УДК 577.152.087:581 doi: 10.15407/biotech8.02.036

JASMONIC ACID: ROLE IN BIOTECHNOLOGY AND THE REGULATION OF PLANTS BIOCHEMICAL PROCESSES

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Received 20.01.2015

Published data and results of our studies concerning the involvement and role of jasmonic acid in the regulation of plant physiological and biochemical processes have been analyzed and summarized. The basic stages of jasmonates synthesis are reviewed. Properties of enzymes involved in jasmonate biosynthesis are described. Data on the jasmonic acid involvement in the regulation of seed germination, maintaining of aging processes, sex determination, cellulose synthesis, features of interaction with ABA as well as in gene expression, formation of the immune system in stress and pathogene effect conditions are presented. Jasmonic acid effects on the cell ultrustructure are discussed. Prospects of using jasmonates in biotechnology are dealt with.

Key words: biotechnology of jasmonic acid, regulation of metabolism reactions.

Jasmonates were first identified in volatile oil of *Jasminum grandiflorum* L. [1]. However, active studies on their physiological and biochemical properties began only at the end of the eighties of the last century [2]. Jasmonic acid (JA) and its derivatives: methyl jasmonate (Me-JA), 7-isojasmonate, jasmonic acid glucosides, amino-acid conjugates are widely spread in the plant kingdom. Using the radioimmunology technique with JA-specific antiserums, jasmonates have been identified in 206 plant species that belong to 150 genera including algae, mosses, horsetail, pteridophytes, gymnosperms and fungi. Their greatest diversity is found in fungi but a biological function of jasmonates in fungi is unknown [3]. To date there still discussion continues of the problem what jasmonates are: hormones or stress factors formed during organs ageing? The jasmonates hormonal nature is confirmed by their expansion, plant specific responses to an exogenous treatment, interaction with other phytormones. However, as compared to other classes of plant hormones, physiological concentrations, at which jasmonates execute their action, are higher. Jasmonates are physiologically active substances, which affect plant growth and development, show stimulating and inhibiting effects [4]. Jasmonic acid and its derivatives accumulation in plant organs and tissues occurs as a result of jasmonate-induced gene expression. JA is involved in the regulation of quite a number of processes, namely: embryo and generative organs development, ageing, sex determination, seed germination, root growth, tuber formation, leaf movement (phototropism) and sensitivity, adaptation to stress factors [3–9]. It is thought that there are some similarities between the patterns of response to JA and ABA actions [10]. The aim of this review was to summarize available published data and results of our studies concerning a biological role and involvement of JA and its derivatives in the regulation of physiological and biochemical processes in plants.

Jasmonic acid biosynthesis

Biosynthesis of jasmonic acid and its methyl esters was described in the eighties of the last century in reports [2, 4, 11]. Jasmonates are specific cyclopentane derivatives of the lipoxygenase pathway of polyunsaturated

fatty acid oxidation. The lipoxygenase family (linoleate: oxygen oxidoreductase –LOX), (EC 1.13.11.12.) unites dioxygenase enzymes that catalyze a regio- and stereo-spesific addition of molecular oxygen to cis,cis-1,4 pentadiene fragment of polyunsaturated fatty acids (PUFAs) (linoleic, linolenic and α-linolenic acids. PUFAs oxydation is the first link of the enzyme cascade that results in the formation of a biologically active compound — oxylipin. Most of LOX oxydize linoleic and linolenic acids at C–9 or C–13 positions producing 9– and 13–hydroperoxides respectively, which form at least six enzyme pathways [12,13]. LOX substrates are both free fatty acids and fatty acids that are components of storage triacylgycerols, phospohlipids and galactolipids [14, 15]. Their greatest part is represented by soluble cytoplasmatic enzymes though some of them are also found in chloroplasts, mitochondria and vacuoles. [16]. Plant LOX were isolated and purified to a homegenous state, their structure and properties were characterized in detail. JA synthesis starts in chloroplasts and ends in peroxisomes; it is initiated by the release of α-linolenic acid (18:3) from the chloroplast membrane involving the enzyme of phospholipase D (Fig. 1, 2) [6,7].

It was established that in cells of *Arabidopsis thaliana* and tomato JA can be synthesized from 16:3 substrate 7 (Z), 10 (Z), 13 (Z)- hexadecatrienoic acid via the hexadecanoid pathway [17]. 13-LOX catalyses the molecular oxygen addition to cis-cis-1,4-pentadienic system. A hydroperoxide product resulting from this process contains conjugated cis-trans set (Fig. 1) that is produced following a double binding migration during the catalytic cycle [6, 18–20]. 13-hidroperoxylinoleic acid (after separation pathways of traumatin and JA biosynthesis) is converted to epoxide by 13-allene oxide syntase (AOS) and cyclized by allene oxide cyclase (AOC) to obtain cyclopentanone of (cis)-12-oxo phytodienoic acid (OPDA). Phospholipase enzymes, 13-LOX, AOS and AOC, are localized in chloroplasts (Fig. 1). Transformation of the cyclopentanone ring by reductase enzyme with subsequent three cycles of β-oxydation are occurs in peroxisomes (Fig. 2). Residual (+)-7-iзo-JA can change to (–)-JA [6]. One stage of the JA conversion takes place in cytosol, namely: JA isoleucine conjugation resulting in the production of an amino-acid conjugate or methylation generating Me-JA [21]. *Arabidopsis thaliana* cells were shown to have an additional source of an intermediate substrate to synthesize JA, named „Arabidopside A" — galactolipid, etherified with 12-oxo phytodienoic acid that is formed in response to injury and synthesized with LOX 2 [22]. 12-oxo phytodienoic acid involved in transformation processes of the JA synthesis, is released with the participation of galactolipase (Fig. 3).

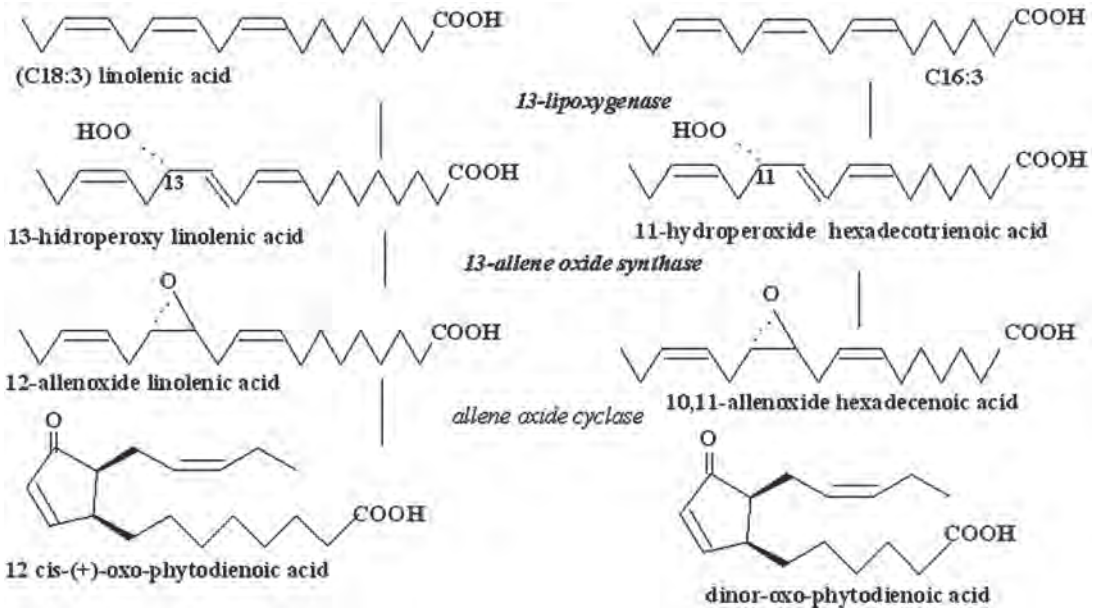

Fig. 1. **Schematic diagram of the jasmonic acid synthesis first stage that begins in chloroplasts (cited data by Wasternack, Forner, 2013)**

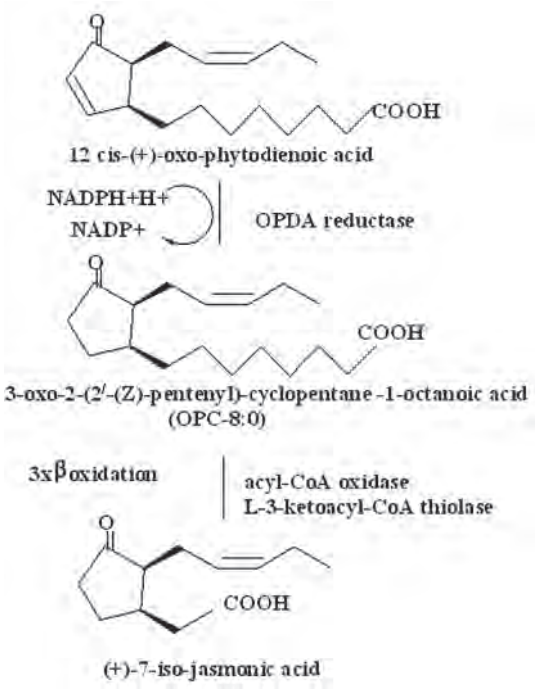

Fig. 2. **Schematic diagram of the jasmonic acid synthesis second stage that occurs in peroxysomes [6]**

Thus, the final stage of the JA biogenesis occurs in peroxisomes while enzymes that take part in the initial stages of the biosynthesis are localized in plastids [23–25]. It was published about transporter PXA1 which helps intermediates to transport to peroxisome. However, it is still unknown how intermidiates of the JA synthesis are transferred between plastids and peroxisomes.

Molecular mechanism of jasmonate action

The jasmonate regulation of physiological processes in the plant cell goes on at the transcriptional and translational levels [26, 27]. That was first revealed in studies on barley ageing leaves [28]. Regulation at the transcriptional level shows itself in activation of some genes under presence of JA and production of a considerable number of iRNA and specific proteins while at the translational level it exhibits itself in inhibiting the „normal" proteins synthesis and preserving an appropriate iRNA synthesis. There were identified some genes that are JA-activated. In *Solanum tuberosum* L., these are genes inhibiting proteinase (p.pin I and

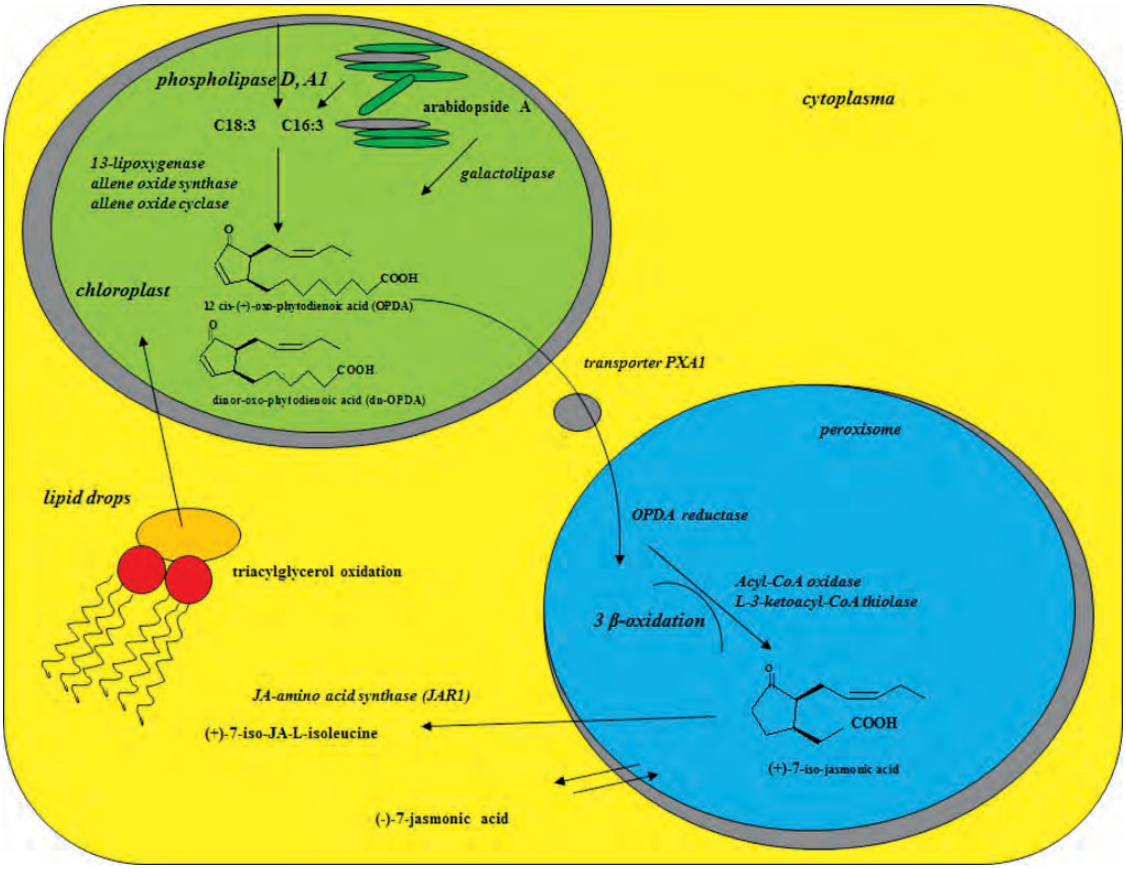

Fig. 3. **Schematic diagram of the jasmonic acid synthesis cascade in *Arabidopsis thaliana* [6]**

p.pin II), in *Lycopersion esculentum* L. — t.pin I gene, LOX (lox-3) gene and storage protein genes (vsp A and vsp B), in *Glycine max* L. — gene of phenylalanine-ammonium -lyase (pal) from yeast fungus *Rhodotorula rubra* L., in *Petroselinium sativa* L. — gene of chalcosynthase (chs), in *Agrobacterium rhizogenes* — gene of nopalinsynthase (nos) from tumor tissues, which causes desease "hairy root". Deletion of promoter site in the above-mentioned genes were found to lead to the loss of their sensitivity to JA effects. There were decoded DNA sections, which are responsible for the interaction with jasmonates. In addition, such section of p.pinII gene is between 500 and 620 nucleotiode sequences (n.s.), vsp A gene– between 1170 and 1270 n.s., vsp B gene — between 480 and 580 n.s., chs gene — between 120 and 170 n.s. [26]. However, the section significant dimensions impugn the suggestion regarding a direct interaction between the phytohormone and DNA. Most probably, there takes place an interaction with protein, which forms a complex with JA. So, in the promotion site of jasmonate-dependent genes (vsp A, vsp B, p.pin II, chs) there was isolated a specific nucleotide sequence G-box, which contains gexanucleotide CACGTG that is associated with the transcription initiation factor. The G-box sequence was detected in gene promotion sites of yeast, bacteria, plants and mammals. In addition to jasmonates, the gene activity is affected by other phytohormones including ABA and IAA. It was revealed that at the distance of 10–50 n.s. from G-box the genes vsp A, vsp B, p.pin II and chs have two homologous sequences — boxes I and III. The homologous boxes dimensions (within one turn of the DNA helix) and a significant distance between them indicate that not one but several regulating proteins, producing a complex to interact with JA, are bound to the gene regulating sites. This suggestion is confirmed by studies on the p.pin II gene from *Solanum tuberosum* L. An isolated DNA fragment was cloned in the plasmid pTE2pb. As a result there was obtained an affine sorbent used to isolate from the protein mixture and describe four proteins which were desorbed from the affine sorbent with the presence of 4 μM solution of ME-JA. The obtained proteins proved to be subunits of two transcription repressors whose inducer is methyljasmonate. The protein repressor binding with the gene regulator sites involves boxes-G, I and III, similarly sensitive to effects of ABA and JA [26]. The similarity of gene expression variation, resulting from JA and ABA action, a question raises if these phytohormones act successively on one pathway or there are formed two independent signaling pathways. To study the mechanisms of ABA and JA interaction during gene expression, some models enabling changes in the endogenous jasmonic acid and ABA content have been proposed. To inhibit the LOX-pathway in barley leaves, a hundred-fold increase in the JA content by means of a 24-hour sorbitol induction was applied. An impact on the LOX-pathway effectiveness was evaluated on the basis of the JA content and synthesis of jasmonate-induced proteins (JIP). Changes in the endogenous JA content were regulated under ibuprophen and aspirin — the LOX-pathway inhibitors that inhibit JIP gene expression. The JIP synthesis blocking was found to occur via a suppression of the JA synthesis [29]. Such a suppression of the LOX-pathway involving some decrease in the JA content was a result of decline in the gene expression caused by damages in injured tomato leaves [30]. Leaf dehydration in ABA-deficit (Az34) and carotenoid-deficit (albozonata) barley mutants evoked by sorbitol had no effect on the ABA content but caused the accumulation of jasmonate-induced mRNA and proteins (JIP) [31]. During wild barley leaf dehydration control samples showed, on the contrary, some ABA accumulation that did not lead to JIP synthesis. Thus, the JIP gene expression involved jasmonic acid but not ABA. Since under the exogenous treatment both phytohormones were involved in the JIP synthesis induction, it can be suggested that most probably there exist different signaling pathways.

Jasmonate biological activity

JA and its derivatives activity is regulated both by external and internal factors [10]. An exogenous JA treatment at concentration 10^{-3} M resulted in inhibition of seedling and root growth, pollen germination and catarantus callus growth [4]. Phytochrome A was revealed to stimulate genes of JA biosynthesis that leads to the production of JA amino-acid conjugates [32]. JA suppressed growth of hypocotyls in *Arabidopsis thaliana*, whose regulation involves receptors of the phytochrome families of red (A) and long-wave red light (E). There was found a correlation between a jasmonate suppression of chloroplast transcript activity, chlorophyll production and light intensity. ME-JA reduced the photosynthesis rate in

Cucurbita pepo cotyledons [33]. Jasmonates also stimulated the synthesis of alkaloids and root formation from potato tuber meristems. Plant organs were shown to differ in their jasmonate content. The overground organs of *Vicia faba* L. (flowers, young leaves and fruits), for example, contained a significant quantity of jasmonates (10–30 μg/g of fresh weight), while in roots, mature and old leaves there were detected only trace quantities [4]. In mature soya fruits the highest content of JA (0.4 μg /g of fresh weight) was detected in the pericarp (in its vascular bundles in particular), cicatricle and seed skin, the lowest one — in cotylidons and embryonic axis (0.2 μg/g of fresh weight). After a 12-hour seed soaking, the JA content increased up to 2 μg /g of fresh weight. In soya seedlings the JA level in the hypocotyl, cell division zones and in young buds was higher than that in the extension zone, old parts of the stem and root and in old leaves [34]. In soya leaves a high expression level of jasmonate-sensetive genes is typical for mesophyll cells that enclose conducting bundles. In epidermis cells it is relatively low. The similar pattern of a jasmonate distribution in organs is also characteristic of monocotyledons [4].

JA plays a significant role in the cell wall formation because it is involved in cellulose synthesis regulation. So, some increase in the JA level in cellulose-deficit mutants of *Arabidopsis thaliana* was associated with a cell extension and compensatory rise of lignin in the cell wall on the background of cellulose losses [35]. JA induces the lipoxygenase gene expression that is engaged in the biosynthesis of octadecanoids and forms responses to a pathogenic damage involving oxidation products. JA and ME-JA express genes of decaturase that catalyzes the linoleic acid conversion in linolenic acid which is one of the basic derivative compounds required for the JA synthesis. Intermediate products of PUFAs oxidizing degradation execute function of circle ionophore and stimulate calcium-dependent processes [36].

JA and its metabolic precursor (OPDA) initiate the production of stress proteins including proteinase inhibitors [37]. OPDA actively affect on protective proteins synthesis and is the main gene expression inducers in response to a local stress action while the signal transduction to organs and tissues remote from the action site as well as systemic resistance formation are carried out with JA and ME-JA [38, 39].

Regulation of seed germination

Seed germination is one of the most important steps of higher plant ontogenesis, in which the metabolic activity is resumed and growth processes are activated. Mature seeds of most plant species, growing in the moderate climat areas, can be dehydrated to an air-dry condition and still retain their viability [40]. As a rule, the seed life cycle consists of three steps: formation, dormancy and germination. Seed germination can, to some extent, be regarded as a number of successive structural and functional changes resulting in a gradual increase of metabolic activity and transformation of the embryo to a seedling. Morphologically, the germination initial stage takes place after some parts of the embryo emerge from the seed coating. Water is decisive factor, on which the seed transition to the germination stage depends. The first stage of germination, swelling, starts with water uptake by seed cells. After a required level of seed water imbibition is achieved, seeds begin germinating. For different plant species this level differs and depends on their structural specificity, dimensions, storage substances and other factors. Fundamental metabolic processes that are involved in germination can not be confined only to growth and nevertheless growth is the basic indicator of germination. When solving many problems on seed life activity and seedling formation we face the challenge of studying the mechanisms of growth processes triggering and the possibility of their regulation by means of natural or synthetic physiologically active substances. By using exogenous phytohormones, we may accelerate ripening, break dormancy, stimulate germination and, vice versa, prolongate dormancy and repress germination. The jasmonic acid precursor — 12–OPDA, when interacting with ABA, inhibited germination of *Arabidopsis thaliana* seeds, stimulating the content of ABA-insensitive proteins. A significant quantity of this cis-OPDA is etherified to the galactolipid content and produces arabidopsin — an intermediate substrate additional source to synthesize JA [21]. Me-JA (10^{-3} M) repressed seed germination in yellow lupine, inactivating α-galactose that caused, in its turn, the termination of α-D-galactoside utilization. Some delay in germination of *Amaranthus caudatus* seeds occurred after an exogenous exposure to Me-JA (10^{-3} M) [8]. When studying an exogenous JA influence on seed germination more than 20 years ago,

T. Daletzka and G. Zembdner suggested that this process depended on a type of storage substances in seeds. JA, for example, repressed germination in wheat and rye seeds that are characterized by a forced dormancy whereas the main storage substance of these plants is starch. In rye, germination inhibition was observed at JA concentration of 1mg/l, while at the concentration of 25mg/l seeds lost their germinability completely. Other events were observed in studies on flax seeds whose basic storage substances are lipids. Germination of JA-treated seeds started already in 48 hours and had practically no differences from control. Only at higher JA concentrations (500 mg/l) germination was inhibited [41]. In our studies we applied orthodox seeds of *Acer tataricum* L., which at the final step of ripening are dehydrated, going to the state of a deep physiological dormancy [40]. Mature seeds imbibition is 10% . Air-dry seeds are able to germinate following a long-term storage. Under conditions that are favourable for growing, moisture uptake and dwarf seedling growth are taken place [42]. When studying the embryonic axis cell ultrustructure, we discovered that the cell membrane system of *A. tataricum* mature seeds showed substantial changes. Standard techniques of cell preparation for ultrastaructural studies enabled to identify lipid drops and protein bodies [43]. It was found that storage lipids in mature seed cells are dominant and they generate dense layers around the plasmalemma, protein bodies and are freely arranged in the cytoplasm. No starch grains were detected in mature seed embryo cells (Fig. 4). Recovery of the cell membrane structure that normally occurred after a cold stratification at 0–3 °C and took 120 days was replaced by a 24-hour JA treatment at concentration of 500 mg/l [44]. In germination of JA-treated and stratified seeds there were observed similar ultrastructural changes that included recovery of the membrane lamellar structure in cytoplasmic components, lipid drop degradation, protein body proteolysis (Fig. 4). It should be noted that JA-treated seeds germinated somewhat later than stratified ones but they formed normal seedlings.

Similar JA effects also took place during *A. tataricum* seed ripening. 60–65 days after flowering (DAF), that coincides with the stage of high metabolic and growth activities and also 90–95 DAF — during the termination of storage substance synthesis — we observed hydrolysis of lipid drops and formation of glyoxysomes. Studies on *Aesculus hippocastanum* L. seeds that belong to a recalcitrant type showed that after the termination of ripening they retained a high moisture level (60–70%) and immediately germinated, and in dehydration they lost their germinability because of the absence of the dehydration protection mechanism. Ultrastructural studies on the mature seed emryo of *A. hippocastanum* revealed that by the time of a full maturity it was formed from functionally active cells. It is typical of embrio cells in freshly harvested mature seeds of *A. hippocastanum* to have a great number of mitochondria with a well developed crista system, among plastids there prevail aminoplasts that contain numerous starch grains, the cell membrane system is fully developed, nuclei are located in cell centers and include nucleoli. A specific feature of seed embryo cells of *A. hippocastanum* is that after the termination ripening they do not produce protein bodies and contain insignificant quantities of stored lipids localized along plasmalemma (Fig. 5).

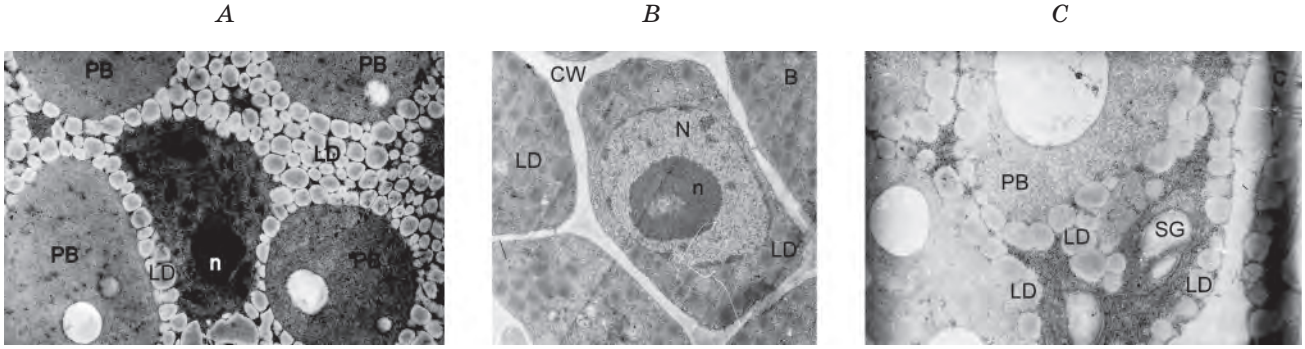

Fig. 4. **Cell substructure in the embryo axis of *Aesculus tataricum* L.:**
A — dry seed (deep physiological dormancy): PB — protein bodies, LD — lipid drops, N — nucleus, n — nucleolus (8000×); *B* — 120 days after cold stratification (12 000×): CW —cell wall; *C* — after JA treatment, 500 мг/л 48 hour (20 000×) [43]

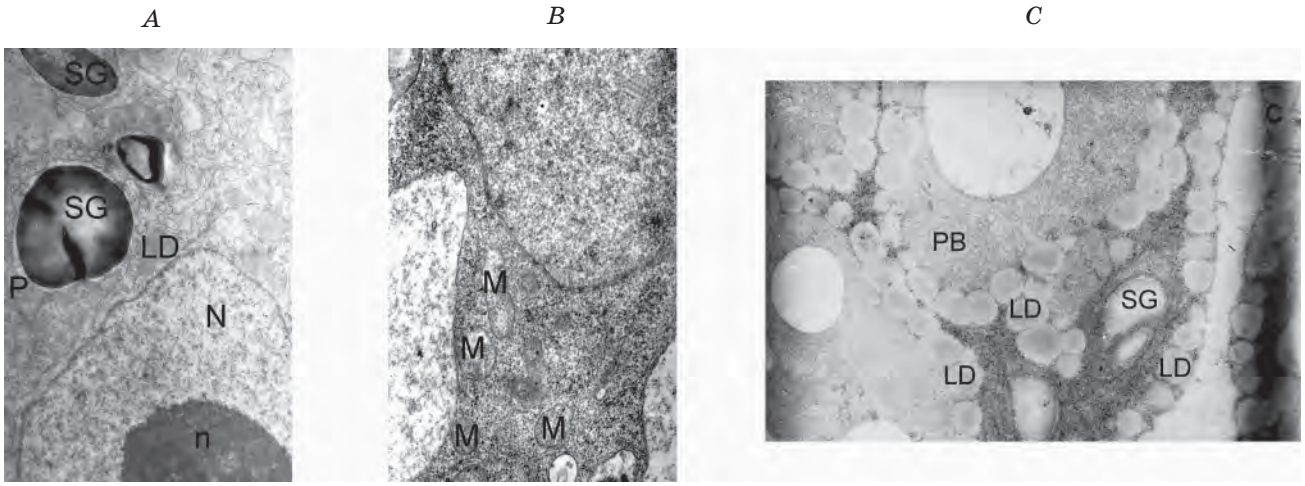

Fig. 5. **Cell substructure in the embryo axis of freshly harvested ripe *A. hippocastanum* seeds incubated on L.** P — plastid; LD — lipid drops; SG — starch grains; M — mitochondrion; *A* — (25 000×); *B* — (30 000×); *C* — (40 000×) [45]

Ultrastructural studies on cells of the embryonic axis incubated in water for 24 hours revealed the formation of the central vacuole, the cytoplasm was in a parietal position, the nucleus had a clear-cut double membrane envelope and was shifted to the plasmalemma, quite a number of lipid drops was hydrolyzed, quantity of starch grains in plastids decreased. The occurrence of such changes indicated that growth processes in the axis had begun (Fig. 6).

Exposure to JA at the concentration of 100 mg/l stimulated an isolated axis growth.

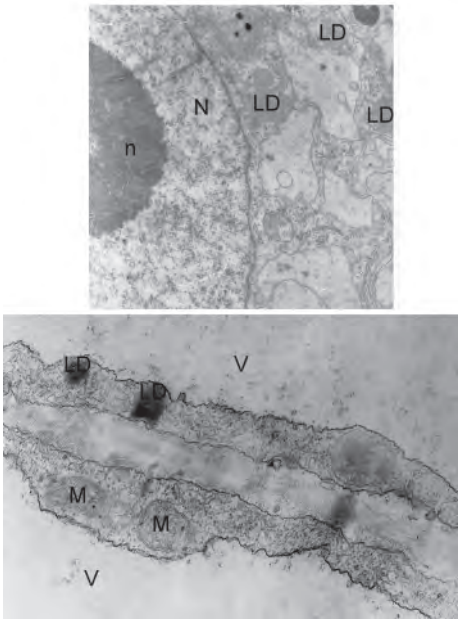

Fig. 6. **Cell substructure in the embryo axis of freshly harvested ripe *A. hippocastanum* L. seeds incubated in water:** LD — lipid drops; M — mitochondrion; N — nucleus, n — nucleolus, V — vacuole (40 000×) [45]

Lower hormone concentrations (10–50 mg/l) had almost no impact on morphometric parameters. JA concentrations of 250 mg/l completely inhibited the axis growth. Nevertheless, quite a number of lipid drops were generated along the plasmalemma, the central vacuole became more osmophilic (filled with precipitate). In aminoplasts, starch grains were visualized but organelles themselves swelled and their matrix gained an electronic transperancy (Fig. 7). The observed changes indicate that organelles decomposition are occurid [45]. Similar results were obtained when we studied recalcitrant seeds of *A. saccharinum* L. However, among plastids in mature embryo cells there dominated chloroplasts with a well- developed crista system and a greate number of protein bodies. Ptrotein bodies were also available. Chloroplast occurrence resulted in a bright green colouring of *A. saccharinum* L. mature seeds. Exposure to JA caused embryo tissue yellowing. A significant amount of lipid drops along the plasmalemma were produced. Chloroplasts swelled and their matrix lost its structuredness. Cell organelles were decomposed [43]. Thus, the pattern of JA action depended both on a stored substance type and seed physiological state. JA -treatment of *A. tataricum* L. orthodox seeds, whose basic stored substances are lipids, led to their degradation, deep dormancy release and germination initiation. However, in recalcitrant seeds of *A. hippocastanum* and *A. saccharinum*, which contained an insignificant amount of stored lipids, exposure to JA resulted in ultrastructural changes incompatible with seed germination.

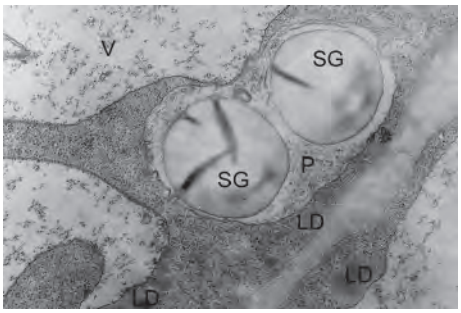

Fig. 7. **Cell substructure in the embryo axis of freshly harvested ripe *A. hippocastanum* L. seeds incubated in JA solution (250 мг/л):** P — plastid; LD — lipid drops; SG — starch grains; V — vacuole (40 000×) [45]

Influence on ageing processes

The effect of JA on organs ageing was studied in detail. Such typical syndromes of ageing as cell respiration, proteolytic and peroxydase activities were promoted in leaf segments through JA treatment. Structural chloroplast damages, photosynthetic activity reduction (as a marker of regular ageing) also had place following a jasmonate exposure. At the same time there was seen a quick decline in activity and decomposition of ribulose-1,5-bisphosphatcarboxylase, which as compared to other enzymes, is the most sensitive to JA influence [46, 47]. However, JA-treatment of isolated chloroplasts had no impact on ribulose-1,5- bisphosphatcarboxylase activity and chlorophyll content that is a proof of an indirect action of the hormone, which first affected other (non-chloroplast) cell components. Chloroplast ageing symptoms *in situ* may be evoked by signals from the cytoplasm. A clear evidence regarding a cellular mechanism of jasmonate action in ageing is missing. It was observed that JA and its derivatives caused a loss of the membrane integrity. The idea of a detrimental role of JA in ageing processes is based on the fact that jasmonates are synthesized from linoleic acid produced under effect of phospholypase D [3, 4]. Me-JA exogenous treatment during tomato fruit ripening terminated the lycopine accumulation and stimulated β-carotin synthesis that made fruits unripe and yellow. Me-JA was revealed to stimulate the ethylene biosynthesis, but repressed the activity of polygalacturonase — the key enzyme that affects the fruit softening [5].

Jasmonic acid and sex determination

One of the basic physiological functions of JA is the regulation of the plant male and female reproductive organs creation [48–52]. JA regulates the development of anthers and pollen maturation [53]. It was shown that *Arabidopsis thaliana* mutants with disturbances in the JA synthesis are sterile in the male line. Sterility caused by mutations in the JA biosynthesis may be overcome via a jasmonate exogenous treatment [54]. It was discovered that the corn gene TS1 that brings about the pollen supplier feminization in inflorescence is involved in the JA biosynthesis. When there was no functioning gene TS1, LOX activity was missing and endogenous JA content in developing inflorescences decreased [55].

In *Arabidopsis thaliana*, for which there had been obtained quite a number of mutants with disturbances in the hormonal status and developing flowers the regulation of flowering and floral development was studied most thoroughly [56–58]. The signaling systems of the floral morphogenesis and sex expression regulation are characterized by the hierarchy and plurality. Plurality of internal signals involving proteins and phytohormones ensures the gene expression hierarchy in flower development [56–59]. Almost all phytohormones, for example, participate in androecium formation, petel development is controlled mainly by IAA and JA while gynoecium development is regulated by IAA [57]. Phytohormone content and ratio vary in response to internal and external factors impact. The pattern of JA and protein-switches action depend on the level of their concentration and activity. Homeotic genes that control the flower structure are regarded to be targets for a phytohormonal signal, in particular for JA [60]. Class C homeotic genes (AGAMOUS) control processes of stamen and carpel formation and can affect the phytohormone synthesis producing feedback loops. It was revealed that phytohormones act on the floral development through interrelations and cross-regulation [61]. Thus, IAA and JA regulate elongation of floral organs making them more attenuatous [57]. Studies on stamen development in *Arabidopsis thaliana* showed that synthesis of proteins DELLA (named after the similar amino-acid sequence) is controlled by gibberellic acid (GA) that interacts with other phytohormones [62]. GA is seen as a negative signal for DELLA proteins. DELLA proteins interact with the

jasmonate-ZIM domain and activate JA-pathway preventing AtMYC2 repression.

It was shown that JA is involved in the regulation of the gametophyte development early steps and in the cultivation of sporophyte protoplasts in the fern *Platycerium bifurcalum* (Cav.) C. Chr. JA had no impact on spore germination and production of primary rhizoids, but it contributed to an early development of gametophytes that was confirmed by the length and number of primary rhizoids as well as by an increase in the cell quantity. JA concentration of 1 μM stimulated gametophyte transition from a thread-like protenema to a flat prothallium. Optimal elongations of primary rhizoids and the highest cell division activity were observed at JA concentrations between 0.01–1 μM while the greatest amount of rhizoids was produced at concentrations of 0.1–1 μM. At JA concentrations being higher than 1 μM, we observed the cell elongation and division repression except for studies on JA effects on spore germination processes [63].

Involvement in adaptation processes

JA and its derivatives are involved not only in the regulation of growth and development but in adaptation to stress factors too [64]. In recent years intensive studies have substantially advanced our understanding of jasmonates physiological role and mechanisms of their action. The data obtained indicate that jasmonates may mediate chemical reactions associated with the plant stress resistance. They directly affect the activity of individual enzymes (it is doubtful that the phytohormone, acting in very low concentrations, may directly have impact on enzymes activity) and also express the jasmonate-induced proteins synthesis. Among them there are inhibitors of proteinase and tripsin, napain, crucipherin, vegetative storage proteins, phenilalanin-amonium-lyase i chalcon synthetase [65] ω-3 fatty acids desaturase [66], LOX-1 and LOX-2, and also allen oxide synthase [67–69]. Exogenous Me-JA evokes the formation of lipid bodies in *Brassica napus* embryos [70] that are developing and can be utilized as an additional resource in cold or osmatic stresses [71]. Studies on *Arabidopsis thaliana* provided proof that depending on the type of stress JA synergetically interacts with ethylene [72] and synergetically and antagonistically with salycilic [73] and abscisic acids (ABA) [74].

Studies on tomato mutants def1 with disturbances in the JA biosynthesis that manifest themselves in a low amount of synthesized JA in response to an injury demonstrated their sensitivity to *Manduca sexta*. That is an indirect evidence of octadecanoids metabolic products involvement in protection against insects [75, 76]. Exposure of potato leaves to exogenous LA led to a local protection against pathogens [77, 78]. In response to applied elicitors and incompatible phytophthtora strains, potato plant tissues accumulated JA and OPDA [79, 80], and on the contrary, no JA synthesis occurred in pathogen-sensetive potato species affected by *Phytophthora infestans* [81, 82]. It means that jasmonates were accumulated when there was some antagonism between a host plant and pathogen. JA applied in combination with biogenic elicitors enables to increase the effectiveness and protection reaction rates of the latter and to promote reparation processes after injuries resulting from PI gene expression [83]. A combined elicitor and JA application increased the velocity of an induced protective effect propagation in potato tissues. A high intensity of propagation of the systemic immune response made it possible to promote the onset of the induced resistance period in higher plants.

Terpenoid volatile organic compounds (VOC) are produced in spore-bearing plants via JA-dependent pathway. Nevertheless, the VOC content in ferns injured by plant feeders or after other mechanical damages is much lower than that of other higher plants. So, in *Pteridium aquilinum* with fronds injured by *Spodoptera littoralis* and by *Strongylogaster multifasciata*, and also with mechanical damages there was produced an insignificant number of attractants, among which terpinoids were dominant. Release of such substances was stimulated by application of exogenous JA, which activates the attractant synthesis in flower plants. Mechanically injured leaves of bean, corn, cotton, poplar, tobacco, potato and other angiosperms were shown to generate a substantial amount of JA [84]. And vice versa, exposure of fern fronds to exogenous JA resulted in an intensive release of VOC mixtures. An exogenous application of JA precursors — 12-OPDA and α-linolenic acid also caused a VOC release, but it was less intensive than after a direct JA treatment. Phosmidomicine and mevinoline that are inhibitors of the mevalonic and non-mevalonic pathways in angiosperms blocked a release of terpenoids. It is assumed that injuries of fern fronds in *C. multifasciata* and *C. littoralis* prevent the synthesis of JA in quantities

required for activation of the mevalonic and non-mevalonic pathways and a further release of VOC. It means that in contrast to flower plants, ferns need no attractants for protection although they possess this mechanism [85]. Thus, biotic and abiotic stress factors activate various signaling systems in plant cells that optimize the complex of protective responses. Such responses depend not only on a stress type, pathogen species specificity but also on the plant evolutionary level. In addition to JA, the signaling compound group also include salycilic acid, ethylene, ABA and some other metabolites. The interralation between the various signaling systems may be independent, synergetic and antagonistic. This enables the plant to form strategically optimal protective responses to biotic and abiotic stresses. So, potato signaling molecules (salicylic and jasmonic acids) affect the development of an injury periderm in different ways. As JA locally and systematically stimulated the reparation of potato tissues and evoked some increase in proteinase inhibitor levels, salicylic acid did not promote these processes but even blocked proteinase inhibitor formation [86]. In high concentrations salicylic and jasmonic acid showed antagonism in pea plants whereas in low concentrations, vice versa, they demonstrated synergism. Both acids produced mainly specific and in some cases unidirectional changes in protein content. Salicylic acid evoked the gene expression in some proteins. Changes provoked by Me-JA were related to a less number of proteins as compared to those caused by salicylic acid. Combined salicylic acid and Me-JA action resulted in summation of changes effects in protein content [87]. Between JA and ethylene there occurs an additive effect. These phytohormones act interactively, activating genes that code for proteinase inhibitors and protective proteins defencine [88]. There is an evidence that in some cases jasmonates and ethylene promote a signaling function of salicylic acid that causes PR-gene expression [89].

Jasmonic acid and immunity

Pathogens activate JA production in plant cells and it indirectly affects the reorganization of cortical and transvacuolar microfilaments, the octine-dependent polar transport of vesicles with secretion products in the infection place and a local activation of caloci synthesis [90]. It is known that closed stomata in plant leaves prevent the pathogen bacteria penetration. However, microorganism virulent strains, producing a phytotoxic compound coranatin that is a biological analogue of JA, are able to overcome this protective barrier and evoke stomata reopening [91]. Cytoskeleton restructuring that occurs during the formation of plant protective responses is associated with cells repolarization and creates physical barriers against pathogen penetration [92]. JA and Me-JA were found to disturb the cortical microtubule organization in tobacco suspension culture cells of the line BY-2 and in potato [93]. Exogenous jasmonates contributed to the colonization and arbuscular structure further development while the level of endogenous jasmonates controlled the activity of arbuscle structures [94]. Nevertheless, the signaling pathway involving JA was required also to repress the development of symbiotic arbuscalar mycorhiza of the fungus *Glomus intraradices* on tomato plants [95, 96].

The jasmonate physiological functions include the induction of plant immune reactions. However, it is still unclear if JA and its methyl ether are systemic signal molecules or intracellular messengers and they probably combine these two functions. It was revealed that JA is activated by elicitors and systemine. The protein systemine, produced in affected tissues after the hydrolysis of predecessor protein prosystemine, is transported via phloem to target cells, is bound to plasmalemma receptors and activates the synthesis of JA, which, in its turn, stimulates the expression of quite a number of genes. They include genes, which code: 1) peptides that form mechanical barriers to infection in cell walls; 2) enzymes involved in the synthesis of phytoalexines and phenol compounds that are characterized by protective effects; 3) synthesis of protease inhibitors that protect plants attacked by leaf-eating insects or infected by pathogens; 4) sulfurous peptides with fungicide properties — thionine, osmotin and protein RIP 60 [96].

Transduction of jasmonate signals

A systemic signal generated in an affected leaf was found to activate protective responses in remote unaffected parts of the plant. Jasmonates are important components of the mobile injury systemic signal [97, 98]. Localization of JA biosynthesis enzymes in vascular bundles indicates that JA is brobably involved in the alarm signal transduction. It is also proved by the prosystemine availability and by production of systemine in vascular bundle parenchyma cells. [99, 100]. Localization of prosystemine and JA biosynthesis enzymes in cells of various types

testifies to the fact that systemine is bound to SR160 protein on the cell surface. This binding initiates the synthesis of JA and its futher transport along the phloem [100, 101]. That requires an intact phloem since a period of the system response depends on a speed of JA transportation along the phloem. JA locally applied on the leaf surface and also local *P. syringae* infection evoked a systemic expression of proteinase inhibitor genes [102]. Studies on expression of proteinase inhibitor genes 2 hours after a mechanical damage or insect attack showed that a speed of signal propagation in a tomato leaf was 5 sm/h [103–105]. ^{14}C-labelled JA applied locally was transferred along the phloem to parts remote from the injection site for several hours [106]. Thus, the synthesis of JA *de novo* is not required as prior condiotion for a systemic response [106, 107].

It was revealed that leaf-eating caterpillar excrements applied to a tobacco affected leaf surface caused an increase in the JA content while only a mechanical injury separately did not produce that effect [108]. It appears that caterpillar excrement composition includes elicitors that complement and complicate the effect of a negative biotic factor. It is also possible that plants are able to distinguish a mechanical injury from that caused by insects and thus they determine whether it is necessary to activate the system protective mechanisms or just confine themselves to a local protection.

JA in biotechnology

Jasmonic acid and its derivatives are applied in agriculture as biologically active substances that regulate plant metabolic processes. It was found that an exposure of vegetable vegetative plants (potato, tomato, cucumber, onion) to JA in the fields prior to the first affection symptoms contributed to a substantial improvement of plant resistance [109]. A presowing treatment of barley seeds by jasmonic and succinic acid solutions promoted plant growth at the early development stages, reduced moisture losses in leaves and growth inhibition in drought conditions [110]. A jasmonic and salycilic acid mixture is used in potato plant cultivation in vitro to obtain an improved sowing material resistant to phytophthora [111]. A presowing exposure of millet seeds to JA improved the heat resistance in seedlings and adult plants due to the reduction in the content of lipid peroxidation products and increase in chlorophyll content. It was obsereved a rise in the number and mass of grains in panicles. A positive JA effect substantially showed itself in unfavourable ground conditions that is an evidence of its prolonged influence on the plant stress-protective systems [112]. A presowing exposure of Triticum aestivum seeds to a salycilic and jasmonic acid mixture reduced a degree of *Septoria nodorum* development on leaves [113]. Reports by M. Zenk showed that in suspension cultures *Corydalis claviculata, Crotolaria cobalticola, Eschscholtzia californica, Glycin max, Lactuca sativa, Lycopersicum esculentum, Rauvolfia canescens, Rubia tinctorum, Ruta chalepensis* and *Sarcocapnos crassifolia* affected by an exogenous elicitor (a fragment of the fungus cell wall) there occurred a quick synthesis of JA. An exogenous ME-JA applied to the suspension culture of the above plants initiated de novo the transcription of phenilalanin-amonium-lyase enzyme gene, which is involved in plant protection [114]. At the same time, Me-JA applied to the infiltration medium had no effect on *Agrobacterium*-mediated transient expression and accumulation of the recombinant protein in *Nicotiana excelsior* that should be taken into account in biotechnological developments aimed at the protein-oriented production [115].

Jasmonic acid was discovered more than half a century ago. Intensive studies in recent years have substancially advanced our knowledge on the biological significance, metabolism and mechanisms of jasmonate effects. Jasmonic acid is a powerful tool in the study and explanation of such physiological processes as seed germination, ageing, sex determination. Jasmonates are regarded as key compounds in the systemic signaling. However, knowledge about pathways and mechanisms of signaling induced in plant cells by jasmonic acid is rather limited and they require further investigations. To date, jasmonic acid and its derivatives are applied in biotechnology, medicine, industry, agriculture as highly technological regulators of metabolic processes both as independent biologically active substances and in combination with other compounds.

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ЖАСМОНОВА КИСЛОТА: РОЛЬ У БІОТЕХНОЛОГІЇ ТА РЕГУЛЯЦІЇ БІОХІМІЧНИХ ПРОЦЕСІВ РОСЛИН

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Проаналізовано дані літератури та результати власних досліджень авторів щодо ролі жасмонової кислоти в регуляції біохімічних процесів рослин та її можливого застосування в біотехноогії. Розглянуто основні етапи синтезу жасмонатів. Висвітлено властивості ензимів, які беруть участь у біосинтезі жасмонатів. Наведено дані щодо участі жасмонової кислоти та її похідних у регуляції проростання насіння, процесів старіння, детермінації статі, утворенні целюлози, особливостей взаємодії з абсцизовою кислотою, а також в експресії генів, формуванні імунної реакції за стресів та уражень патогенами. Описано вплив жасмонової кислоти на ультраструктуру клітин. Розглянуто перспективи використання жасмонатів у біотехнологічних розробках.

Ключові слова: біотехнологія жасмонової кислоти, регуляція реакцій метаболізму.

ЖАСМОНОВАЯ КИСЛОТА: РОЛЬ В БИОТЕХНОЛОГИИ И РЕГУЛЯЦИИ БИОХИМИЧЕСКИХ ПРОЦЕССОВ РАСТЕНИЙ

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Проанализированы данные литературы и результаты собственных исследований авторов о роли жасмоновой кислоты в регуляции биохимических процессов растений и ее возможном применении в биотехнологии. Рассмотрены основные этапы синтеза жасмонатов. Описаны свойства энзимов, которые принимают участие в биосинтезе жасмонатов. Приведены данные об участии жасмоновой кислоты и ее производных в регуляции прорастания семян, процессов старения, детерминации пола, образовании целлюлозы, особенностях взаимодействия с абсцизовой кислотой, а также в экспрессии генов, формировании иммунной реакции при стрессах и поражениях патогенами. Освещено влияние жасмоновой кислоты на ультраструктуру клеток. Рассмотрены перспективы использования жасмонатов в биотехнологических исследованиях.

Ключевые слова: биотехнология жасмоновой кислоты, регуляция реакции метаболизма.