be a promising alternative to modern plant protection products used in agriculture. The table shows examples of treating various plants with phytohormones and a description of the effects caused by the treatment.

Thus, the modern literature provides a significant amount of information on the effects of abscisic acid, jasmonates and salicylates on various crops, but most of the data is based on the results of lab tests, and there is an obvious lack of information on the physiological effects caused by these substances in field conditions. The widespread use of these compounds is largely limited by the possibility of their production, since the production of some phytohormones and their functional analogues on an industrial scale still remains a difficult task. If the cost of producing drugs based on salicylates is economically feasible, then the production of jasmonates, and especially abscisic acid, requires the use of expensive processes. Chemical stability of such compounds is an important aspect. It should be remembered that plant hormones are low-molecular substances (≤ 500 Da), except for polypeptide hormones, which serve as derivatives of basic biochemical compounds of plants, namely amino acids, carotenoids, terpenoids, phytosterols and fatty acids. Therefore, the most promising way to produce phytohormones seems to be the reconstruction of biosynthetic pathways in a living cell and the creation of bioproducers. Most likely, it is the successful development of biotechnologies with the use of bioproducers that will determine the scale of production and introduction of new drugs based on plant hormones in agriculture in the near future.

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