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ACTION OF METHYL JASMONATE AND SALT STRESS ON ANTIOXIDANT SYSTEM OF *ARABIDOPSIS* PLANTS DEFECTIVE IN JASMONATE SIGNALING GENES

T. O. YASTREB[1], Yu. E. KOLUPAEV[1,2], N. V. SHVIDENKO[1], A. P. DMITRIEV[3]

[1]Dokuchaev Kharkiv National Agrarian University, Ukraine;
e-mail: plant_biology@ukr.net;
[2]Karazin Kharkiv National University, Ukraine;
[3]Institute of Cell Biology and Genetic Engineering,
National Academy of Sciences of Ukraine, Kyiv;
e-mail: dmitriev.ap@gmail.com

Role of jasmonate signaling in the regulation of stress-protective systems in Arabidopsis under salt stress remains insufficiently studied. For its clarification, comparative studies with mutants lacking various protein components of jasmonate signaling are advisable. In this connection, effects of methyl jasmonate (MJ, 50 μM) and salt stress (NaCl, 150 mM) on functioning of antioxidant and osmoprotective systems of wild-type Arabidopsis plants (Col-0) and ones defective in jasmonate signaling, namely coi1 (mutant for gene coding the protein COI1, which participates in removal of repressor proteins of transcription factors of jasmonate signaling) and jin1 (mutant defective in gene encoding the transcription factor JIN1/MYC2, one of the key in jasmonate signaling), were investigated. Salt stress inhibited growth of plants of all three genotypes. Treatment with MJ before salt stress positively influenced only the growth of wild-type plants. In contrast to mutants coi1 and jin1, Col-0 plants treated with MJ, under conditions of salt stress, kept close to the control values of water and total chlorophylls content, and the content of carotenoids increased. The coi1 plants under normal conditions differed from wild-type plants and jin1 mutants by reduced activity of guaiacol peroxidase and catalase and increased proline content. Treatment with MJ did not affect the activity of antioxidant enzymes and proline content in both mutants defective in jasmonate signaling. Under salt stress, the activity of superoxide dismutase, catalase and guaiacol peroxidase, as well as the content of proline and anthocyanins, in wild-type plants treated with MJ, were significantly higher than in control plants. The role of jasmonate-dependent protective systems in resistance of Arabidopsis plants to salt stress is discussed.

K e y w o r d s: Arabidopsis thaliana, coi1, jin1, methyl jasmonate, signaling, salt stress, stress-protective systems.

At present, specific proteins have been identified for the transduction of jasmonic acid (JA) signal into the genetic apparatus of plant cell [1, 2]. It is known that the physiological activity of JA is manifested after its transformation into jasmonoyl-L-isoleucine. In this regard, the JAR1 protein, displaying activity of aminoacyl synthetase, which conjugates amino acids with jasmonic acid, is considered as one of the first components of chain of transduction of its signal into the genetic apparatus [3]. At the same time, the COI1 protein, which is part of the SCF/COI1 complex conjugated with ubiquitin enzymes, is considered to be the jasmonate receptor specifically binding jasmonoyl-L-isoleucine [4]. An interaction of jasmonoyl-L-isoleucine with COI1 leads to its activation and interaction with JAZ- (Jasmonate-Zim-Domain) proteins, JA-signal repressors that are sent to 26S proteasomes for degradation [5]. Consequently, a signaling pathway of JA is opened for specific transcription factors MYC2, MYC3 and MYC4 [4]. It is believed that JIN1/MYC2 is one of the major positive regulators in jasmonate-inducible gene expression in *Arabidopsis thaliana* [5, 6].

Recently, JA and its derivatives are considered to be important regulators of plant resistance not only to biotic, but also to abiotic stresses, incl. to

salt [7, 8]. Earlier, we showed less effective functioning of stress-protective systems under conditions of salt stress in *Arabidopsis* mutant *jin1* treated with JA compared to wild-type plants [9]. However, the transcription factor JIN1/MYC2 is involved in the effects of not only JA but also abscisic acid (ABA) [10-13] and, probably, nitric oxide [14, 15]. Moreover, a number of studies have indicated the involvement of the transcription factor JIN1/MYC2, previously activated by jasmonate signal, in the regulation of ABA-dependent salt stress reactions [16]. Therefore, it remains unclear whether the low salt tolerance of the *jin1* mutants is due to the violation of jasmonate signaling, or the differences in salt tolerance of wild-type plants and the *jin1* mutants are due to the involvement of the JIN1/MYC2 transcription factor in other signaling pathways. On the other hand, it is known that the transduction of jasmonate signal occurs not only with the help of the JIN1/MYC2 transcription factor, but also with the ERF family proteins (ERF1, ERF2, ERF5 and ERF6), which combine effects of JA and ethylene and are involved in regulation of expression of a number of genes [5, 17].

Thus, it is relevant to carry out comparative studies with mutants lacking various protein components in order to clarify the role of jasmonate signaling in the regulation of stress-protective systems of *Arabidopsis* under salt stress. Functioning of the antioxidant and osmoprotective systems in the *Arabidopsis* mutant defective in COI1 jasmonate receptor under salt stress has not yet been studied, although there are data indicating its role in regulating biosynthesis of flavonoid compounds, expression of non-specific peroxidase and ascorbate peroxidase genes [18, 19], which are important for adaptation to salinity and other stress factors.

In connection with the foregoing, the aim of the study was to compare the functioning of the antioxidant and osmoprotective systems of *coi1* (*coronatine insensitive 1*) and *jin1* (*jasmonate insensitive 1*) mutants, defective in jasmonate signaling, and wild-type *Arabidopsis thaliana* plants under salt stress in the presence and absence of exogenous methyl jasmonate (MJ).

Materials and Methods

Five-week-old plants of *Arabidopsis thaliana* L. wild-type (Col-0) and *coi1* and *jin1* lines were used in experiments. Plants were grown in water culture on Hoagland medium with modifications [20] at 24/18 °C (day/night), illumination of 6000 lux and 10 h photoperiod [9]. MJ (Sigma–Aldrich, USA) at a concentration 50 μM was inserted into the culture medium and plants were incubated on it for 24 h. The optimal concentration of MJ was determined in preliminary experiments, where the effect of 10-200 μM MJ on growth parameters of Col-0 under the salt stress (150 mM) was evaluated. At the end of the MJ treatment time, plants of three genotypes, treated and untreated with phytohormone, were subjected to salt stress by transferring to the medium supplemented with 150 mM NaCl and keeping for 24 h.

For determination of the water content and biochemical analyzes, plates of mature leaves of the basal rosette were used. The assays were performed 24 h after the transfer of the plants to the medium with sodium chloride or to the nutrient medium without MJ.

The amount of water in the leaves was determined by the usual weighing method, drying the samples at 103 °C to a constant mass.

Photosynthetic pigments were extracted from the leaves with ethanol and their content was determined by spectrophotometric method [21]. The pigment content was expressed as mg/g dry weight of the leaves.

The activity of antioxidant enzymes was determined by methods described in detail earlier [22]. The weighed leaves were homogenized in the cold in 0.15 M K, Na-phosphate buffer (pH 7.6) containing EDTA (0.1 mM) and dithiothreitol (1 mM). The homogenate was centrifuged at 8000 g for 10 min at 4 °C on MPW 350R centrifuge (Poland). The supernatant after centrifugation was used for the analysis. The activity of cytosolic superoxide dismutase (SOD, EC 1.15.1.1), represented predominantly by Cu/Zn-SOD [23], was determined at pH 7.6 using a method based on the ability of the enzyme to compete with nitroblue tetrazolium for superoxide anions, formed due to the aerobic interaction of NADH and phenazine methosulfate. Catalase activity (EC 1.11.1.6) was determined at pH 7.0 by the amount of decomposed hydrogen peroxide per unit of time. The activity of guaiacol peroxidase (EC 1.11.1.7) was determined using guaiacol as the hydrogen donor and hydrogen peroxide as the substrate. The activity of SOD and guaiacol peroxidase was expressed as arbitrary units/(g dry weight·min), catalase activity – as mM H_2O_2/(g dry weight·min).

The proline content in the leaves was analyzed using a ninhydrin reagent according to Bates et al. [24] and expressed as μM/g dry weight.

To determine the content of anthocyanins, the weighed plant material was homogenized in 1% HCl solution in methanol [25]. After centrifugation of the homogenate at 8000 g for 15 min, the optical density of the supernatant was determined at 530 and 657 nm. When calculating the content of anthocyanins, the amount of nonspecific absorption at 657 nm was taken into account [26]. The content of anthocyanins was expressed in conventional units as the value $(A_{530} – 0.25A_{657})$/g dry weight.

The experiments were performed in triplicate biological replication and each experiment was independently reproduced 3 times. The data are presented as mean values and standard errors and are considered significant at $P \leq 0.05$ except the specially stipulated cases. The significance of the differences was evaluated by Student's *t*-test.

Results and Discussion

Growth indicators of plants under conditions of salt stress. Under the action of 150 mM NaCl, a decrease in the growth of biomass of wild-type plants and both *Arabidopsis* mutants defective in jasmonate signaling was observed (Fig. 1). Treatment with MJ under conditions of salt stress improved the growth of wild-type plants and did not have a positive effect on growth rates of *coi1* and *jin1* mutants.

Water content in leaves under salt stress conditions. Under normal conditions, the water content in plant leaves of different genotypes did not differ significantly (Table). Treatment with MJ did not affect its content under these conditions. After salt stress, the water content in leaves of plants of all genotypes decreased. Pre-treatment with MJ promoted the maintenance of water proportion close to normal in the wild-type plants under salt stress. At the same time, it did not significantly affect the water content in leaves of both mutants defective in jasmonate signaling (Table).

Content of photosynthetic pigments in leaves. It is known that one of the markers of plant resistance to the action of stress factors, incl. salinity, is the ability to preserve a pool of photosynthetic pigments [27]. The content of chlorophylls and carotenoids in leaves of *Arabidopsis* of three genotypes did not differ significantly under normal conditions (Fig. 2). In the absence of salt stress, the treatment of plants with MJ did not significantly affect the content of photosynthetic pigments.

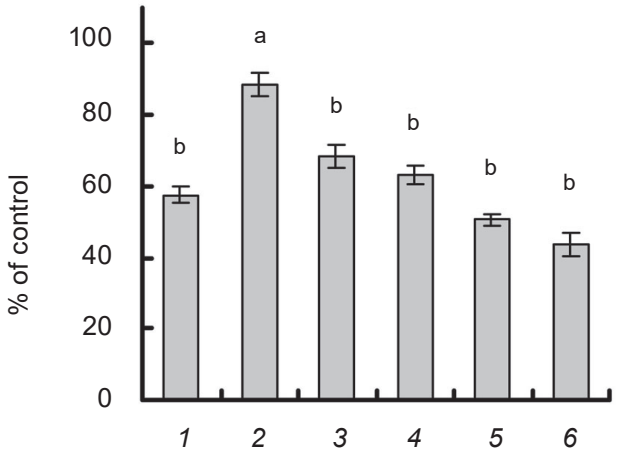

Fig. 1. Growth of biomass of Arabidopsis plants under salt stress (150 mM NaCl). Here and in Fig. 2-4: 1 – Col-0 (control); 2 – Col-0 (methyl jasmonate, 50 μM); 3 – coi1 (control); 4 – coi1 (methyl jasmonate, 50 μM); 5 – jin1 (control); 6 – jin1 (methyl jasmonate, 50 μM); values with the same superscript letters are not significantly different (P ≤ 0.05)

Under the influence of salt stress, the chlorophylls content in plants of all genotypes decreased. Treatment with MJ contributed to the preservation of the chlorophylls pool in wild-type plants and did not significantly affect its value in *coi1* and *jin1* genotypes (Fig. 2). Also under salt stress conditions, MJ treatment promoted an increase in the content of carotenoids in leaves of Col-0 plants.

Activity of antioxidant enzymes in plant leaves. The activity of the key antioxidant defense enzyme, SOD, in the various genotypes of *Arabidopsis* under normal conditions somewhat differed (Fig. 3, *A*).

Water content in leaves of Arabidopsis plants (%)

Genotype	Control	Methyl jasmonate (50 μM)	NaCl (150 mM)	Methyl jasmonate (50 μM) + NaCl (150 mM)
Col-0	91.30 ± 0.21^{a}	91.00 ± 0.24^{a}	88.60 ± 0.22^{b}	91.6 ± 0.2^{a}
coi1	92.0 ± 0.2^{a}	91.80 ± 0.28^{a}	89.30 ± 0.32^{b}	89.50 ± 0.25^{b}
jin1	92.10 ± 0.27^{a}	91.5 ± 0.3^{a}	89.70 ± 0.25^{b}	$90.20 \pm 0.22^{a,b}$

Values with the same superscript letters are not significantly different ($P \leq 0.05$)

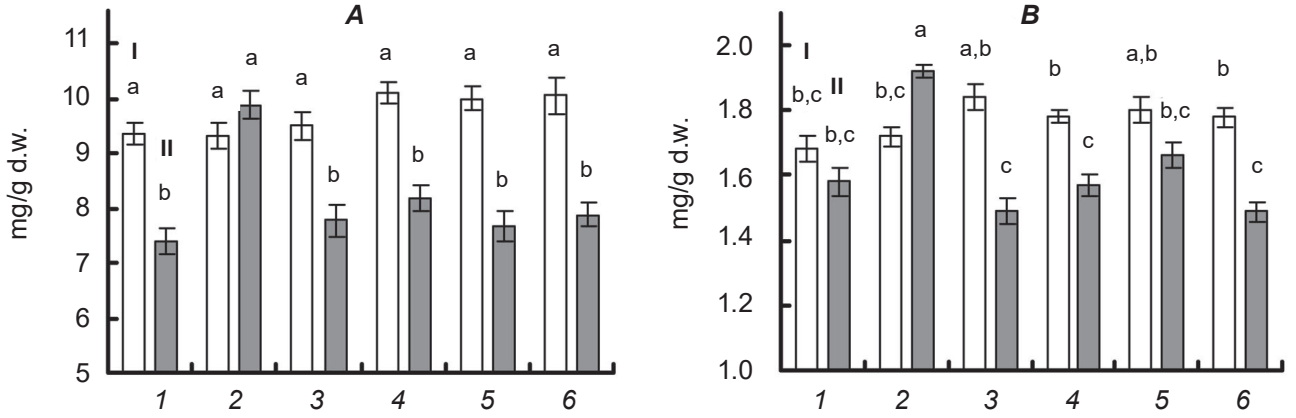

*Fig. 2. Content of chlorophyll (**A**) and carotenoids (**B**) in leaves of Arabidopsis. Here and in Fig. 3-4: I – without stress, II – NaCl (150 mM)*

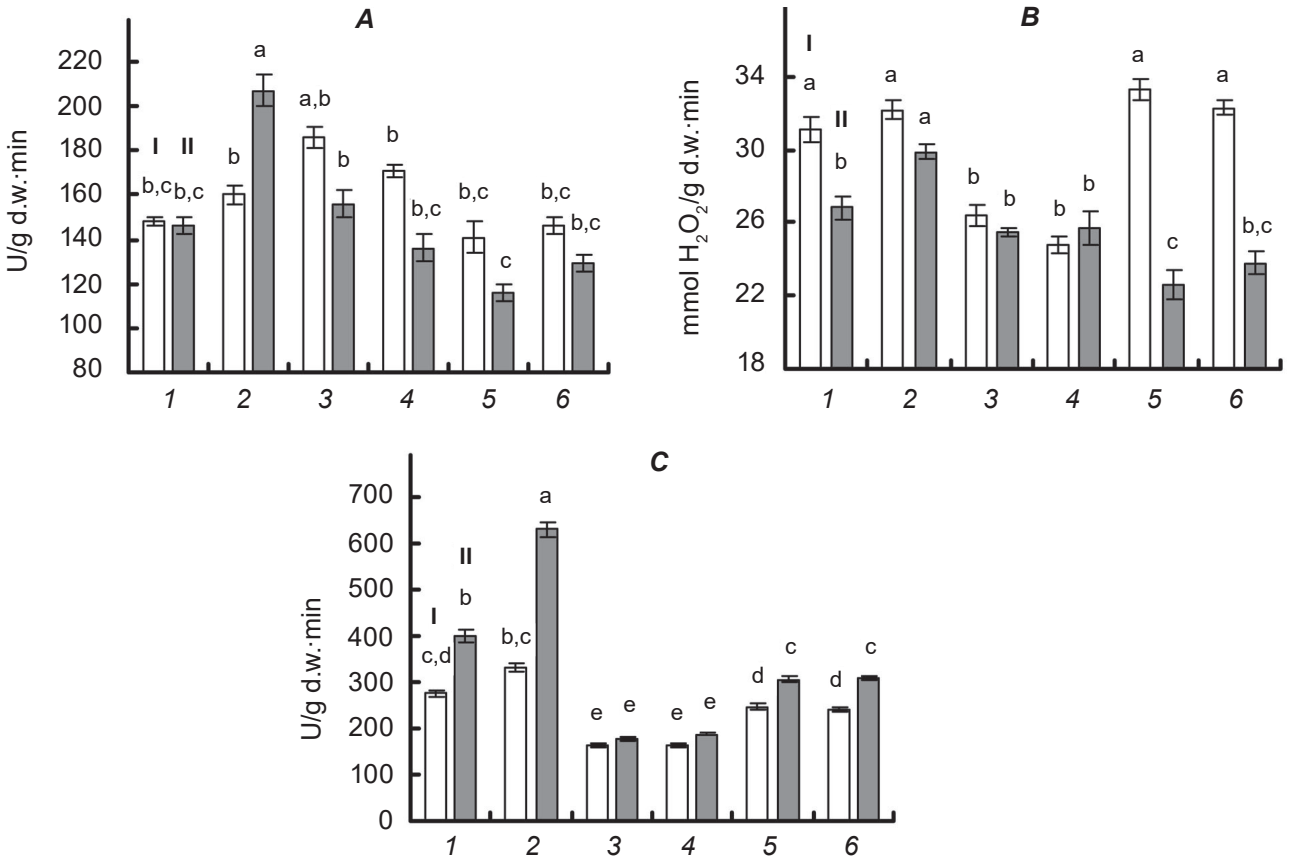

*Fig. 3. Activity of SOD (**A**), catalase (**B**) and guaiacol peroxidase (**C**) in leaves of Arabidopsis*

Thus, its value in *coi1* plants was higher than that in wild-type plants. Treatment with MJ in the absence of stress did not significantly affect the enzyme activity in leaves of plants of all the investigated genotypes.

Under salt stress, the SOD activity in wild-type plants did not change significantly, but it decreased slightly in mutants defective in jasmonate signaling (Fig. 3, *A*). Treatment with MJ caused an increase in the activity of SOD under salt stress only in wild-type plants.

The catalase activity under physiologically normal conditions in plants of the *jin1* genotype did not differ from that in the wild-type, while at the same

time it was noticeably lower in *coi1* plants (Fig. 3, *B*). Treatment with MJ had no effect on catalase activity in all three genotypes in the absence of stress.

Under the influence of salt stress, the enzyme activity was significantly reduced in *jin1* plants and to a lesser extent in wild-type plants. In *coi1* plants, it did not change significantly. Treatment with MJ contributed to the preservation of values of catalase activity, characteristic to normal conditions, in wild-type plants (Fig. 3, *B*).

Basic values of the activity of guaiacol peroxidase in *Arabidopsis* plants of different genotypes differed markedly (Fig. 3, *C*). Thus, in *jin1* and especially *coi1* plants, it was lower in comparison with the value of wild-type plants. Treatment with MJ promoted an increase in the activity of the enzyme in wild-type plants and did not affect its values in mutants defective in jasmonate signaling.

Under salt stress, the activity of guaiacol peroxidase increased in wild-type plants and to a lesser extent in the *jin1* mutants, and in the *coi1* mutant it remained low. Treatment with MJ caused an additional increase in the enzyme activity in wild-type plants after salt stress (Fig. 3, *C*).

Proline content in leaves. Under physiologically normal conditions, the amount of proline in leaves of *coi1* mutants was approximately twice as high as in wild-type plants and in the *jin1* mutants (Fig. 4, *A*). In the absence of stress, MJ treatment did not cause changes in proline content in all three genotypes.

In MJ-untreated Col-0 plants, under salt stress, the proline content increased more than 4-fold, and in plants pretreated with phytohormone it increased approximately 6-fold. The *jin1* and *coi1* mutants also showed an increase in proline content in response to salt stress, but pretreatment with MJ did not significantly affect its amount (Fig. 4, *A*).

Content of anthocyanins in leaves. Under normal conditions, the content of anthocyanins in plants of all three genotypes did not differ (Fig. 4, *B*). Treatment with MJ caused its increase in wild-type plants, but did not affect this index in *coi1* and *jin1* mutants.

After salt stress, the content of anthocyanins in plants of three genotypes decreased. MJ treatment mitigated this effect only in Col-0 plants (Fig. 4, *B*).

Jasmonate-dependent regulation of protective systems in Arabidopsis plants. Discussing the results, first of all, it should be noted that there are noticeable differences in biochemical indicators studied in *Arabidopsis* plants of different genotypes. Thus, the *Arabidopsis coi1* mutant differed from wild-type plants by a higher SOD activity, but reduced catalase and especially guaiacol peroxidase activities (Fig. 3). Also, for these plants, characteristic proline content was higher than in other genotypes (Fig. 4, *A*). It can be assumed that an increase in the proline content, which has antioxidant properties [28], compensates to a certain extent the low activity of enzymes that destroy hydrogen peroxide for the plants of this genotype (Fig. 3). The literature describes the effects of functional interaction of enzymatic antioxidants and proline, as well as their interchangeability [29]. Note that the differences in biochemical parameters in the *jin1* mutants from those in wild-type plants were not as significant as those of the *coi1* mutants. Apparently, the closure of jasmonate signal associated with the *coi1* mutation (gene coding the jasmonate receptor COI1) is more stringent than the *jin1* mutation. This may be due to the fact that other

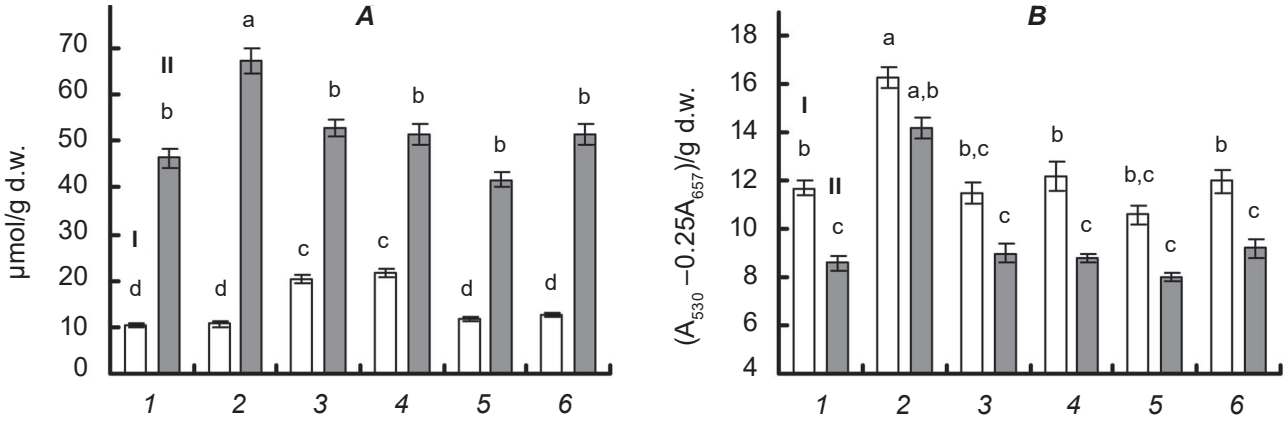

*Fig. 4. Proline (**A**) and anthocyanins (**B**) content in leaves of Arabidopsis*

protein components are involved in transfer of jasmonate signal to genetic apparatus, in particular, the already mentioned ERF protein [5]. It is possible that the presence of alternative transcription factors in *jin1* plants can provide a partial transduction of the jasmonate signal in genetic apparatus. So, after pretreatment with MJ, these plants showed a tendency to increase the proline content on the background of salt stress (Fig. 4, *A*). Under stress conditions, the activity of guaiacol peroxidase increased in *jin1* plants (Fig. 3, *C*). Such effects were not characteristic for *coi1* mutants defective in the gene encoding the immediate receptor of jasmonate.

On the whole, in both mutants defective in jasmonate signaling (*coi1* and *jin1*), after MJ treatment, unlike wild-type plants, there was practically no increase in salt tolerance. This was expressed in the absence of a positive effect of MJ on the growth, water and photosynthetic pigments content in these genotypes under salt stress (Fig. 1, 2, Table). In literature, there are data on the participation of proteins both COI1 [18] and JIN1/MYC2 [6] in the positive regulation of flavonoid content, incl. anthocyanins. The jasmonate signal appears to be important for the regulation of the prolin content, a multifunctional protector participating in osmoregulation, antioxidant protection and maintenance of protein functional activity under salt stress [28]. Thus, the proline content in soybean leaves [30] and banana fruits [31] increased under the influence of exogenous MJ. A positive relationship was established between expression level of JIN1/MYC2 gene and accumulation of proline. It is noteworthy that proline can have a positive effect on the accumulation of anthocyanins in plants under stress conditions [32]. However, the mechanisms of this influence are still unclear. In the conditions of our experiments, wild-type *Arabidopsis* plants treated with MJ under conditions of salt stress showed an increased proline content and a pool of anthocyanins was preserved (Fig. 4), that probably prevented oxidative damage.

An important component of the effect of jasmonate under salt stress, apparently, is its participation in the regulation of antioxidant enzyme activity. As already noted, in both jasmonate signaling mutants, *jin1* and especially *coi1*, a decreased activity of enzymes that neutralize hydrogen peroxide was observed (Fig. 3). Treatment with exogenous MJ promoted an increase in the activity of SOD, guaiacol peroxidase and preservation of catalase activity only in wild-type *Arabidopsis* plants, but not these mutants. It should be noted that an increase in the activity of antioxidant enzymes under the influence of JA was also shown in a number of other objects [33-35]. It was also reported that JA and MJ induced the emergence of new molecular forms of SOD and peroxidase in leaves of wheat and castor plants [33, 36].

Thus, jasmonic acid and its derivatives appear to be involved in the regulation of functioning of complex of protective systems, including antioxidant enzymes, proline, flavonoid compounds, under an action of stressors (including salinity). Transduction of jasmonate signal regulating these systems includes protein complexes containing COI1 and JIN1/MYC2. However, it is possible that part of the physiological (stress-protective) effects of jasmonate can be realized without the participation of transcription factors of the MYC family, for example, with ERF proteins involved in the ethylene signaling [5]. On the other hand, as already noted, the transcription factors of the MYC family can be involved in the transduction of signals not only of jasmonate, but also ABA and NO, which are also involved in plant adaptation to salinity. In addition, ROS, lipid signaling components and other mediators can participate in the realization of jasmonate effects [34, 35]. Their possible functional interaction with the main components of jasmonate signaling, in particular, with proteins COI1 and MYC2, remains unexplored.

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ДІЯ МЕТИЛЖАСМОНАТУ І СОЛЬОВОГО СТРЕСУ НА АНТИОКСИДАНТНУ СИСТЕМУ РОСЛИН АРАБІДОПСИСУ, ДЕФЕКТНИХ ЗА ГЕНАМИ ЖАСМОНАТНОГО СИГНАЛІНГУ

Т. О. Ястреб[1], Ю. Є. Колупаєв[1,2], М. В. Швиденко[1], О. П. Дмитрієв[3]

[1]Харківський національний аграрний університет ім. В. В. Докучаєва, Україна;
e-mail: plant_biology@ukr.net;
[2]Харківський національний університет ім. В. Н. Каразіна, Україна;
[3]Інститут клітинної біології та генетичної інженерії НАН України, Київ;
e-mail: dmitriev.ap@gmail.com

Роль жасмонатного сигналінгу в регуляції стреспротекторних систем арабідопсису за сольового стресу залишається недостатньо вивченою. Для її з'ясування доцільні порівняльні дослідження з мутантами за різними протеїновими компонентами жасмонатного сигналінгу. У зв'язку з цим досліджували вплив метилжасмонату (МЖ, 50 мкМ) і сольового стресу (150 мМ NaCl) на функціонування антиоксидантної та осмопротекторної систем рослин арабідопсису дикого типу (Col-0) і дефектних за жасмонатним сигналінгом: *coi1* (мутант за геном, що кодує протеїн COI1, який бере участь у видаленні протеїнів-репресорів транскрипційних факторів жасмонатного сигналінгу) і *jin1* (мутант, дефектний за геном, що кодує транскрипційний фактор JIN1/MYC2 – один із ключових у жасмонатному сигналінгу). Сольовий стрес інгібував ріст рослин всіх трьох генотипів. Обробка МЖ перед сольовим стресом позитивно впливала тільки на ріст рослин дикого типу. Також у рослин Col-0, оброблених МЖ, на відміну від мутантів *coi1* і *jin1*, в умовах сольового стресу зберігалися близькі до контролю величини вмісту води, сумарного вмісту хлорофілів і підвищувався вміст каротиноїдів. Рослини генотипу *coi1* у звичайних умовах відрізнялися від рослин дикого типу і мутантів *jin1* зниженою активністю гваяколпероксидази і каталази і підвищеним вмістом проліну. Обробка МЖ не впливала на активність антиоксидантних ензимів і вміст проліну в обох мутантів, дефектних за жасмонатним сигналінгом. За сольового стресу показники активності супероксиддисмутази, каталази і гваяколпероксидази, а також вмісту проліну і антоціанів у рослин дикого типу, оброблених МЖ, були помітно вищими, ніж у контрольних. Обговорюється роль жасмонатзалежних протекторних систем у забезпеченні стійкості рослин арабідопсису до сольового стресу.

Ключові слова: *Arabidopsis thaliana*, *coi1*, *jin1*, метилжасмонат, сигналінг, сольовий стрес, стреспротекторні системи.

ДЕЙСТВИЕ МЕТИЛЖАСМОНАТА И СОЛЕВОГО СТРЕССА НА АНТИОКСИДАНТНУЮ СИСТЕМУ РАСТЕНИЙ АРАБИДОПСИСА, ДЕФЕКТНЫХ ПО ГЕНАМ ЖАСМОНАТНОГО СИГНАЛИНГА

Т. О. Ястреб[1], Ю. Е. Колупаев[1,2], Н. В. Швиденко[1], А. П. Дмитриев[3]

[1]Харьковский национальный аграрный университет им. В. В. Докучаева, Украина;
e-mail: plant_biology@ukr.net;
[2]Харьковский национальный университет им. В. Н. Каразина, Украина;
[3]Институт клеточной биологии и генетической инженерии НАН Украины, Киев;
e-mail: dmitriev.ap@gmail.com

Роль жасмонатного сигналинга в регуляции стресспротекторных систем арабидопсиса при солевом стрессе остается недостаточно изученной. Для ее выяснения целесообразны сравнительные исследования с мутантами по различным протеиновым компонентам жасмонатного сигналинга. В связи с этим исследовали влияние метилжасмоната (МЖ, 50 мкМ) и солевого стресса (150 мМ NaCl) на функционирование антиоксидантной и осмопротекторной систем растений арабидопсиса дикого типа (Col-0) и дефектных по жасмонатному сигналингу: *coi1* (мутант по гену, кодирующему протеин COI1, который участвует в удалении протеинов-репрессоров транскрипционных факторов жасмонатного сигналинга) и *jin1* (мутант, дефектный по гену, кодирующему транскрипционный фактор JIN1/MYC2 – один из ключевых в жасмонатном сигналинге). Солевой стресс ингибировал рост растений всех трех генотипов. Обработка МЖ перед солевым стрессом положительно влияла только на рост растений дикого типа. Также у растений Col-0, обработанных МЖ, в

отличие от мутантов *coi1* и *jin1*, в условиях солевого стресса сохранялись близкие к контролю величины содержания воды, суммарного содержания хлорофиллов и повышалось содержание каротиноидов. Растения генотипа *coi1* в обычных условиях отличались от растений дикого типа и мутантов *jin1* пониженной активностью гваяколпероксидазы и каталазы и повышенным содержанием пролина. Обработка МЖ не влияла на активность антиоксидантных энзимов и содержание пролина у обоих мутантов, дефектных по жасмонатному сигналингу. При солевом стрессе показатели активности супероксиддисмутазы, каталазы и гваяколпероксидазы, а также содержания пролина и антоцианов у растений дикого типа, обработанных МЖ, были заметно выше, чем у контрольных. Обсуждается роль жасмонатзависимых протекторных систем в обеспечении устойчивости растений арабидопсиса к солевому стрессу.

Ключевые слова: *Arabidopsis thaliana*, *coi1*, *jin1*, метилжасмонат, сигналинг, солевой стресс, стресспротекторные системы.

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