

GIBBERELLINS IN REGULATION OF PLANT GROWTH AND DEVELOPMENT UNDER ABIOTIC STRESSES

I. V. KOSAKIVSKA, V. A. VASYUK

Kholodny Institute of Botany of the National Academy of Sciences of Ukraine, Kyiv

E-mail: irynakosakivska@gmail.com, vasyuk@ukr.net

Received 29.01.2021

Revised 08.02.2021

Accepted 30.04.2021

Background. Gibberellins (GAs), a class of diterpenoid phytohormones, play an important role in regulation of plant growth and development. Among more than 130 different gibberellin isoforms, only a few are bioactive. GA₁, GA₃, GA₄, and GA₇ regulate plant growth through promotion the degradation of the DELLA proteins, a family of nuclear growth repressors — negative regulator of GAs signaling. Recent studies on GAs biosynthesis, metabolism, transport, and signaling, as well as crosstalk with other phytohormones and environment have achieved great progress thanks to molecular genetics and functional genomics.

Aim. In this review, we focused on the role of GAs in regulation of plant growth in abiotic stress conditions.

Results. We represented a key information on GAs biosynthesis, signaling and functional activity; summarized current understanding of the crosstalk between GAs and auxin, cytokinin, abscisic acid and other hormones and what is the role of GAs in regulation of adaptation to drought, salinization, high and low temperature conditions, and heavy metal pollution. We emphasize that the effects of GAs depend primarily on the strength and duration of stress and the phase of ontogenesis and tolerance of the plant. By changing the intensity of biosynthesis, the pattern of the distribution and signaling of GAs, plants are able to regulate resistance to abiotic stress, increase viability and even avoid stress. The issues of using retardants — inhibitors of GAs biosynthesis to study the functional activity of hormones under abiotic stresses were discussed. Special attention was focused on the use of exogenous GAs for pre-sowing priming of seeds and foliar treatment of plants.

Conclusion. Further study of the role of gibberellins in the acquisition of stress resistance would contribute to the development of biotechnology of exogenous use of the hormone to improve growth and increase plant yields under adverse environmental conditions.

Key words: gibberellins, DELLA, phytohormones, abiotic stresses, retardants, growth, stress resistance.

Plant growth and development are regulated and coordinated by the interaction of phytohormones — low molecular weight compounds that act directly or remotely from the site of their synthesis, and mediate genetically programmed developmental changes and respond to environmental challenges [1]. GAs form the most numerous class of plant hormones and number more than 130 isoforms, but physiological activity is typical only of certain gibberellic acids (GA₁, GA₃, GA₄, GA₅, GA₆ and GA₇), while others belong to their precursors and inactive

forms [2]. GAs regulate plant growth and development by affecting the degradation of DELLA (aspartic acid-glutamic acid-leucine-leucine-alanine) proteins, a family of transcriptional repressors that inhibit cell proliferation and elongation [3]. GAs content reduction resulting from stressors effects limits growth, while enhanced hormone biosynthesis prevents possible damage to plants [4]. Regulation of endogenous GAs levels and the use of their synthesis inhibitors are among the main strategies for the formation of stress resistance of crops. Because one of the key

functions of GAs is to determine plant height, they are a major target for stress-induced growth modulation. It is important that the expression of genes encoding the synthesis of enzymes that catalyze the main stages of GAs synthesis, such as soluble GA2-oxidases, is normally regulated by environmental signals, making endogenous GAs extremely sensitive to environmental changes [4].

Biosynthesis and Signalling

GAs biosynthesis (Fig. 1) consists of three stages that occur in plastids, endomembranes and cytosol. GAs are synthesized from *trans*-geranylgeranyl diphosphate through methyl erythritol phosphate pathway due to the sequential action of two plastid terpene cyclases with subsequent oxidation on the endoplasmic reticulum by cytochrome P450 monooxygenases and subsequent dissolution by 2-oxoglutarate-dependent dioxygenases GA20ox and GA3ox. Under the action of abiotic stresses, GA2ox are activated, which inhibit the synthesis of GAs [4].

Since the biosynthesis of active GAs is a complex multistage process involving the formation of various intermediates [5, 6], it is quite difficult to accurately identify tissues or organs, in which the hormone is synthesized or localized. Genes involved in the biosynthesis of GAs are localized in different cells and tissues

and their activity depends on the stage of ontogenesis. The maxima of local accumulation of GAs correspond to the active growth of root and hypocotyl cells and flower formation. Long-distance transportation is mainly limited to inactive GAs precursors [7]. Genetic studies have identified components of gibberellin signaling [5, 8]. DELLA proteins, which form one of the subfamilies of GRAS transcription factors, have been universal participants in signaling pathways that coordinate plant growth and development [9]. The involvement of DELLA proteins in the formation of the responses of plants to external influences has been established [3, 4]. Five DELLA proteins (RGA, GAI, RGA-LIKE1 (RGL1), RGL2, and RGL3) have been identified for *Arabidopsis thaliana* plants that inhibit GAs activity [10]. At the N-terminal of DELLA proteins is a conservative amino acid sequence for all higher plants — DELLA domain. It is responsible for binding to activated gibberellin receptors (GA INSENSITIVE DWARF1, GID1). DELLA proteins serve as negative regulators of genes whose expression is activated by GAs [3, 4, 11]. It has been found that increasing the content of GAs and their binding to the GID1 receptor causes degradation of DELLA proteins, inhibits their action and releases the GID1 receptor, which interacts with other DELLA protein molecules [12]. DELLA proteins are involved in maintaining gibberellin homeostasis through

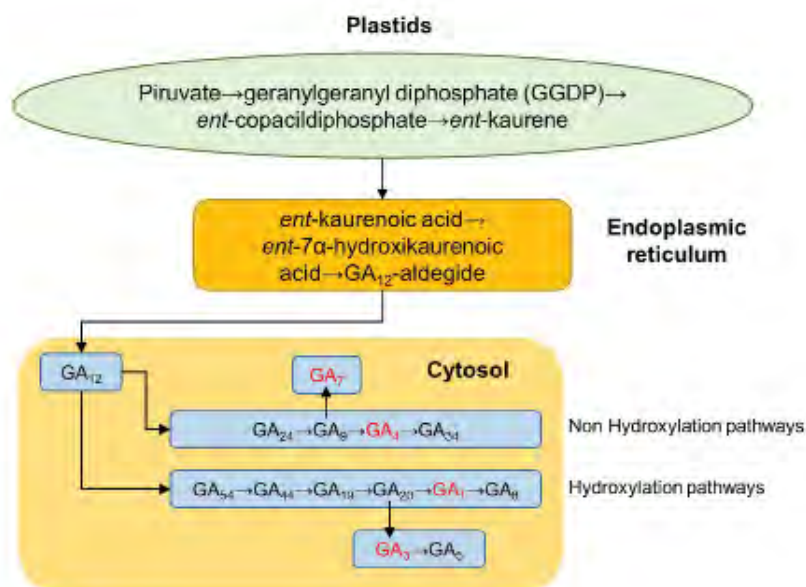


Fig. 1. Scheme of gibberellins synthesis:

ent-kaurene, the universal precursor of GA, is formed in plastids, and GA₁₂-aldehyde is formed in the endoplasmic reticulum. The synthesis branches into the Non Hydroxylation and Hydroxylation pathways in cytosol. Precursors and inactive forms of GAs, which have weak physiological activity, and active forms (highlighted in red) are synthesized. Arrows indicate the different stages of synthesis, which are catalyzed by individual enzymes

inhibition the expression of GA deactivation genes. Thus, in *della* mutants, the expression level of genes responsible for the synthesis of GAs was significantly lower [13]. The DELLA protein antagonist SCARECROW-LIKE 3 protein (SCL3) is activated under shading and flooding conditions that lead to the accumulation of GAs and elongation of the stem. *SCL3* expression is induced by DELLA and repressed by GAs. *SCL3* regulates its own transcription by interacting directly with DELLA [14].

Therefore, DELLA proteins are the main negative regulators of gibberellin signaling. They interact with transcription factors and modulate gene expression, which allows us concluding about their involvement in the cross-system interaction between GAs and the environment.

Functional activity

The main functions of gibberellins are the regulation of seed germination, and seeds' embryogenesis, coordination of cell division and elongation, sex determination, pollen and flower development, flowering induction, seed and fruit formation [15,16, 17]. GAs activate the so-called «initial effects» of germination of cereal grains: they stimulate the linear growth of organs and leaf surface. The effects of GAs on embryo growth are due to the induction of hydrolytic enzymes, which are involved in starch conversion, protein and lipid cleavage, and seed coat softening by GA20-oxidase and GA3-oxidase gene expression [18]. These genes are expressed in the epithelium of the embryo during germination and induce the synthesis of active GAs [19]. GAs are transported to the aleurone layer, where they express the α -amylase gene through the transcription factors SLN1 and GAMYB [20], while DELLA SLN1 inhibits the activity of GAs [21]. GAs play an important role in cell elongation and internode elongation [22]. Thus, during the elongation of rice internodes (*Oryza sativa* L.), the expression of genes encoding xyloglucan endotransglucosylase synthesis was regulated by gibberellins. This enzyme is involved in the reorganization of xyloglucan by cleaving and re-ligation of polymers, thereby increasing the plasticity of the cell wall [23]. Localized in the intercalary meristem of the root and hypocotyl GAs regulate the activity of genes of cyclin-dependent protein kinases — key enzymes of the cell cycle [24]. The accumulation of active GAs occurs in the area of elongation of the root and hypocotyl and corresponds to the

maximum cell growth. Thus, the synthesis of the protein NTH15, which is located in the apical meristem of the tobacco shoot, led to the negative regulation of the GA20 oxidase gene, GAs hypersynthesis, enhanced cell division [25]. GAs have a positive effect on root growth. The early transition from root cell division to elongation, mediated by HDT1/2 (histone deacetylase), occurs due to inhibition of *GA2ox2* gene transcription [26]. Studies of mutant and transgenic Arabidopsis plants indicate that GAs and their signaling pathway are necessary and sufficient to directly stimulate enhanced xylogeny in the hypocotyl [27]. The synthesis of GAs in flowers occurs only in the stamens and is regulated by GA20ox and GA3ox. Moving active GAs (but not their precursors) short distances from the stamen to other flower organs and peduncles is important and sufficient for flower development. GAs also stimulate flowering and cause fruit set and initiate their growth [16].

Endogenous GAs under stress

Under stress plants are known to have changes in the balance of endogenous hormones that affect growth processes and promote adaptation. Thus, mutant lines with low GAs content showed salt and drought resistance due to reduced biosynthesis or increased hormone degradation [28]. Dwarf varieties of rice and barley (*Hordeum vulgare* L.) with low levels of GAs were stress resistant. GAs levels manipulation led to increased grain yield, branching of the root system and enhanced drought resistance and resistance to negative biotic factors [29, 30]. Maize leaves (*Zea mays* L.) and bean shoots (*Phaseolus vulgaris* L.) significantly decreased GA₃ content during drought [28, 31]. In the early stages of pouring rice grains under drought, there was a reduction in the level of endogenous GAs [32]. Drought-affected roots of wild emmer wheat (*Triticum turgidum* ssp. *Dicoccoides*) exhibited some increase in the content of GAs, higher root growth and inhibited shoot growth [33].

The expression of genes encoding enzymes involved in the biosynthesis of GAs is regulated by external signals. Thus, under the influence of negative factors, the synthesis of GAs is inhibited due to the expression of *GA2ox* genes, which encode GA2-inactivating enzymes, as well as the *DELLA RGL3* gene, which encodes a gibberellin suppressor. The genes *SD1*, *GDD1*, *SLR1*, *EUI*, *GID1*, *SD1* and *D1* involved in the synthesis and signaling

of GAs regulate the growth and development of rice plant organs and their architecture, yield and stress response [4, 34].

Under salinization conditions, the content and signaling of GAs decreased that led to delayed growth and development of wheat plants (*Triticum aestivum* L.) [35, 36]. Excessive expression of *DWARF AND DELAYED FLOWERING 1 (DDF1)* activated the *GA2ox7* promoter and the accumulation of DELLA proteins, which resulted in a rapid decline in the level of endogenous GAs in Arabidopsis plants and inhibition of their growth and facilitated adaptation [37]. Salt stress inhibited the activity of GAs, which caused a delay in the germination of soybean seeds (*Glycine max* L. Merr.) [38].

Heat stress caused morphological and physiological changes in rice plants and reduced their yield due to a decrease in GA_1 content in inflorescences [39]. At the same time, hyperthermia caused a higher level of endogenous GA_3 in wheat plants during the early development of the kernels, which resulted in less kernel number and lower grain-filling rate [40]. It was found that the activity of GA20-oxidase genes (*GA20ox1*, *GA20ox2*, *GA20ox3*) and GA3-oxidase genes (*GA3ox1*, *GA3ox2*), which regulate the late stages of GAs biosynthesis, was inhibited under heat stress [41]. However, information on the effects of high temperature on the early stages of GAs biosynthesis and hormone catabolism is scarce and needs further study [39].

Cold stress reduced the levels of endogenous GA_4 and GA_7 in rice anthers and did not affect the content of their precursor GA_{12} that was due to decrease in *GA20ox3* and *GA3ox1* expression [42]. The low level of GAs in coldsensitive rice genotypes was found to be due to the repression of hormone biosynthesis genes, rather than the catabolism of active GA_4 and GA_7 [43]. At low temperature, wheat leaves inhibited growth and accumulated active GAs that stimulated cell elongation. Under these conditions, the threshold of sensitivity to the action of GAs raised [44]. The recessive dwarf mutant of rice *gid1* (*gibberellin insensitive dwarf1*) was shown to be resistant to low temperatures and fungal diseases [45].

Soil contamination with aluminum inhibited the germination of rice seeds and reduced GAs, while exogenous hydrogen (H_2) reduced metal toxicity by increasing the GA/ABA ratio. Further detailed analysis indicated that H_2 promoted the expression of GAs *GA20ox1* and *GA20ox2* biosynthesis genes and ABA catabolism genes *ABA8ox1* and *ABA8ox2*

[46]. High concentrations of zinc induced an increase in GA_3 , isopentenyladenosine and salicylic acid and a decrease in levels of indole-3-acetic acid (IAA), zeatin and ABA in winter wheat seedlings [47].

The main attention in studying the role of GAs in the formation of responses to adverse environmental conditions is focused on the metabolism, signaling and mechanisms of interaction with other phytohormones [4, 48]. Interhormonal signaling plays an important role in the formation of the response to stress (Fig. 2). The adaptive changes that occur in stressor-affected plants depend on the character of the cross-talk (synergistic or antagonistic) of hormonal signaling [49]. The interaction of the gibberellin repressor DELLA proteins with the main components of the signaling cascades of other hormones has been studied in the most detail [8].

The interaction between GAs and ABA during the regulation of plant growth and development is antagonistic [38, 50, 51]. Thus, GAs activate seed germination, while ABA provides its dormancy. High levels of ABA in mature dry seeds activate transcription factors ABI3 and ABI5, which adversely affect the synthesis of GAs [52]. Under high temperature, the interaction between DELLA proteins, ABI3 and ABI5 occurs, which promotes the expression of high-temperature inducible genes, reduces GAs synthesis and increases ABA levels, and inhibits the germination of arabidopsis seeds [53]. Expression of GAs biosynthesis genes *GA20ox1* and *GA20ox2* and ABA catabolism genes *ABA8ox1* and *ABA8ox2* was observed during rice seeds germination under aluminum pollution [46]. At low temperatures, ABA levels in barley cells became higher and ABA-induced protein kinase (PKABA1) was activated, which reduced GAs activity and delayed germination [54, 55]. The *TaMYB73* gene, which is expressed under salinity and associated with ABA and GAs, was identified in wheat [56]. The relationship between the content of GAs and ABA affects the temporal organization of plant growth. In barley, wheat and maize plants, active GAs were shown to accumulate during early embryogenesis, the concentration of which gradually decreases until maturation with a simultaneous increase in ABA levels [57, 58].

Indole-3-acetic acid (IAA) induces cell elongation, especially in shoots, and causes apical dominance and root development, whereas GAs regulate stem, leaf, and other aboveground organ growth, causing cell

elongation and internode length to increase [59]. Activation of DELLA proteins under stress conditions prevents the production of IAA, which provides control over fruit ripening [60]. Heat stress inhibited the accumulation of GA₁ in rice inflorescences, also decreased the content of active cytokinins and IAA and increased ABA levels, which caused yield reduction [39].

GAs inhibit the effects of cytokinins during plant growth, from germination to aging. Cytokinins act in the initial stages of development, control the growth of the meristem, and GAs in the later ones, regulating the division and stretching of shoot cells. SPINDLY (SPY) protein is involved in the interaction between cytokinins and GAs, which through DELLA proteins enhances the effects of cytokinins and inhibits gibberellin signaling. SPY plays a key role in the regulation of crosstalk between cytokinins and GAs, acts as a repressor of the effects of GAs and a positive regulator of cytokinin signaling under stress conditions [61]. Rice plants with the enzyme OsCYP71D8L from the CYP450 family maintained a high content of chlorophyll and low levels of reactive oxygen species (ROS) had increased resistance to drought and salt stress. The enzyme was found to coordinate the homeostasis of GAs and

cytokinins, regulate root development, and control multiple agronomic traits of plants and their responses to abiotic stress [62]. Jasmonic acid (JA) is considered the main signal molecule that regulates plant growth and resistance to abiotic stresses and pathogens. JASMONATE ZIM DOMAIN PROTEIN (JAZ) and MYC2 transcriptional activator, which regulate the balance between growth and plant defence, were identified as key components of crosstalk [63].

Thus, the interaction of phytohormones enables to integrate different signals of stressors, as a result of which plants respond to them properly. Coordination of growth and stress responses essential for signals for each hormone and their ability to cross-talk at different levels of signaling. Plants can control the action of the hormone by regulating its biosynthesis and localization, as well as by regulating signaling pathways.

Applying of growth retardants as valuable tools to identify the role of GAs in stress resistance

Inhibitors of GAs biosynthesis include retardants — synthetic non-toxic compounds that inhibit shoot growth without changing the patterns of plant development. This is

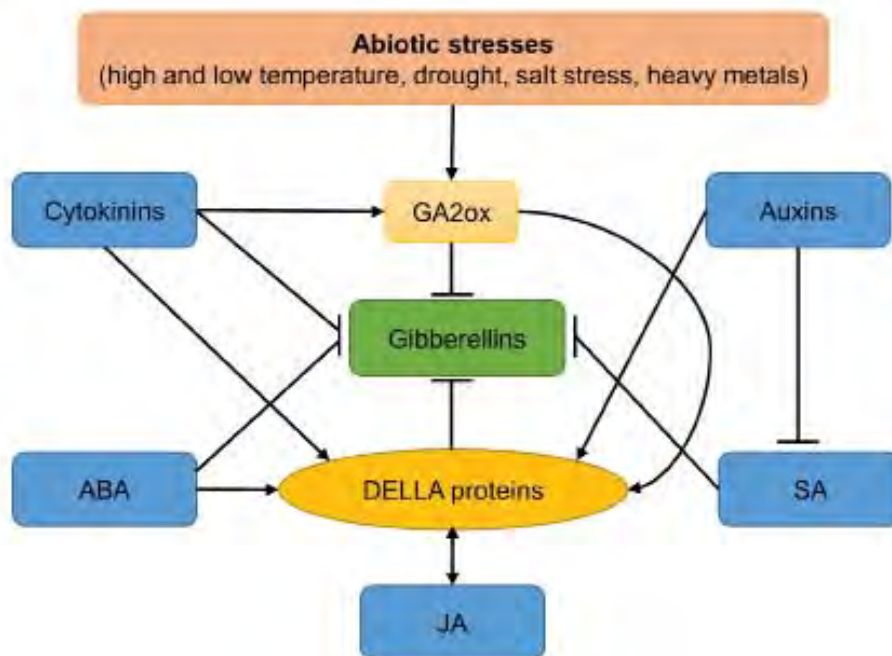


Fig. 2. The crosstalk between gibberellins and other phytohormones regulates plant growth and development under abiotic stresses:

positive interactions are indicated by arrows and T bars indicate repression between GA and individual phytohormones: ABA — abscisic acid, SA — salicylic acid, JA — jasmonic acid, GA2ox — gibberellin 2-oxidase

achieved primarily by delaying the elongation of cells and reducing the rate of their division. The effects of retardants on the morphological structure and plants growth are antagonistic to effects of GAs and auxins. Under the intense prolonged stress GAs do not have a stress-protective effect, and such one is manifested by their antagonists — retardants. Inhibitors of gibberellin synthesis increased drought resistance and plant yield, stimulated biomass accumulation. Retardants form the most commercially important group of plant bioregulators, although compared to herbicides, insecticides and fungicides, they play a relatively small role and account for only a few percent of the world's crop protection chemicals [64]. Chemicals with anti-GAs activity are able to inhibit and even remove apical dominance, which leads to the development of more leaves, flowers and fruits, increased yields. The excess of assimilates, which accumulates due to the slowing down of growth processes, is directed to the organs and tissues that are formed and actively developing. The height of plant is a key agronomic feature, which determines the plants architecture and yield, response to stress and is controlled by integrated phytohormone signaling networks [34]. Inhibitors of GAs biosynthesis have been shown to reduce the size of barley plants and increase their resistance to high temperatures [65]. The use of paclobutrazol (PBZ) has led to the emergence of dwarf forms of wheat, but has not always been accompanied by drought resistance [66]; in barley, promoted the transformation of GA₂₀ into GA₁ and GA₉ into GA₄, which enhanced the stress resistance of plants to high temperatures [29]; in rice, the number of spikelets on the panicle increased and contributed to better grain filling [67]; in teff (*Eragrostis tef* (Zucc.) Trotter) decreased height and increased drought resistance of plants, due to higher chlorophyll content and blocking of the gibberellin pathway [68]; reduced the height of flax plants, accelerated seed maturation and improved fruit yield [69]. The use of GAs and PBZ, as well as their mixtures, affected the growth, content of endogenous phytohormones and productivity of radish (*Raphanus sativus* L.). PBZ inhibited the linear growth of radish plants, enhanced cell proliferation, increased the mass and size of the root crop. Under the action of GAs, the growth of shoots was activated and the roots were inhibited, the weight of the root crop did not change. PBZ significantly reduced the content of endogenous GAs [70]. At the same time, a negative effect of PBZ on teff yield

was reported, the low productivity of which was associated with a 98% reduction in plant height [71].

Uniconazole (UN) under salt stress improved the resistance of barley plants, stimulated the accumulation of ABA and cytokinins and reduced the content of GA₃ and IAA. Under UN action in the grain increased the content of proteins and proline [72]. UN and the ethylene producer ethephon (ETH) inhibited the growth of maize plants, increased dry weight accumulation, and accelerated grain uptake, in which increased ABA, zeatin, and zeatin riboside, and decreased GAs content. The accumulation of ABA and cytokinins was positively correlated with the rate of grain fullness. The use of the GAs inhibitor UN has been shown to be more effective than ethylene-producing ETH [73].

Exogenous GA in the regulation of stress resistance

An alternative strategy to overcome abiotic stresses is the exogenous use of plant growth regulators. GAs induce resistance to mild and moderate stress, but reduce it under the action of strong impact. Exogenous GAs are able to eliminate the inhibitory effect of drought. Thus, treatment with a solution of GA₃ isogenic wheat lines with *Rht-B1a* (high) and *Rht-B1b* (semi-dwarf) alleles initiated root development and restored leaf growth [74]. Foliar treatment of corn with GA₃ solution improved morphophysiological characteristic. Increases in leaf surface index, growth rate and dry weight, cob length and diameter, number and weight of grains, improvement of stability and yield were observed [75]. Priming of rye (*Secale montanum* L.) seeds with GA₃ and SA solutions enhanced the germination index and germination rate coefficient. After treatment with phytohormones, the content of antioxidant enzymes catalase and ascorbate peroxidase increased [76]. Exogenous GA₃ stimulated wheat growth and increased the weight of 1000 grains [77]. Exogenous GAs contributed to the stabilization of cell membranes, the growth of dry weight, the content of nutrients and chlorophyll, the preservation of relative humidity in the leaves of corn [78].

Under conditions of salt stress after pre-sowing priming of wheat seeds with GA₃ in shoots and roots of plants ionic homeostasis was stabilized, the concentration of polyamines and ABA decreased, and the content of endogenous SA has enlarged. The improvement of yield was

due to an increase in the number of productive stems and grain mass in the spike [79]. Also, foliar treatment with GA³ in maize plants contributed to better calcium absorption, higher chlorophyll levels, but decreased superoxide dismutase (SOD), peroxidase (POD) and polyphenol oxidase (PPO) activity and proline content, although these indexes exceeded the corresponding control ones [80]. Pre-sowing primer of wheat seeds with GA₃ виправити на Pre-sowing priming of wheat seeds with GA₃ had a positive effect on germination and subsequent growth in conditions of soil salinity, induced protein synthesis, including the gibberellin receptor of 74.41 kDa [81].

Foliar spraying with GA₃ restored the normal development of rice anthers that was disrupted due to microsporogenesis under moderate low temperatures, which significantly promoted yields [42]. After short-term heat stress (+50 °C) GA₃ treatment of dwarf barley plants resumed normal growth, but the content of photosynthetic pigments decreased [29].

Conclusion. Exogenous GAs are able to improve plant resistance to heavy metals (HMs), which contributes to agroecological benefits under adverse conditions [82, 83]. Exogenous GAs play a crucial role in protecting plants from cadmium stress [84]. In Arabidopsis plants, gibberellin signaling was shown to enhance the activity of the key enzyme of sulfate assimilation — adenosine-5'-phosphosulfate reductase, which enabled to optimize sulfur metabolism under stressful conditions [85]. Pre-sowing primer of wheat seeds with GA₃ and Ca²⁺ softened the inhibitory effect of nickel on the growth of wheat seedlings, stabilized the content of chlorophyll and proline, increased POD, CAT, SOD, ascorbate peroxidase and glutathione reductase activity [86]. Addition of 0.5 μM GA₃ to the nutrient medium of barley and rice reduced the inhibitory effects of cadmium and molybdenum, due to the activation of four hydrolytic enzymes, which resulted in an increase in sugars and amino acids level in the endosperm and partial resumption of mobilization of proteins and starch from the endosperm to the roots [87]. Foliar spraying with GA₃ (200 mg/l) and sulfur enhanced the growth of industrial crops (flax and kenaf) and remediation of the soil. GAs improved the assimilation of Co and Cr by kenaf, and Cd and Mn by flax [88]. Addition of GA₃ (14 μM) together with Cd and Ni to rice culture partially reduced the effect of HMs, stimulated growth, mobilized carbohydrate storage in seeds, increased sugar content in roots and leaves, changed the distribution of carbohydrates.

Unlike GA₃, ABA (19 μM) enhanced the action of HMs, inhibited the growth of young leaves [89].

The effects of priming with GAs depended on hormone concentration, plant species and the conditions of their cultivation. Thus, wheat yield increased significantly after treatment of seeds with 10–100 μM GA₃ [90]. After pre-sowing priming of *Leymus chinensis* seeds with 50 μM of GA₃, germination accelerated by 14–27%, biomass accumulation increased, plant height bushiness increased. The stimulating effect persisted for the second year of vegetation [91]. Gibberellins and inhibitors of their synthesis are widely used in modern agriculture, horticulture and viticulture. Application of exogenous GA₃ was found to increase the eggplant (*Solanum melongena* L.) height, number of leaves per plant, the fresh weight of the stems and roots, as well as the dry weight of the whole plant. The treatment with GA₃ resulted in some increase of the content of endogenous GA₃, IAA and ABA in the stems and especially in the leaves, whereas the pool of cytokinins in the leaves decreased significantly. The inactive isoforms of zeatin-O-glucoside (ZG) and isopentenyladenosine (iPa) dominated in the stems [92]. To increase the yield and quality of agricultural products, mainly exogenous GA₃ is used [64].

Thus, treatment with exogenous plant growth regulators optimizes development, enhances stress resistance and improves plant productivity, through the induction of changes in metabolism, hormonal balance, morphological and physiological transformations (Table).

Gibberellins, which are known to be the most numerous class of plant hormones, were found in all higher plants. They are involved in regulation of growth and development by elongating and dividing cells, activating the germination and maturation of seeds and induction of flowering. The biosynthesis of gibberellins proceeds in three stages in plastids, endomembranes and cytosol. By means of the specific proteins transporter, gibberellins are transported between cells through the plasma membrane. By changing the intensity of biosynthesis, the pattern of the distribution and signaling of these hormones, plants are able to regulate resistance to abiotic stress, increase viability and even avoid stress. The important role of gibberellins in the acquisition of stress resistance has more and more evidence and proof. The effects of GAs depend primarily on the strength and

Exogenous gibberellins application in mitigation of abiotic stresses

Plant	Effect	References
Drought		
<i>Zea mays</i> L.	Increased the leaf surface, dry weight, length and diameter of the cob, the number and weight of grains, improved drought resistance and yield	[75]
<i>Secale montanum</i> L.	Induced seed germination	[76]
<i>Triticum aestivum</i> L.	Induced seed germination, enhanced growth	[89]
<i>Zea mays</i> L.	Increased leaf dry weight, chlorophyll content, relative humidity, stabilized cell membranes.	[78]
<i>Triticum aestivum</i> L.	Increased root growth and restored leaf growth	[74]
<i>Triticum turgidum</i> ssp. <i>dicoccoides</i>	Increased root growth	[33]
Salinization		
<i>Triticum aestivum</i> L.	Stimulated growth and increased grain weight	[77]
<i>Hordeum vulgare</i> L.	Induced protein synthesis, including gibberellin receptor 74.41 kDa	[81]
<i>Triticum aestivum</i> L.	Maintained ionic homeostasis in shoots and roots	[79]
Low temperature		
<i>Zea mays</i> L.	Increased Ca ²⁺ absorption and chlorophyll content, decreased SOD, POD and polyphenol oxidase activity; and proline content	[80]
High temperature		
<i>Oryza sativa</i> L.	Restored normal development of pollen grains	[42]
Heavy metals pollution		
<i>Hordeum vulgare</i> L.	Restored the normal growth of dwarf plants, but decreased photosynthetic pigments content during recovery	[29]
<i>Triticum aestivum</i> L.	Reduced negative effects of toxicity by improving the antioxidant system and proline accumulation	[86]
<i>Arabidopsis thaliana</i> L.	Decreased nitric oxide (NO) levels reduce <i>IRT1</i> expression	[84]
<i>Oryza sativa</i> L.	Increased growth, mobilization of carbohydrate reserves in seeds, increased sugar content in roots and leaves, changed carbohydrate distribution	[89]

duration of stress and the phase of ontogenesis and tolerance of the plant. In the formation of the response to stress, the signaling pathways of gibberellins, ABA, cytokinins, auxins, jasmonic and salicylic acids, which are mainly mediated by DELLA proteins, are crossed. Further study of the role of gibberellins in the acquisition of stress resistance will contribute to the development of biotechnology of exogenous use of the hormone to improve growth and increase plant yields under adverse environmental conditions.

Acknowledgements

The authors are grateful to M. M. Shcherbatiuk, PhD, for the help in the graphical design.

This review was supported by Grant № III-82-17.463 "Plant hormonal regulation of the growth and development of cereal plants under influence of negative climatic factors" from the National Academy of Sciences of Ukraine.

REFERENCES

1. Davies P. J. The plant hormones: their nature, occurrence, and function. *Plant Hormones: Biosynthesis, Signal Transduction, Action*. Davies P. J. (Ed.). Dordrecht: Springer. 2010, P. 1–15. https://doi.org/10.1007/978-1-4020-2686-7_1
2. Sponsel V., Hedden P. Gibberellin Biosynthesis and Inactivation. *Plant Hormones*. Davies P. J. (Ed.). Springer, Dordrecht. 2010, P. 63–94. https://doi.org/10.1007/978-1-4020-2686-7_4
3. Vera-Sirera F., Gomez M. D., Perez-Amador M. A. DELLA proteins, a group of GRAS transcription regulators that mediate gibberellin signaling. *Plant Transcription Factors. Evolutionary, Structural and Functional Aspects*. Gonzalez D. H. (Ed.). Elsevier. 2016, P. 313–328. <https://doi.org/10.1016/B978-0-12-800854-6.00020-8>
4. Colebrook E. H., Thomas S. G., Phillips A. L., Hedden P. The role of gibberellin signalling in plant responses to abiotic stress. *J. Exp. Biol.* 2014, 217 (1), 67–75. <https://doi.org/10.1242/jeb.089938>
5. Hedden P. The Current Status of Research on Gibberellin Biosynthesis. *Plant Cell Physiol.* 2020, 61 (11), 1832–1849. <https://doi.org/10.1093/pcp/pcaa092>
6. Gao X., Zhang Yi., He Z., Fu X. Gibberellins. *Hormone Metabolism and Signaling in Plants*. Li J. (Ed). 2017, P. 107–160. <https://doi.org/10.1016/B978-0-12-811562-6.00004-9>
7. Binenbaum J., Weinstain R., Shani E. Gibberellin localization and transport in plants. *Trends Plant Sci.* 2017, 23 (5), 410–421. <https://doi.org/10.1016/j.tplants.2018.02.005>
8. Davière J. M., Achard P. A Pivotal Role of DELLAs in Regulating Multiple Hormone Signals. *Mol. Plant.* 2016, 9 (1), 10–20. <https://doi.org/10.1016/j.molp.2015.09.011>
9. Xue L., Cui H., Buer B., Vijayakumar V., Delaux P-M., Junkermann S., Bucher M. Network of GRAS transcription factors involved in the control of arbuscule development in *Lotus japonicus*. *Plant Physiol.* 2015, 167 (3), 854–871. <https://doi.org/10.1104/pp.114.255430>
10. Dill A., Sun T. Synergistic derepression of gibberellin signaling by removing RGA and GAI function in *Arabidopsis thaliana*. *Genetics.* 2001, 159 (2), 777–785.
11. Hirsch S., Oldroyd G. E. D. GRAS-domain transcription factors that regulate plant development. *Plant Signal Behav.* 2014, 4 (8), 698–700. <https://doi.org/10.4161/psb.4.8.9176>
12. Hirano K., Kouketu E., Katoh H., Aya K., Ueguchi-Tanaka M., Matsuoka M. The suppressive function of the rice DELLA protein SLR1 is dependent on its transcriptional activation activity. *Plant J.* 2012, 71 (3). 443–453. <https://doi.org/10.1111/j.1365-313X.2012.05000.x>
13. Weston D. E., Elliott R. C., Lester D. R., Rameau C., Reid J. B., Murfet I. C., Ross J. J. The Pea DELLA proteins LA and CRY are important regulators of gibberellin synthesis and root growth. *Plant Physiol.* 2008, 147 (1), 199–205. <https://doi.org/10.1104/pp.108.115808>
14. Zhang Z. L., Ogawa M., Fleet C. M., Zentella R., Hu J., Heo J-O., Lim J., Kamiya Y., Yamaguchi S., Sun T-P. Scarecrow-like 3 promotes gibberellin signaling by antagonizing master growth repressor DELLA in Arabidopsis. *Proc. Natl. Acad. Sci. USA.* 2011, 108 (5), 2160–2165. <https://doi.org/10.1073/pnas.1012232108>
15. Gantait S., Sinniah U. R., Ali M. N., Sahu N. C. Gibberellins — a multifaceted hormone in plant growth regulatory network. *Curr. Protein Pept. Sci.* 2015, 16 (5), 406–412. <https://doi.org/10.2174/1389203716666150330125439>
16. Gupta R., Chakrabarty S. K. Gibberellic acid in plant: Still a mystery unresolved. *Plant Signal Behav.* 2013, 8 (9), e25504. <https://doi.org/10.4161/psb.25504>
17. Tsygankova V. A. Genetic Control and Phytohormonal Regulation of Plant Embryogenesis. *Int. J. Med. Biotechnol. Genetics (IJMBG).* 2015, 3(1), 9–20. <http://scidoc.org/IJMBG-2379-1020-03-101.php>
18. Finkelstein R., Reeves W., Ariizumi T., Steber C. Molecular aspects of seed dormancy. *Ann. Rev. Plant Biol.* 2008, V. 59, P. 387–415. <https://doi.org/10.1146/annurev.arplant.59.032607.092740>
19. Kaneko M., Itoh H., Inukai Y., Sakamoto T., Ueguchi-Tanaka M., Ashikari M., Matsuoka M. Where do gibberellin biosynthesis and gibberellin signaling occur in rice plants? *Plant J.* 2003, 35 (1), 104–115. <https://doi.org/10.1046/j.1365-313x.2003.01780.x>
20. Gubler F., Kalla R., Roberts J. K., Jacobsen J. V. Gibberellin-regulated expression of a myb gene in barley aleurone cells: evidence for Myb transactivation of a high-pI alpha-amylase gene promoter. *Plant Cell.* 1995, 7(11), 1879–1891. <https://doi.org/10.1105/tpc.7.11.1879>
21. Zentella R., Yamauchi D., Ho T. H. Molecular dissection of the gibberellin/abscisic acid signaling pathways by transiently expressed RNA interference in barley aleurone cells. *Plant Cell.* 2002, V. 14, P. 2289–2301. <https://doi.org/10.1105/tpc.003376>

22. Sun T. Gibberellin Signal Transduction in Stem Elongation & Leaf Growth. *Plant Hormones*. Davies P. J. (Ed.). Springer, Dordrecht. 2010, P. 308–328. https://doi.org/10.1007/978-1-4020-2686-7_15
23. Uozu S., Tanaka-Ueguchi M., Kitano H., Hattori K., Matsuoka M. Characterization of XET-related genes of rice. *Plant Physiol.* 2000, 122 (3), 853–859. <https://doi.org/10.1104/pp.122.3.853>
24. Fabian T., Lorbiecke R., Umeda M., Sauter M. The cell cycle genes *cycA1;1* and *cdc2Os-3* are coordinately regulated by gibberellin in planta. *Planta*. 2000, 211 (3), 376–383. <https://doi.org/10.1007/s004250000295>
25. Sakamoto T., Kamiya N., Ueguchi-Tanaka M., Iwahori S., Matsuoka M. KNOX homeodomain protein directly suppresses the expression of a gibberellin biosynthetic gene in the tobacco shoot apical meristem. *Genes Dev.* 2001, V. 15, P. 581–90. <https://doi.org/doi:10.1101/gad.867901>
26. Li H., Torres-Garcia J., Latrasse D., Benhamed M., Schilderink S., Zhou W., Kulikova O., Hirt H., Bisseling T. Plant-specific histone deacetylases HDT1/2 regulate GIBBERELLIN 2-OXIDASE2 expression to control Arabidopsis root meristem cell number. *The Plant Cell*. 2017, V. 29, P. 2183–2196. <https://doi.org/10.1105/tpc.17.00366>
27. Ragni L., Kaisa Nieminen K., Pacheco-Villalobos D., Sibout R., Schwechheimer C., Hardtke C. S. Mobile gibberellin directly stimulates Arabidopsis hypocotyl xylem expansion. *The Plant Cell*. 2011, V. 23, P. 1322–1336. <https://doi.org/10.1105/tpc.111.084020>
28. Llanes A., Andrade A., Alemano S., Luna V. Alterations of endogenous hormonal levels in plants under drought and salinity. *Am. J. Plant Sci.* 2016, V. 7, P. 1357–1371. <https://doi.org/10.4236/ajps.2016.79129>
29. Vettakkorumakankav N. N., Falk D., Saxena P., Fletcher P. R. A. A crucial role for gibberellins in stress protection of plants. *Plant Cell Physiol.* 1999, 40 (5), 542–548.
30. Lo S. F., Ho T. H. D., Liu Y. L., Jiang M. J., Hsieh K. T., Chen K. T., Yu L.-C., Lee M.-H., Chen C.-Y., Huang T.-P., Kojima M., Sakakibara H., Chen L.-J., Yu S.-M. Ectopic expression of specific GA₂ oxidase mutants promotes yield and stress tolerance in rice. *Plant Biotechnol. J.* 2017, 15 (7), 850–864. <https://doi.org/10.1111/pbi.12681>
31. Abass S., Mohamed H. Alleviation of Adverse Effects of Drought Stress on Common Bean (*Phaseolus vulgaris* L.) by Exogenous Application of Hydrogen Peroxide. *Bangladesh J. Bot.* 2011, V. 40, P. 75–83. <http://dx.doi.org/10.3329/bjb.v40i1.8001>
32. Yang J. C., Zhang J. H., Wang Z. Q., Zhu Q. S., Wang W. Hormonal Changes in the Grains of Rice Subjected to Water Stress during Grain Filling. *Plant Physiol.* 2001, 127 (1), 315–323. <http://dx.doi.org/10.1104/pp.127.1.315>
33. Krugman T., Peleg Z., Quansah L., Chagu V., Korol A. B., Nevo E., Saranga Y., Fait A., Chalhou B., Fahima T. Alteration in expression of hormone-related genes in wild emmer wheat roots associated with drought adaptation mechanisms. *Funct. Int. Genom.* 2011, V. 11, P. 565–583. <https://doi.org/10.1007/s10142-011-0231-6>
34. Liu F., Wang P., Zhang X., Li X., Yan X., Fu D., Wu G. The genetic and molecular basis of crop height based on a rice model. *Planta*. 2018, 247 (1), 1–26. <https://doi.org/10.1007/s00425-017-2798-1>
35. Ashraf M., Karim F., Rasul E. Interactive effects of gibberellic acid (GA₃) and salt stress on growth, ion accumulation and photosynthetic capacity of two spring wheat (*Triticum aestivum* L.) cultivars differing in salt tolerance. *J. Plant Growth Regul.* 2002, 36 (1), 49–59. <https://doi.org/10.1023/A:1014780630479>
36. Irfan A., Shahzadm A. B., Amir I. The effects of seed soaking with plant growth regulators on seedling vigor of wheat under salinity stress. *J. Stress Physiol. Biochem.* 2005, 1 (1), 6–14.
37. Magome H., Yamaguchi S., Hanada A., Kamiya Y., Oda K. The DDF1 transcriptional activator upregulates expression of a gibberellin-deactivating gene, *GA2ox7*, under high-salinity stress in Arabidopsis. *Plant J.* 2008, 56 (4), 613–626. <https://doi.org/10.1111/j.1365-313X.2008.03627.x>
38. Shu K., Qi Y., Chen F., Meng Y., Luo X., Shuai H., Zhou W., Ding J., Du J., Liu J., Yang F., Wang Q., Liu W., Yong T., Wang X., Feng Y., Yang W. Salt stress represses soybean seed germination by negatively regulating GA biosynthesis while positively mediating ABA biosynthesis. *Front. Plant Sci.* 2017, 10 (8), 1372–1384. <https://doi.org/10.3389/fpls.2017.01372>
39. Wu C., Tang S., Li G., Wang S., Fahad S., Ding Y. Roles of phytohormone changes in the grain yield of rice plants exposed to heat: a review. *Peer J.* 2019, V. 7, P. e7792. <https://doi.org/10.7717/peerj.7792>
40. Yang D., Li Y., Shi Y., Cui Z., Luo Y., Zheng M., Chen J., Li Y., Yin Y., Wang Z. Exogenous Cytokinins Increase Grain Yield of Winter Wheat Cultivars by Improving Stay-Green

- Characteristics under Heat Stress. *PLoS One*. 2016, 11 (5), e0155437. <https://doi.org/10.1371/journal.pone.0155437>
41. Toh S., Imamura A., Watanabe A., Nakabayashi K., Okamoto M., Jikumaru Y., Hanada A., Aso Y., Ishiyama K., Tamura N., Iuchi S., Kobayashi M., Yamaguchi S., Kamiya Y., Nambara E., Kawakami N. High temperature-induced abscisic acid biosynthesis and its role in the inhibition of gibberellin action in Arabidopsis seeds. *Plant Physiol*. 2008, 146 (3), 1368–1385. <https://doi.org/10.1104/pp.107.113738>
42. Sakata T., Oda S., Tsunaga Y., Shomura H., Kawagishi-Kobayashi M., Aya K., Saeki K. Reduction of Gibberellin by Low Temperature Disrupts Pollen Development in Rice. *Plant Physiol*. 2014, 164 (4), 2011–2019. <https://doi.org/10.1104/pp.113.234401>
43. Sharma K. D., Nayyar H. Regulatory Networks in Pollen Development under Cold Stress. *Front. Plant Sci*. 2016, V. 7, P. 402–416. <https://doi.org/10.3389/fpls.2016.00402>
44. Tonkinson C. L., Lyndon R. F., Arnold G. M., The effects of temperature and the *Rht3* dwarfing gene on growth, cell extension, and gibberellin content and responsiveness in the wheat leaf. *J. Exp. Bot*. 1997, 48 (4), 963–970. <https://doi.org/10.1093/jxb/48.4.963>
45. Tanaka N., Matsuoka M., Kitano H., Asano T., Kaku H., Komatsu S. *Gid1*, a gibberellin-insensitive dwarf mutant, shows altered regulation of probenazole-inducible protein (PBZ1) in response to cold stress and pathogen attack. *Plant Cell Environ*. 2006, 29 (4), 619–631. <https://doi.org/10.1111/j.1365-3040.2005.01441.x>
46. Xu D., Cao H., Fang W., Pan J., Chen J., Zhang J., Shen W. Linking hydrogen-enhanced rice aluminum tolerance with the reestablishment of GA/ABA balance and miRNA-modulated gene expression: a case study on germination. *Ecotoxicol. Environ. Saf*. 2017, V. 145, P. 303–312. <https://doi.org/10.1016/j.ecoenv.2017.07.055>
47. Kosakivska I. V., Voytenko L. V., Vasyuk V. A., Shcherbatiuk M. M. Effect of zinc on growth and phytohormones accumulation in *Triticum aestivum* L. Seedlings priming with abscisic acid. *Dopov. Nats. akad. nauk Ukr*. 2019, N 11, P. 93–99. <https://doi.org/10.15407/dopovidi2019.11.093>
48. Abhinandan K., Skori L., Stanic M., Hicker-son N. M. N., Jamshed M., Samuel M. A. Abiotic Stress Signaling in Wheat — An Inclusive Overview of Hormonal Interactions During Abiotic Stress Responses in Wheat. *Front. Plant Sci*. 2018, V. 9, P. 734–742. <https://doi.org/10.3389/fpls.2018.00734>
49. Verma V., Ravindran P., Kumar P. P. Plant hormone-mediated regulation of stress responses. *BMC Plant Biol*. 2016, 16 (1), 86. <https://doi.org/10.1186/s12870-016-0771-y>
50. Ye N., Zhang J. Antagonism between abscisic acid and gibberellins is partially mediated by ascorbic acid during seed germination in rice. *Plant Signal Behav*. 2012, 7 (5), 563–565. <https://doi.org/10.4161/psb.19919>
51. Kosakivska I. V., Voytenko L. V., Vasyuk V. A., Vedenichova N. P., Babenko L. M., Shcherbatyuk M. M. Phytohormonal regulation of seed germination. *Fiziologia rastenii i henetyka*. 2019, 51 (3), 187–206. (In Ukrainian). <http://www.frg.org.ua/articles/51030187a.pdf>
52. Piskurewicz U., Jikumaru Y., Kinoshita N., Nambara E., Kamiya Y., Molin L-L. The Gibberellic Acid Signaling Repressor RGL2 Inhibits Arabidopsis Seed Germination by Stimulating Abscisic Acid Synthesis and ABI5 Activity. *Plant Cell*. 2008, V. 20, P. 2729–2745. <https://doi.org/10.1105/tpc.108.061515>
53. Lim S., Park J., Lee N., Jeong J., Toh S., Watanabe A., Kim J., Kang H., Kim D. H., Kawakami N., Choi G. ABA-insensitive₃, ABA-insensitive₅, and DELLAs Interact to activate the expression of SOMNUS and other high-temperature-inducible genes in imbibed seeds in *Arabidopsis*. *Plant Cell*. 2013, 25 (12), 4863–4878. <https://doi.org/10.1105/tpc.113.118604>
54. Gómez-Cadenas A., Verhey S. D., Holappa L. D., Shen Q., Ho T. H., Walker-Simmons M. K. An abscisic acid induced protein kinase, PKABA1, mediates abscisic acid-suppressed gene expression in barley aleurone layers. *Proc. Natl. Acad. Sci. USA*. 1999, 96 (4), 1767–1772. <https://doi.org/10.1073/pnas.96.4.1767>
55. Yamauchi D., Zentella R., Ho T. H. Molecular analysis of the barley (*Hordeum vulgare* L.) gene encoding the protein kinase PKABA1 capable of suppressing gibberellin action in aleurone layers. *Planta*. 2002, 215 (2), 319–326. <https://doi.org/10.1007/s00425-002-0740-6>
56. He Y., Li W., Lv J., Jia Y., Wang M., Xia G. Ectopic expression of a wheat MYB transcription factor gene, *TaMYB73*, improves salinity stress tolerance in *Arabidopsis thaliana*. *J. Exp. Bot*. 2012, 63 (3), 1511–1522. <https://doi.org/10.1093/jxb/err389>
57. Jacobsen J. V., Pearce D. W., Poole A. T., Pharis R. P., Mander L. N. Abscisic acid,

- phaseic acid and gibberellin contents associated with dormancy and germination in barley. *Physiol. Plant.* 2002, V. 115, P. 428–441. <https://doi.org/10.1034/j.1399-3054.2002.1150313>
58. White C. N., Proebsting W. M., Hedden P., Rivin C. J. Gibberellins and seed development in maize. I. Evidence that gibberellin/abscisic acid balance governs germination versus maturation pathways. *Plant Physiol.* 2000, V. 122, P. 1081–1088. <https://doi.org/10.1104/pp.122.4.1081>
 59. Bora R. K., Sarma C. M. Effect of gibberellic acid and cycocel on growth, yield and protein content of pea. *Asian. J. Plant Sci.* 2006, 5 (2), 324–330. <https://doi.org/10.3923/ajps.2006.324.330>
 60. Hu J., Israeli A., Ori N., Suna T. The Interaction between DELLA and ARF/IAA Mediates Crosstalk between Gibberellin and Auxin Signaling to Control Fruit Initiation in Tomato. *The Plant Cell.* 2018, V. 30, P. 1710–1728. <https://doi.org/10.1105/tpc.18.00363>
 61. Greenboim-Wainberg Y., Maymon I., Borochov R., Alvarez J., Olszewski N., Ori N., Eshed Yu., Weiss D. Cross Talk between Gibberellin and Cytokinin: The Arabidopsis GA Response Inhibitor SPINDLY Plays a Positive Role in Cytokinin Signaling. *Plant Cell.* 2005, 17 (1), 92–102. <https://doi.org/10.1105/tpc.104.028472>
 62. Zhou J., Li Z., Xiao G., Zhai M., Pan X., Huang R., Zhang H. CYP71D8L is a key regulator involved in growth and stress responses by mediating gibberellin homeostasis in rice. *J. Exp. Bot.* 2020, 71 (3), 1160–1170. <https://doi.org/10.1093/jxb/erz491>
 63. Yang J., Duan G., Li C., Liu L., Han G., Zhang Y., Wang C. The Crosstalks Between Jasmonic Acid and Other Plant Hormone Signaling Highlight the Involvement of Jasmonic Acid as a Core Component in Plant Response to Biotic and Abiotic Stresses. *Front. Plant Sci.* 2019, V. 10, P. 1349. <https://doi.org/10.3389/fpls.2019.01349>
 64. Rademacher W. Chemical regulators of gibberellin status and their application in plant production. *Ann. Plant Rev.* 2016, V. 49, P. 359–403. <https://doi.org/10.1002/9781119210436.ch12>
 65. Sarkar S., Michel R., Falk D., Zhang R. Relationship between gibberellins, height, and stress tolerance in barley (*Hordeum vulgare* L.) seedlings. *J. Plant. Growth. Regul.* 2004, 42 (2), 125–135. <https://doi.org/10.1023/B:GROW.0000017492.56792.64>
 66. Crook M. J., Ennos A. R. Stem and root characteristics associated with lodging resistance in 4 winter-wheat cultivars. *J. Agric. Sci.* 1994, V. 123, P. 167–174.
 67. Pan S., Rasul F., Li W., Tian H., Mo Z., Duan M., Tang X. Roles of plant growth regulators on yield, grain qualities and antioxidant enzyme activities in super hybrid rice (*Oryza sativa* L.). *Rice.* 2013, V. 6, article number: 9. <https://doi.org/10.1186/1939-8433-6-9>
 68. Plaza-Wüthrich S., Blösch R., Rindisbacher A., Cannarozzi G., Tadele Z. Gibberellin deficiency confers both lodging and drought tolerance in small cereals. *Front. Plant Sci.* 2016, V. 7, P. 1–14. <https://doi.org/10.3389/fpls.2016.00643>
 69. Kim S-K., Han C-M., Shin J-H., Kwon T-Y. Effects of paclobutrazol and prohexadione-Ca on seed yield, and content of oils and gibberellin in flax grown in a greenhouse. *Korean J. Crop. Sci.* 2018, 63 (3), 265–271. <https://doi.org/10.7740/KJCS.2018.63.3.265>
 70. Jabir B. M. O., Kinuthia K. B., Faroug M. A., Awad F. N., Everlyne M. M., Ahmadzai Z., Liu L. Effects of gibberellin and gibberellin biosynthesis inhibitor (paclobutrazol) applications on radish (*Raphanus sativus* L.) taproot expansion and the presence of authentic hormones. *Int. J. Agric. Biol.* 2017, 19 (4), 779–784. <https://doi.org/10.17957/IJAB/15.0359>
 71. Gebre E., Schlüter U., Hedden P., Kunert K. Gibberellin biosynthesis inhibitors help control plant height for improving lodging resistance in *Eragrostis tef*. *J. Crop. Improv.* 2012, V. 26, P. 375–388. <https://doi.org/10.1080/15427528.2011.646056>
 72. Bakheta M. A., Hussein M. M. Uniconazole effect on endogenous hormones, proteins and proline contents of barley plants (*Hordeum vulgare*) under salinity stress (NaCl). *Nusantara Biosci.* 2014, 6 (1), 39–44. <https://doi.org/10.13057/nusbiosci/n060107>
 73. Ahmad I., Kamran M., Meng X., Ali S., Bilegjargal B., Cai T., Liu T., Han Q. Effects of plant growth regulators on seed filling, endogenous hormone contents and maize production in semiarid regions. *J. Plant Growth Regul.* 2019, V. 38, P. 1467–1480. <https://doi.org/10.1007/s00344-019-09949-2>
 74. Coelho Filho M. A., Colebrook E. H., Lloyd D. P. A., Webster C. P., Mooney S. J., Phillips A. L., Hedden P., Whalley W. R. The involvement of gibberellin signalling in the effect of soil resistance to root penetration on leaf elongation and tiller number in wheat. *Plant Soil.* 2013, V. 371, P. 81–94. <https://doi.org/10.1007/s11104-013-1662-8>

75. Sarwar N., Atique-ur-Rehman, Farooq O., Mubeen N., Wasaya A., Nourman W., Zafar Ali M., Shehzad M. Exogenous application of gibberellic acid improves the maize crop productivity under scarce and sufficient soil moisture condition. *Cercet. Agron. Mold.* 2018, 50 (4), 65–73. <https://doi.org/10.1515/cerce-2017-0036>
76. Ansari O., Azadi M. S., Sharif-Zadeh F., Younesi E. Effect of Hormone Priming on Germination Characteristics and Enzyme Activity of Mountain Rye (*Secale montanum*) Seeds under Drought Stress Conditions. *J. Stress. Physiol. Biochem.* 2013, 9 (3), 61–71.
77. Arabshahi M., Mobasser H. R., Rad M. R. N. Effect of drought stress and gibberellin on some characteristics of wheat. *Chem. Res. J.* 2017, 2 (2), 154–158. Available online www.chemrj.org
78. Kaya C., Tuna A. L., Alves A. Gibberellic acid improves water deficit tolerance in maize plants. *Acta Phisiol. Plant.* 2006, 28 (4), 331–337. <https://doi.org/10.1007/s11738-006-0029-7>
79. Iqbal M., Ashraf M. Gibberellic acid mediated induction of salt tolerance in wheat plants: Growth, ionic partitioning, photosynthesis, yield and hormonal homeostasis. *Environ. Exp. Bot.* 2013, V. 86, P. 76–85. <https://doi.org/10.1016/j.envexpbot.2010.06.002>
80. Tuna A. L., Kaya C., Dikilitas M., Higgs D. The combined effects of gibberellic acid and salinity on some antioxidant enzyme activities, plant growth parameters and nutritional status in maize plants. *Environ. Exp. Bot.* 2008, 62 (1), 1–9. <https://doi.org/10.1016/j.envexpbot.2007.06.007>
81. Amal M. E. Abdel-Hamid, Heba I. M. The effect of the exogenous gibberellic acid on two salt stressed barley cultivars. *Europ. Sci. J.* 2014, 10 (6), 1857–1881. <https://doi.org/10.19044/esj.2014.v10n6p%25p>
82. Gangwar S., Singh V. P., Tripathi D. K., Chauhan D. K., Prasad S. M., Maurya J. N. Plant responses to metal stress: the emerging role of plant growth hormones in toxicity alleviation. In: *Emerging technologies and management of crop stress tolerance*. Academic Press. 2014, P. 215–248.
83. Sytar O., Kumari P., Yadav S., Brestic M., Rastogi A. Phytohormone Priming: Regulator for Heavy Metal Stress in Plants. *J. Plant. Growth Regul.* 2019, V. 38, P. 739–752. <https://doi.org/10.1007/s00344-018-9886-8>
84. Zhu X. F., Jiang T., Wang Z. W., Lei G. J., Shi Y. Z., Li G. X., Zheng S. J. Gibberellic acid alleviates cadmium toxicity by reducing nitric oxide accumulation and expression of IRT1 in *Arabidopsis thaliana*. *J. Hazard. Mater.* 2012, V. 239–240, P. 302–307. <https://doi.org/10.1016/j.jhazmat.2012.08.077>
85. Koprivova A., North K. A., Kopriva S. Complex Signaling Network in Regulation of Adenosine 5'-Phosphosulfate Reductase by Salt Stress in Arabidopsis Roots. *Plant Physiol.* 2008, V. 146, P. 1408–1420. <https://doi.org/10.1104/pp.107.113175>
86. Siddiqui M. H., Al-Whaibi M. H., Basalah M. O. Interactive effect of calcium and gibberellin on nickel tolerance in relation to antioxidant systems in *Triticum aestivum* L. *Protoplasma.* 2010, 248 (3), 503–511. <https://doi.org/10.1007/s00709-010-0197-6>
87. Amri B., Khamassi K., Ali M. B., Teixeira da Silva J. A., Kaab L. B. B. Effects of gibberellic acid on the process of organic reserve mobilization in barley grains germinated in the presence of cadmium and molybdenum. *South Afr. J. Bot.* 2016, V. 106, P. 35–40. <https://doi.org/10.1016/j.sajb.2016.05.007>
88. Shehata S. M., Badawy R. K., Aboulsoud Y. I. E. Phytoremediation of some heavy metals in contaminated soil. *Bull. Natl. Res. Cent.* 2019, V. 43, Article number 189. <https://doi.org/10.1186/s42269-019-0214-7>
89. Picazo I., Moya J. L. Heavy metal hormone interactions in rice plants: effect on growth, photosynthesis and carbohydrate distribution. *J. Plant Growth Regul.* 1995, V. 14, P. 61–67. <https://doi.org/10.1007/BF00203115>
90. Ulfat A., Majid S. A., Hameed A. Hormonal seed priming improves wheat (*Triticum aestivum* L.) field performance under drought and non-stress conditions. *Pak. J. Bot.* 2017, V. 49, P. 1239–1253. <https://www.researchgate.net/publication/319313045>
91. Ma H. Y., Zhao D., Ning Q., Wei J., Li Y., Wang M., Liu X., Jiang C., Liang Z. A Multi-year Beneficial Effect of Seed Priming with Gibberellic Acid-3 (GA₃) on Plant Growth and Production in a Perennial Grass, *Leymus chinensis*. *Sci. Rep.* 2018, V. 8, P. 13214. <https://doi.org/10.1038/s41598-018-31471-w>
92. Rogach V. V., Voytenko L. V., Shcherbatiuk M. M., Kosakivska I. V., Rogach T. I. Morphogenesis, pigment content, phytohormones and productivity of eggplants under the action of gibberellin and tebuconazole. *Regul. Mech. Biosyst.* 2020, 11 (1), 116–122. <https://doi.org/10.15421/022017>

ГІБЕРЕЛІНИ У РЕГУЛЯЦІЇ РОСТУ ТА РОЗВИТКУ РОСЛИН ЗА ДІЇ АБІОТИЧНИХ СТРЕСІВ

І. В. Косаківська, В. А. Васюк

Інститут ботаніки ім. М. Г. Холодного
НАН України, Київ

*E-mail: irynakosakivska@gmail.com,
vasyuk@ukr.net*

Вступ. Гібереліни (ГБ), клас дитерпеноїдних фітогормонів, відіграють важливу роль у регуляції росту та розвитку рослин. Серед більш ніж 130 різних ізоформ гіберелінів лише окремі мають біологічну активність. ГК₁, ГК₃, ГК₄ і ГК₇ регулюють ріст рослин завдяки деградації DELLA протеїнів — негативних регуляторів генів, експресія яких активується ГБ. Нещодавні дослідження в галузі молекулярної генетики та функціональної геноміки суттєво поглибили наші уявлення щодо біосинтезу, метаболізму, транспортування, сигналіngu та взаємодії ГБ з іншими фітогормонами та факторами довкілля.

Мета. В огляді зосереджено увагу на участі ГБ у регулюванні росту і розвитку рослин за дії абіотичних стресів.

Результати. Подано ключову інформацію про біосинтез, сигналіng та функціональну активність ГБ, узагальнено відомості про перехресну взаємодію (кросс-ток) між ГБ, ауксинами, цитокинінами, абсцизовою кислотою та іншими фітогормонами; висвітлено роль ГБ в адаптації до умов посухи, засолення, високої та низької температури, забруднення важкими металами. Ефекти ГБ залежать передусім від інтенсивності й тривалості стресового впливу, а також від фази онтогенезу і толерантності рослини. Змінюючи інтенсивність біосинтезу, характер розподілу і передавання сигналів ГБ, рослини можуть регулювати стійкість до абіотичних стресів, підвищувати життєздатність і навіть уникати стресу. Обговорено питання використання ретардантів — інгібіторів біосинтезу ГБ із метою вивчення функціональної активності гормонів за дії абіотичних стресів. Особливу увагу приділено новим біотехнологічним підходам, у яких використовують екзогенні ГБ для передпосівного праймування насіння та фоліарної обробки рослин.

Висновки. Подальше вивчення ролі гіберелінів у набутті стресостійкості сприятиме розвитку біотехнології екзогенного використання гормону для поліпшення росту й підвищення врожайності рослин в несприятливих умовах довкілля.

Ключові слова: гібереліни, DELLA, фітогормони, абіотичні стреси, ретарданти, ріст, стресостійкість.

ГИББЕРЕЛИНЫ В РЕГУЛЯЦИИ РОСТА И РАЗВИТИЯ РАСТЕНИЙ В УСЛОВИЯХ АБИОТИЧЕСКИХ СТРЕССОВ

И. В. Косаковская, В. А. Васюк

Институт ботаники им. Н. Г. Холодного
НАН Украины, Киев

*E-mail: irynakosakivska@gmail.com,
vasyuk@ukr.net*

Вступление. Гиббереллины (ГБ), класс дитерпеноидных фитогормонов, играют важную роль в регуляции роста и развития растений. Среди более чем 130 различных изоформ гиббереллинов лишь немногие обладают биологической активностью. ГК₁, ГК₃, ГК₄ и ГК₇ регулируют рост, влияя на деградацию DELLA протеинов, — негативных регуляторов генов, экспрессия которых активизируется ГБ. Недавние исследования в области молекулярной генетики и функциональной геномики существенно расширили наши представления о биосинтезе, метаболизме, транспортировке, сигналинге и взаимодействии ГБ с другими фитогормонами и факторами окружающей среды.

Цель. В обзоре сосредоточено внимание на роли ГБ в регуляции роста и развития растений при действии абитических стрессов.

Результаты. Приведена ключевая информация о биосинтезе, сигналинге и функциональной активности ГБ, обобщены сведения о перекрестном взаимодействии (кросс-ток) между ГБ, ауксинами, цитокининами, абсцизовою кислотой и другими фитогормонами, о роли ГБ в адаптации к условиям засухи, засоления, высокой и низкой температуры, загрязнения тяжелыми металами. Эффекты ГBB зависят в первую очередь от интенсивности и продолжительности стрессового воздействия, а также от фазы онтогенеза и толерантности растения. Изменяя интенсивность биосинтеза, характер распределения и передачи сигналов ГБ, растения могут регулировать устойчивость к абитическому стрессу, повышать жизнеспособность и даже избегать стресса. Обсуждены вопросы использования ретардантов — ингибиторов биосинтеза ГБ с целью изучения функциональной активности гормона в условиях абитических стрессов. Особое внимание уделено новым биотехнологическим подходам, которые используют экзогенные ГБ для предпосевного праймирования семян и фоліарной обработки растений.

Выводы. Дальнейшее изучение роли гиббереллинов в приобретении стрессоустойчивости будет способствовать развитию биотехнологии экзогенного использования гормона для улучшения роста и повышения урожайности растений в неблагоприятных условиях окружающей среды.

Ключевые слова: гиббереллины, DELLA, фитогормоны, абитические стрессы, ретарданты, рост, стрессоустойчивость.