METHYL JASMONATE – A MULTIFUNCTIONAL MOLECULE THROUGHOUT THE WHOLE PLANT LIFE

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ABSTRACT

Methyl jasmonate (MJ) is a widely occurring molecule. Since it is synthesized constitutively, its presence is substantial to plant normal growth and development. Moreover, its elevated concentration detected under abiotic and biotic stress conditions seems to be crucial to plant in reacting to adverse events and its ability to survive. Because of the sophisticated biochemical machinery inside the plant body, MJ, among other molecules, helps the plant to adopt to the surrounding environmental changes and is involved in its defense system.

Key words: methyl jasmonate, abiotic stress, biotic stress, heavy metal stress, chilling

INTRODUCTION

Methyl jasmonate called methyl jasmonic acid (MJ) is an endogenous plant hormone belonging to jasmonate family (JAs) [Wasternack and Strnad 2016, Han et al. 2019] and acting in a wide range of physiological processes, e.g. growth, reproduction, photosynthesis and stress responses [Wasternack and Hause 2013, Dar et al. 2015, García-Pastor et al. 2019]. Functioning of MJ depends on a plant species, its age, and physiological and hormonal status acting synergistically or antagonistically with i.e. auxin, ethylene (ET), abscisic acid (ABA), salicylic acid (SA) [Cheong and Choi 2003]. MJ is transported from upper part of plants to roots *via* phloem [Dai et al. 2017]. It is a signaling molecule participating in the intra-plant and inter-plants communication [Das et al. 2013] and triggering the genome instability in response to genotoxic stress agents [Donà et al. 2013].

The most bioactive metabolite in jasmonic acid (JA) signaling is (+)-7-*iso*-jasmonoyl-L-isoleucine (JA-Ile), the conjugate of JA and amino acid [Wasternack and Strnad 2016]. Moreover, the crucial regulator of jasmonate hormonal response is jasmonate ZIM-domain (JAZ) [Staswick 2008, Wasternack and Strnad 2016]. For exogenous application of MJ, the primary source of this molecule was jasmine (*Jasminum grandiflorum*) oil [Sembdner and Parthier 1993]. MJ is used by fragrance and chemical companies in fragrance mixtures with well-passed toxicology and dermatology tests [Scognamiglio et al. 2012].

Due to MJ importance in food and pharmaceutical industry as an enhancer of quantity of desired molecules and bioactive compounds with health-promoting properties, we reviewed the effects of

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exogenous application of MJ in non-stressful conditions and its role in alleviating the abiotic and biotic stresses in plants.
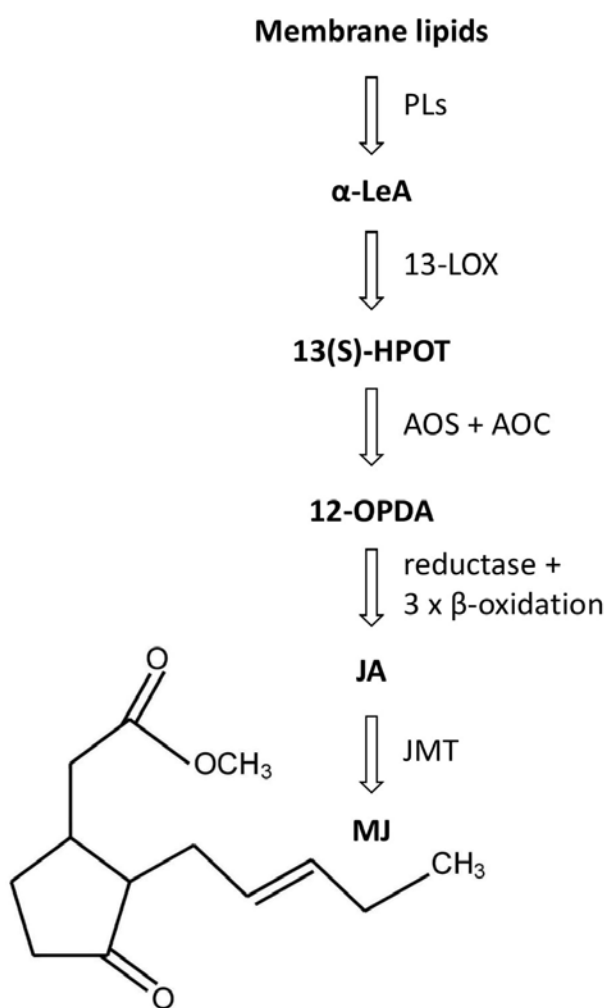
Membrane lipids

$\Downarrow$ PLs

α-LeA

$\Downarrow$ 13-LOX

13(S)-HPOT

$\Downarrow$ AOS + AOC

12-OPDA

$\Downarrow$ reductase +
3 × β-oxidation

JA

$\Downarrow$ JMT

MJ

Fig. 1. The key reactions in MJ biosynthesis. Abbreviations: PLs – phospholipases, α-LeA – α-linolenic acid, 13-LOX – 13-lipoxygenase, 13(S)-HPOT – 13-hydroperoxy-9,11,15-oktadecatrienoic acid, AOS – allene oxide synthase, AOC – allene oxide cyclase, 12-OPDA – 12-oxo--phytodienoic acid, JA – jasmonic acid, JMT – JA carboxyl methyltransferase, MJ – methyl jasmonate

Biosynthesis of MJ. Chemical structure of MJ comprises a hydrocarbon ring with two functional groups: a carbonyl group (ketone) and a methyl ester group (carboxylic acid) [Creelman and Mullet 1997]. MJ is biosynthesized in plants *via* the octadecanoid pathway and its details are discussed in previous reports [Cheong and Choi 2003, Wasternack 2007, Santino et al. 2013, Dar et al. 2015]. Briefly, MJ production starts from the action of phospholipases (PLs) on α-linolenic acid (α-LeA; C18:3), which is localized in chloroplast membranes. The oxygenation of α-LeA by 13-lipoxygenase (13-LOX) forms 13-hydroperoxy-9,11,15-oktadecatrienoic acid (13(S)-HPOT). Subsequently, 13(S)-HPOT is transformed by allene oxide synthase (AOS) and allene oxide cyclase (AOC) to 12-oxo-phytodienoic acid (12-OPDA). Afterwards, 12-OPDA is reduced and undergoes three steps of β-oxidation in peroxisomes [Wasternack 2007, Ahmad et al. 2016], which gives JA. Finally, as a result of catabolic action of JA carboxyl methyltransferase (JMT) on JA, MJ is synthesized and released into the cytoplasm (Fig. 1). An alternative, less efficient, pathway of MJ biosynthesis is also detected [Wasternack 2007, Santino et al. 2013]. Under PLs action, chloroplast membranes release hexadecatrienoic acid (HDTA; C16:3), which is converted in plastids by the same enzymes as in the above mentioned pathway to dinor-12-oxo-fitodienoic acid (dnOPDA). This molecule is an OPDA structural analog and in peroxisomes it is involved into the first pathway of MJ biosynthesis and is converted to JA. The last step of JA conversion to MJ is the same in both pathways [Wasternack 2007].

The signaling pathway of MJ is partially known [Wasternack and Hause 2013, Reyes-Díaz et al. 2016, Wasternack and Strnad 2016]. The concentration of MJ in plants varies depending on a tissue type, phenological stage and external stimuli [Vick and Zimmerman 1984]. The highest MJ levels are detected in reproductive tissues and flowers, whereas lower – in mature leaves and roots [Lorbeth et al. 1992]. Endogenous levels of MJ are systemically or locally regulated [Senthil-Nathan 2019] and can reach up to 95 µg g^{-1} FW [Preston et al. 2004].

Selected groups of molecules produced under MJ application. The MJ supplementation improves growth and development of plant, modulates levels of endogenous phytohormones, and induces the synthesis of bioactive compounds [Santino et al. 2013,

Ramirez-Estrada et al. 2016]. In plants growing under adverse conditions, such as abiotic stress of salinity, temperature or presence of heavy metals, and biotic stress of pathogen attack and insect-driven wounding, MJ affects the whole plant physiology and biochemistry [Dar et al. 2015].

Secondary metabolites under MJ application. Secondary metabolites (SMs) contribute the plant adaptation to the changes in the surrounding environment and play a crucial role in the plant defense system [Natella et al. 2016]. MJ used exogenously regulates SMs in agriculturally [Ávila-Juárez et al. 2017] and pharmacologically important plants [Ramirez-Estrada et al. 2016].

In crops, the level and composition of SMs differs among plants, e.g. MJ at 0.1 µM elevated quercetin level in tomato [Horbowicz et al. 2011], whereas MJ at 300 µM enhanced resveratrol content in strawberry [Wang et al. 2007]. In *Fagopyrum esculentum*, 1 µM MJ did not change the level of caffeic, gallic, ferulic and coumaric acids or quercetin content [Horbowicz et al. 2011]. Among glucosinolates (GLs), MJ raised accumulation of two of them in broccoli sprouts – neoglucobrassicin and glucobrassicin [Natella et al. 2016]. MJ can also promote anthocyanin production in *Brassica juncea* and *B. oleracea* [Natella et al. 2016, Xie et al. 2019].

Some scientists declare that usually 100–200 µM MJ stimulates production of different SMs, especially those important in pharmaceutical research, i.e. alkaloids, terpenoids, flavonoids and phenylopropanoids [Ramirez-Estrada et al. 2016, Gai et al. 2019, Ji et al. 2019]. Exogenous addition of MJ accelerates production of podophyllotoxin in *Podophyllum* genus, ginsenoides in *Panax ginseng*, taxane in *Taxus* spp., hyoscyamine and scopolamine in *Hyoscyamus niger*, stilbenes and resveratrol in *Vitis vinifera*, artemisin in *Artemisia annua* [Ramirez-Estrada et al. 2016]. Moreover, the MJ treatment enhances the accumulation of bioactive metabolites in *Codonopsis pilosula*, especially polysaccharide, β-D-fructose-butanol glycoside, polyacetylene like lobetyolin, and terpenoid, atractylenolide III [Ji et al. 2019].

Pathogenesis-related proteins. Pathogenesis-related (PR) proteins, classified into 17 families, are quite a diverse group of proteins appearing in plants.

Some of the PR proteins may be MJ dependent [Pluskota et al. 2019] and could be synthesized constitutively [Misra et al. 2016] or appear during development in a specific tissue [Lotan et al. 1989], while others are produced under pathological conditions [Peng et al. 2017, Butt et al. 2019]. PR proteins might be induced by various abiotic and biotic stresses [Van Loon et al. 2006]. PR proteins can be secreted inside the host's infected cells as well as outside the host [Hong and Hwang 2002, He et al. 2013].

Thirty-day *Lilium* spp. seedlings subjected to foliar application of MJ stimulated PR4 synthesis [Wang et al. 2017]. Antifungal potential of MJ against *Fusarium oxysporum* in maize leaves was manifested by *PR* gene expression [Butt et al. 2019]. A *PR10* gene isolated from *Saccharum* was involved in plant defense responses to pathogenic fungus, *Sporisorium scitamineum* and 25-µM MJ stimulation [Peng et al. 2017]. On the other hand, MJ deficiency did not limit the induction of PR1 protein upon chilling [Goyal et al. 2016].

MJ and oxidative stress. MJ mitigates strength of oxidative stress by activating the antioxidant system to scavenge the reactive oxygen species (ROS), such as hydroxyl radicals ($OH^\bullet$), superoxide radicals ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2) [Dar et al. 2015]. Production of antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX) [Hanaka et al. 2016, 2018] inhibits the oxidation of cell biomolecules – lipids, proteins, carbohydrates and DNA. For example, results of *in vivo* and *in vitro* experiments on *Arabidopsis thaliana* suggest that MJ influences the oxidative stress through regulating the gene expression and enzymatic activity [Maksymiec and Krupa 2002]. In the leaves of *A. thaliana*, an elevation of H_2O_2 level was induced after application of MJ through the root system. Activities of SOD and APX increased at 1 µM MJ and decreased at 100 µM MJ. CAT activity lowered proportionally to MJ concentration. The content of ascorbic acid and dehydroascorbate at 1 µM MJ was similar to that for the control, but at higher concentrations, it was elevated due to a higher ascorbate accumulation [Maksymiec and Krupa 2002]. Moreover, MJ enhanced activity of antioxidant enzymes in leaves of *Zea mays*, but in roots its

activity remained mainly similar to control values [Hanaka et al. 2018].

Cross-functional role of MJ during plant growth and development. MJ takes part in different stages of plant growth and development, i.e. seed germination, root growth, tuber formation, flowering and fertility, fruit maturation and senescence [Wasternack and Hause 2013].

Light. Plant development may be light-driven in a MJ signaling pathway [Kazan and Manners 2011]. In fact, light quality affects both development and defense. Far-red (FR) light-enriched environment (red (R) : FR < 1) promotes shade avoidance syndrome in shade-intolerant species. For example, FR light represses the JA-responsive fungal defense genes and the biosynthesis of JA-responsive insect defense compounds – phenolics, and simultaneously activates the transcription of insect defense genes [Kazan and Manners 2011].

Seed germination. MJ inhibited germination of dormant seeds and cooperated with ABA in the jasmonate receptor, Coronatine Insensitive 1 (COI1)--independent manner [Dave et al. 2011]. Exogenous 800 µM MJ treatment inhibited the germination and post-germination growth of *Astragalus membranaceus* [Yang et al. 2018]. It decreased the weight of mobilized seed reserves and seed reserves utilization efficiency, detained the mobilization of proteins and lipids leading to exceeded consumption of carbon energy. It changed the fatty acid composition in cotyledons, with decreasing the double bond index and average carbon chain length [Yang et al. 2018]. On the other hand, there are the opposite reports, in which MJ promotes dormancy release, for example in *Triticum aestivum* and is correlated with a transient increase in JA content and expression of JA biosynthesis genes [Xu et al. 2016].

In fact, the effect of MJ on seed germination and vigor is dose-dependent as was presented in research on the *Oryza sativa* being improved by 2.5 mM MJ and reduced by 5 mM MJ [Sheteiwy et al. 2018]. Moreover, during the germination of *Solanum lycopersicum* seeds, expression of one of the PR proteins, NP24, is mediated independently by MJ and ET. The production of NP24 protein in the endosperm cells is probably a step in the preparation to a possible pathogen attack [Pluskota et al. 2019].

Shoot and root development. Depending on the timespan of MJ (10 µM) stimulation, it produced no effect (1-h pre-incubation) or elevated leaf area, simultaneously reducing the shoot fresh weight (FW) (24-h pre-incubation) in *Phaseolus coccineus*. Moreover, at 10 µM MJ, the length of the main root was inhibited, but root FW was stimulated [Hanaka et al. 2015]. The JA-induced root growth inhibition seems to occur preferentially *via* modulation of the effects of auxin in root growth and development [Wasternack and Hause 2013].

Under osmotic stress, MJ at 2.5 mM improved the growth parameters of *Oryza sativa* seedlings, e.g. root and shoot length, FW and dry weight (DW) [Sheteiwy et al. 2018]. Similar effects were achieved in *Glycine max* after foliar spray with 20 µM MJ and resulted in the increase in shoot length, shoot and root FW and DW [Mohamed and Latif 2017].

Tuberization. The process of tuberization is affected by many internal and external factors, such as nitrogen levels, hormones, temperature and light. Among several plant growth regulators, such as gibberellins (GA), cytokinins, ABA and jasmonates involved in the regulation, MJ significantly controls tuberization in *Solanum tuberosum* [Sohn et al. 2011]. MJ at concentrations from 0.2 to 20 µM induced *in vitro* tuberization in various potato cultivars that differed greatly in ripening time. The lower tuberizing response of late-maturing cultivars to MJ was observed, which could be provoked by high levels of endogenous GA. However, extremely late-maturing cultivar showed high tuberization in response to MJ. These results suggest that also jasmonates are the crucial factors determining the ripeness [Koda and Kikuta 2001].

Flowering. In *Oryza sativa*, external MJ application (40 µM – 4 mM) induces floret opening and the numbers of opening florets are correlated with the concentration applied [Zeng et al. 1999], suggesting that the JA signaling pathway is involved in this process [Xiao et al. 2014]. The activity of promoter (*PvMADS56*) was enhanced by exogenous MJ and ABA and may be a multifunctional gene that regulates the flowering time and is involved in the identity

of floral organs and leaves in bamboo in response to ABA and MJ [Liu et al. 2016].

Fruit maturation. The quality of fruit and vegetables in pre- and postharvest time might be significantly enhanced by MJ treatment, especially important to the marketing period [Reyes-Díaz et al. 2016]. MJ action provokes accumulation of bioactive compounds, e.g. total phenolics and anthocyanin concentration, as a result of elevated phenylalanine ammonialyase (PAL) activity [García-Pastor et al. 2019]. Furthermore, MJ raises the level of lipophilic antioxidant compounds – carotenoids and vitamin E [Serrano et al. 2018, García-Pastor et al. 2019].

MJ applied as pre- and postharvest treatments, affects the fruit ripening and quality parameters at harvest and during the storage [García-Pastor et al. 2019]. For example, MJ applied exogenously at 230 µM to strawberry (*Fragaria × ananassa*) fruits promoted ripening, which was 5 days earlier compared to the control conditions [Han et al. 2019]. MJ treatment enhanced expression of genes related to the fruit ripening, i.e. pigment (anthocyanin) and sugar metabolism genes, as well as fruit softening and hormone synthesis (JA)-related genes. Also, overexpression of *FaAOC* and *FaAOS* (JA biosynthesis genes) promoted the fruit maturation. Reverse results with inhibition of fruit ripening were detected at 400 µM MJ [Han et al. 2019]. Similarly, MJ at 100 µM efficiently accelerated table grape (*Vitis vinifera*) ripening and elevated the content of antioxidant compounds, i.e. total phenolics and anthocyanin concentration. Oppositely, 5 and 10 mM of MJ inhibited berries ripening and reduced their weight, volume and grapevine yield [García-Pastor et al. 2019].

The main idea of postharvest MJ treatment is reduction of stress-induced injuries, e.g. chilling stress, mechanical damage or pathogen infections [García-Pastor et al. 2019, Wang et al. 2019] and positive impact on quality parameters, e.g. color, firmness, weight, soluble solids content associated with health benefits *via* antioxidant activity, like vitamin C production at 1 mM and 10 µM MJ [Akan et al. 2019]. Moreover, the promotion of climacteric and non-climacteric fruit ripening in the presence of MJ is driven by ET increase [Serrano et al. 2018, García-Pastor et al. 2019].

Transport of nitrogen. Exogenous application of MJ to *Oryza sativa* seedlings led to reduced nitrogen (N) uptake in roots and reduced translocation of N from roots to leaves. In turn, shoots treated with MJ resulted in a remobilization of endogenous N from leaves to roots. Roots MJ-treated also increased N accumulation in roots, but did not influence the N accumulation in leaves [Wu et al. 2019].

Guard cells. Involvement of ABA in stomatal closure is a well-established knowledge, but MJ participation emerged recently [Saito et al. 2009, Munemasa et al. 2011]. In the closure of guard cells, MJ signaling depends not only on alkalization of cytosolic pH, which is necessary for ROS and NO production, but also on elevation in concentration of a second messenger, cytosolic Ca^{2+}, caused by activation of slow-type anion channels [Saito et al. 2009, Munemasa et al. 2011]. In guard cells, MJ signaling is regulated by calcium dependent protein kinase and by two NAD(P)H oxidases [Munemasa et al. 2011].

Senescence. After induction of senescence in leaves of *Solanum lycopersicum*, the patterns of chlorophyll degradation of hormonal and photomorphogenic mutants were not significantly different in comparison with control. Moreover, there was no significant change in lipid peroxidation measured as malondialdehyde (MDA) concentration, as well as CAT, APX, and glutathione reductase activities in the hormonal mutants. The results suggest that JA do not participate in light signaling pathway during the leaf senescence-induced oxidative stress [Carvalho et al. 2013]. Also, application of 10 µM MJ promoted the loss of chlorophyll corresponding with the chloroplast degradation in *Avena sativa* leaves. MJ decreased primarily cellulosic polysaccharides, but not hemicellulosic ones [Miyamoto et al. 2013]. Senescence was also stimulated in *Ipomoea nil* cotyledon after 100 µM MJ application [Wilmowicz et al. 2016]. Moreover, SA (1–50 µM) delayed the senescence promoted by 50 µM MJ in *Arabidopsis thaliana* leaves [Ji et al. 2016].

Conversely to the above statements, MJ at 5 mM lowered the ET production and delayed *Solanum*

melongema fruit senescence. Fruit quality during storage was improved by reduction of calyx browning and weight, firmness and anthocyanin loss. Moreover, MJ lowered the total phenolics content [Fan et al. 2016]. Also, pool of chlorophylls and carotenoids did not change after 10 µM MJ application to *Phaseolus coccineus* plants [Hanaka et al. 2015].

MJ in abiotic stress response. The physiological mechanisms governing the plant responses to stress factors, e.g. salinity, drought, extreme temperatures and chemical pollution suggest that they must be perceived by plant as both osmotic and oxidative stresses [Santino et al. 2013].

For example, under osmotic stress induced by polyethylene glycol, 2.5 mM MJ treatment improved the photosynthetic parameters of *Oryza sativa* seedlings, e.g. net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO_2 concentration (Ci) and transpiration rate (Tr), chlorophyll content, photochemical efficiency of PSII (Fv/Fm), water potential, water use efficiency (WUE) and relative water content (RWC), but decreased the electrolyte leakage. The proline content was significantly increased under osmotic stress not only in the presence of 2.5 and 5 mM MJ, but also without MJ application [Sheteiwy et al. 2018].

Salt stress. Salinity influences ±7% of the world's area [Talebi et al. 2018] and more than 20% of cultivated land worldwide [Sadeghipour 2017]. High concentrations of salt (predominantly NaCl) in the plant environment are the reason of hyperosmotic shock manifested as the inhibition of water uptake, decrease of water potential and finally its poor availability and drought stress [Santino et al. 2013, Talebi et al. 2018]. As a consequence, oxidative stress and imbalance of nutrients and ions appear [Santino et al. 2013]. All agents together yield the reduction of plant growth and crops productivity.

The data show that under specific conditions, MJ can aggravate or ameliorate the salt stress. For example, in two almond rootstocks supplemented with 25–50 µM MJ alleviated the effects of salt stress, increasing shoot and root DW, activity of antioxidant enzymes, Pn and membrane integrity [Tavallali and Karimi 2019]. On the other hand, severe stress in *Arabidopsis* plants under combined action of 100 mM NaCl and 20 µM MJ was shown [Chen et al. 2017].

In turn, seeds of cowpea (*Vigna unguiculata*) soaked in 50 µM MJ showed an increased salinity tolerance by enhancing the accumulation of proline, soluble sugars, protein and chlorophyll contents and also improving RWC and Pn [Sadeghipour 2017]. In *Brassica oleracea* under saline conditions (150 mM NaCl), 25 µM MJ also improved the water relation parameters (osmotic and water potentials, and root hydraulic conductivity), and increased GLs content [Hassini et al. 2017]. Similarly, application of 250 µM MJ to *Fragaria × ananassa* reduced the injuries caused by salt stress (30 and 60 mM NaCl), possibly through promoting the K^+ accumulation, decreasing the electrolyte leakage and Na^+ contents in leaves, and elevated proline content [Faghih et al. 2019]. Foliar application of 500 µM MJ to *Ocimum basilicum* also reduced the negative effects of salt stress. At a salinity level of 30 mM NaCl, foliar application of MJ raised the essential oil content: linalool and 1,8-cineole, whereas reduced the content of α-cadinol, α-bergamotene, β-maaliene, and eugenol. MJ also enhanced the antioxidant activity, especially both in control and at 60 mM of NaCl-treated plants [Talebi et al. 2018].

Drought stress. Water stress can decrease 50% of yield of crops in the world [Mohamed and Latif 2017]. Plants tolerate water stress by supporting tissue flexibility and cell turgor and by osmotic adjustment through accumulation of proper solutes (carbohydrates, inorganic ions, sugar alcohols), which are the main reason for reduction of the osmotic potential by water inflow to the cell and regaining the turgor pressure [Bohnert et al. 1995, Munns and Tester 2008]. MJ might help to alleviate the negative consequences of drought stress in plants.

Reduction in turgor and carbon assimilation are the main reasons of lowered root and sucrose yield in water-stressed plants [Fugate et al. 2018]. MJ applied prior to drought allowed plants to maintain greater leaf RWC and higher Pn. Exogenous MJ, at 1 and 10 µM, reduced moderate and severe drought effects on *Beta vulgaris* leaf RWC, Pn, Ci and WUE and altered the drought-induced changes in proline accumulation. MJ delayed dehydration and protected the

photosynthetic apparatus from drought-induced deleterious effects [Fugate et al. 2018]. Similar effects were achieved by foliar spray of *Glycine max* with 20 µM MJ giving the increase in concentration of photosynthetic pigments, saturated and unsaturated fatty acids, flavonoids, phenolic acids, sugar fraction, and RWC and oil content in the shoots [Mohamed and Latif 2017].

Severe drought generally inhibits the induction of SMs by exogenous MJ in *Camellia sinensis*. Furthermore, some volatile metabolites, e.g. methyl salicylate, are more effectively induced by MJ in severe than moderate drought-stressed plants [Scott et al. 2019].

Chilling stress. Chilling stress causes the storage problems for crops, especially those growing in tropical and subtropical areas [Dar et al. 2015]. Chilling injury (CI) in fruit gives usually off-flavor, greater firmness in texture and browning of the skin. Preharvest treatment with 1 and 2 mM MJ improved arils color of *Punica granatum* fruit at harvest and diminished the postharvest CI. Electrolyte leakage increased during the storage and remained higher in control plants than in MJ-treated ones. MJ treatment increased the concentrations of flavonoids, total phenolics, and total anthocyanins, as well as antioxidant activity of fruits [Saba and Zarei 2019]. Postharvest MJ treatment delayed the decrease or elevated unsaturated to saturated fatty acids ratio, thereby elevating the chilling resistance [Pareek et al. 2014]. Application of MJ at 10 µM in loquat (*Eriobotrya japonica*) fruit inhibited the respiration rate, ET production and PAL activity, glutathione content and internal browning. Simultaneously, MJ increased the level of sugars, organic acids (ascorbic acid), total phenolics and flavonoids and activity of APX, glutathione peroxidase, glutathione-S-transferase [Pareek et al. 2014]. The above data are in accordance with other results, i.e. exogenous 10 µM MJ reduced CI of *Capsicum annuum* fruit by decline in MDA level, chlorophyll and vitamin C contents, and by enhancement of the activities and relative gene expressions of CAT and APX [Wang et al. 2019]. Similarly, MJ at 100 µM reduced CI in *Persea americana* fruit *via* changes in fatty acids content and composition and reduction of lipoxygenase activity [Glowacz et al. 2017].

Heavy metal stress. Heavy metals are divided into essential and non-essential ones. At appropriate concentration, essential metals are indispensable to plants, but their exceeded values act similarly to non-essential metals and generate toxicity [Dar et al. 2015]. Toxicity is demonstrated mainly as the series of morphological, physiological and biochemical changes. It was found that MJ might ameliorate Cd and Cu stress [Maksymiec and Krupa 2007, Chen et al. 2014, Hanaka et al. 2016]. Besides ET and NADPH oxidase, 50 µM MJ is involved in Cu^{2+} (25, 50 or 150 µM) inhibitory effect on the roots of *Phaseolus coccineus* and *Zea mays*. Moreover, leaf growth reduction produced by excess of Cu^{2+} seemed to be strongly related to MJ in *Z. mays* and to a lesser extend in *P. coccineus* [Maksymiec and Krupa 2007].

Under Cu excess, MJ did not modulate the growth parameters of *P. coccineus* such as leaf and root growth, shoot and root FW. The content of chlorophylls and carotenoids increased with the increasing Cu content in the leaves. Decrease in the Cu concentration was partially MJ-dependent. Parameters of chlorophyll fluorescence were quite weak indicators of the effect induced by MJ in Cu excess [Hanaka et al. 2015]. Furthermore, MJ modified the activities of antioxidant enzymes and metabolites concentration depending on the timespan of Cu stress (50 µM) [Hanaka et al. 2016]. After short-time Cu influence, MJ reduced the APX and elevated GPX activity in the leaves. After long-time metal application, MJ reduced tartrate, pyruvate, GPX activity in the leaves, and mainly reduced SOD and CAT activities in the roots. Application of MJ under Cu excess partially elevated level of anthocyanin, but did not change the accumulation of MDA, homoglutathione and proline [Hanaka et al. 2016]. Exogenous MJ at 0.1 to 1 µM facilitated reduction of damages caused by Cd in *Kandelia obovata*. It inhibited the translocation of metal to the leaves, which might be driven by stomatal closure and lower transpiration produced by exogenous MJ. Moreover, it evoked an increase in the concentration of ascorbic acid and the activities of CAT and APX [Chen et al. 2014].

MJ in biotic stress. Plants evolved defense mechanisms to cope with biotic stress, which means path-

ogen infection [Donà et al. 2013] or insect attack [Bruce and Pickett 2011]. Two main strategies of plants are resistance, which involves the synthesis of defensive compounds preventing or reducing negative effects and tolerance, which involves the storage of nutrient reserves used for rapid recovery [Wu et al. 2019].

MJ is involved in the stimulation of plant resistance through the induced resistance (IR), the acquisition of systemic acquired resistance (SAR) and systemic wound signal (SWS) and it is able to activate defense responses in neighboring non-stressed plants [Senthil-Nathan 2019] enabling them to prepare for an upcoming stress. Precisely, MJ induces IR in plants serving as elicitor itself (upregulating its level) or improving the action of elicitors [Senthil-Nathan 2019].

MJ enhanced resistance against necrotrophic and partially biotrophic fungal species [Antico et al. 2012]. Soaking of *Solanum lycopersicum* seeds in 100 μM MJ enhanced the resistance against *Fusarium oxysporum*. In the seedlings, enhanced levels of phenolic compounds, such as SA, kaempferol and quercetin were detected [Król et al. 2015].

Furthermore, MJ inhibited the growth and aflatoxin production of *Aspergillus flavus* [Goodrich-Tanrikulu et al. 1995]. Similarly, MJ at 13.56 ng μL^{-1} inhibited conidial germination in *Phaseolus vulgaris* infected by *Colletotrichum lindemuthianum*. This inhibition was dosage-dependent and irreversible [Quintana-Rodriguez et al. 2015].

The exposure of endophyte-symbiotic plants of *Lolium multiflorum* to MJ led to a reduction in the concentration of loline alkaloids (i.e. N-formyllolines and N-acetylnorlolines), consequently decreasing the level of plant resistance to the herbivores [Bastías et al. 2018].

Herbivorous insects use chemicals to recognize an eligible host for feeding and reproduction. Additionally, the relevant mixture and proportion of volatile compounds is crucial in locating the right host among other plants by insects [Bruce and Pickett 2011]. MJ can induce expression of wound-inducible proteinase inhibitors (PIs), which could be useful in induced defense against insects [Howe 2004]. Overall, the results of MJ achieved on insects may vary depend-

ing mainly on plant phenology and sampling method, but generally, MJ treatment contributes to plant defense by attracting natural enemies of pests being the natural pest control method for the precisely characterized goal [Bayram and Tonğa 2018].

Herbivore damage by chewing insects activates MJ signaling in eliciting systemic defense in rice [Wu et al. 2019]. MJ had repellent effects on leaf folders [Senthil-Nathan 2019], aphids, phytophagous thrips species and hoverfly species, the phloem feeder, the potato aphid *Macrosiphum euphorbiae* [Brunissen et al. 2010], the soybean aphid *Aphis glycines* and the soybean thrips *Neohydatothrips variabilis* [Selig et al. 2016]. What is important, with reduced number of the stink bug, *Oebalus pugnax,* also grains per panicle in rice elevated under MJ (2 and 5 mM) treatment [Stella de Freitas et al. 2019], but MJ application also led to reductions in *Triticum aestivum* yield and plant height [Bayram and Tonğa 2018]. Simultaneously, MJ was attractive to wheat stem sawflies, lady beetle species [Bayram and Tonğa 2018], small-flower bug *Orius* spp. in cotton fields [Yu et al. 2018], and lady beetle *Chilocorus kuwanae* on *Diospyros kaki* plants [Zhang et al. 2009].

It is worth mentioning that in MJ-treated seedlings of pine (*Pinus radiata* and *P. pinaster*), lowered damage caused by weevil was dependent on the changing content of monoterpenes [Lundborg et al. 2019]. Furthermore, under attack of the sucking insect, *Trigonotylus caelestialium,* application of 10 μM MJ reduced activities of antioxidant enzymes in leaves of *Z. mays*, whereas elevated their activity in roots [Hanaka et al. 2018].

CONCLUSIONS

Presented knowledge is focused on the role of MJ in plant growth and development. Plant chemical composition can be effectively modified by this phytohormone in order to enhance the amount of desired molecules. This kind of approach is useful and practically applied in food and pharmaceutical industries to achieve better quality of natural products towards producing health promoting bioactive molecules. MJ has also a crucial role in ameliorating the adverse changes in plants mainly caused by water scarcity,

extreme temperatures, metal pollution, and pathogen infection. Effects of its action are strongly dose-, timespan- and way of application-dependent. MJ is especially precious, because according to the U.S. Food and Drug Administration (FDA), it is classified as "generally recognized as safe", which means that this molecule is nonhazardous to human health [FDA-EPA 2013].

REFERENCES

Ahmad, P., Rasool, S., Gul, A., Sheikh, S.A., Akram, N.A., Ashraf, M., Kazi, A.M., Gucel, S. (2016). Jasmonates: multifunctional roles in stress tolerance. Front. Plant Sci., 7, 813. DOI: 10.3389/fpls.2016.00813

Akan, S., Tuna Gunes, N., Yanmaz, R. (2019). Methyl jasmonate and low temperature can help for keeping some physicochemical quality parameters in garlic (*Allium sativum* L.) cloves. Food Chem., 270, 546–553. DOI: 10.1016/j.foodchem.2018.07.085

Antico, C.J., Colon, C., Banks, T., Ramonell, K.M. (2012). Insights into the role of jasmonic acid-mediated defenses against necrotrophic and biotrophic fungal pathogens. Front. Biol., 7(1), 48–56. DOI: 10.1007/s11515-011-1171-1

Ávila-Juárez, L., Torres-Pacheco, I., Ocampo-Velázquez, R.V., Feregrino-Pérez, A.A., Cruz Hernández, A., Guevara-González, R.G. (2017). Integrating plant nutrients and elicitors for production of secondary metabolites, sustainable crop production and human health: a review. Int. J. Agric. Biol., 19(3), 391–402. DOI: 10.17957/IJAB/15.0297

Bastías, D.A., Martínez-Ghersa, M.A., Newman, J.A., Card, S.D., Mace, W.J., Gundel, P.E. (2018). Jasmonic acid regulation of the anti-herbivory mechanism conferred by fungal endophytes in grasses. J. Ecol., 106, 2365–2379. DOI: 10.1111/1365-2745.12990

Bayram, A., Tonğa, A. (2018). Methyl jasmonate affects population densities of phytophagous and entomophagous insects in wheat. Appl. Ecol. Env. Res., 16(1), 181–198. DOI: 10.15666/aeer/1601_181198

Bohnert, H.J., Nelson, D.E., Jensen, R.G. (1995). Adaptations to environmental stresses. Plant Cell, 7, 1099–1111. DOI: 10.1105/tpc.7.7.1099

Bruce, T.J.A., Pickett, J.A. (2011). Perception of plant volatile blends by herbivorous insects – finding the right mix. Phytochemistry, 72, 1605–1611. DOI: 10.1016/j.phytochem.2011.04.011

Brunissen, L., Vincent, C., Le Roux, V., Giordanengo, P. (2010). Effects of systemic potato response to wounding and jasmonate on the aphid *Macrosiphum euphorbiae* (Sternorryncha: *Aphididae*). J. Appl. Entomol., 134(7), 562–571. DOI: 10.1111/j.1439-0418.2009.01493.x

Butt, U.R., Naz, R., Nosheen, A., Yasmin, H., Keyani, R., Hussain, I., Hassan, M.N. (2019). Changes in pathogenesis-related gene expression in response to bioformulations in the apoplast of maize leaves against *Fusarium oxysporum*. J. Plant Interact., 14(1), 61–72. DOI: 10.1080/17429145.2018.1550217

Carvalho, R.F., Monteiro, C.C., Caetano, A.C., Dourado, M.N., Gratão, P.L., Haddad, C.R.B., Peres, L.E.P., Azevedo, R.A. (2013). Leaf senescence in tomato mutants as affected by irradiance and phytohormones. Biol. Plant., 57(4), 749–757. DOI: 10.1007/s10535-013-0333-1

Chen, Y., Wang, Y., Huang, J., Zheng, C., Cai, C., Wang, Q., Wu, C.A. (2017). Salt and methyl jasmonate aggravate growth inhibition and senescence in Arabidopsis seedlings via the JA signaling pathway. Plant Sci., 261, 1–9. DOI: 10.1016/j.plantsci.2017.05.005

Chen, J., Yan, Z.Z., Li, X. (2014). Effect of methyl jasmonate on cadmium uptake and antioxidative capacity in *Kandelia obovata* seedlings under cadmium stress. Ecotox. Environ. Safe., 104, 349–356. DOI: 10.1016/j.ecoenv.2014.01.022

Cheong, J.-J., Choi, Y.D. (2003). Methyl jasmonate as a vital substance in plants. Trends Genet., 19(7), 409–413. DOI: 10.1016/S0168-9525(03)00138-0

Creelman, R.A., Mullet, J.E. (1997). Biosynthesis and action of jasmonates in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol., 48, 355–381. DOI: 10.1146/annurev.arplant.48.1.355

Dai, J., Kong, X., Zhang, D., Li, W., Dong, H. (2017). Technologies and theoretical basis of light and simplified cotton cultivation in China. Field Crops Res., 214, 142–148. DOI: 10.1016/j.fcr.2017.09.005

Dar, T.A., Uddin, M., Khan, M.M.A., Hakeem, K.R., Jaleel, H. (2015). Jasmonates counter plant stress: a review. Environ. Exp. Bot., 115, 49–57. DOI: 10.1016/j.envexpbot.2015.02.010

Das, A., Lee, S.H., Hyun, T.K., Kim, S.W., Kim, J.Y. (2013). Plant volatiles as method of communication. Plant Biotechnol. Rep., 7(1), 9–26. DOI: 10.1007/s11816-012-0236-1

Dave, A., Hernández, M.L., He, Z., Andriotis, V.M.E., Vaistij, F.E., Larson, T.R., Graham, I.A. (2011). 12-

oxo-phytodienoic acid accumulation during seed development represses germination in Arabidopsis. Plant Cell, 23, 583–599. DOI: 10.1105/tpc.110.081489

Donà, M., Macovei, A., Faè, M., Carbonera, D., Balestrazzi, A. (2013). Plant hormone signaling and modulation of DNA repair under stressful conditions. Plant Cell Rep., 32(7), 1043–1052. DOI: 10.1007/s00299-013-1410-9

Faghih, S., Zarei, A., Ghobadi, C. (2019). Positive effects of plant growth regulators on physiology responses of *Fragaria × ananassa* cv. 'Camarosa' under salt stress. Int. J. Fruit Sci., 19(1), 104–114. DOI: 10.1080/15538362.2018.1462291

Fan, L., Shi, J., Zuo, J., Gao, L., Lv, J., Wang, Q. (2016). Methyl jasmonate delays postharvest ripening and senescence in the non-climacteric eggplant (*Solanum melongena* L.) fruit. Postharvest Biol. Technol., 120, 76–83. DOI: 10.1016/j.postharvbio.2016.05.010

FDA-EPA (2013). Methyl jasmonate; Exemption from the requirement of a tolerance. Document 78(74), FR 22789, pp. 22789–22794. Available: federalregister.gov/documents/2013/04/17/2013-08829/methyl-jasmonate-exemption-from-the-requirement-of-a-tolerance

Fugate, K.K., Lafta, A.M., Eide, J.D., Li, G., Lulai, E.C., Olson, L.L., Deckard, E.L., Khan, M.F.R., Finger, F.L. (2018). Methyl jasmonate alleviates drought stress in young sugar beet (*Beta vulgaris* L.) plants. J. Agro. Crop Sci., 204, 566–576. DOI: 10.1111/jac.12286

Gai, Q.-Y., Jiao, J., Wang, X., Zang, Y.-P., Niu, L.-L., Fu, Y.-J. (2019). Elicitation of *Isatis tinctoria* L. hairy root cultures by salicylic acid and methyl jasmonate for the enhanced production of pharmacologically active alkaloids and flavonoids. PCTOC, 137, 77–86. DOI: 10.1007/s11240-018-01553-8

García-Pastor, M.E., Serrano, M., Guillén, F., Castillo, S., Martínez-Romero, D., Valero, D., Zapata, P.J. (2019). Methyl jasmonate effects on table grape ripening, vine yield, berry quality and bioactive compounds depend on applied concentration. Sci. Hortic., 247, 380–389. DOI: 10.1016/j.scienta.2018.12.043

Glowacz, M., Bill, M., Tinyane, P.P., Sivakumar, D. (2017). Maintaining postharvest quality of cold stored 'Hass' avocados by altering the fatty acids content and composition with the use of natural volatile compounds – methyl jasmonate and methyl salicylate. J. Sci. Food Agric., 97, 5186–5193. DOI: 0.1002/jsfa.8400

Goodrich-Tanrikulu, M., Mahoney, N.E., Rodriguez, S.B. (1995). The plant growth regulator methyl jasmonate inhibits aflatoxin production by *Aspergillus flavus*. Microbiology, 141, 2831–2837. DOI: 10.1099/13500872-141-11-2831

Goyal, R.K., Fatima, T., Topuz, M., Bernadec, A., Sicher, R., Handa, A.K., Mattoo, A.K. (2016). Pathogenesis-related protein 1b1 (PR1b1) is a major tomato fruit protein responsive to chilling temperature and upregulated in high polyamine transgenic genotypes. Front. Plant Sci., 7, 901. DOI: 10.3389/fpls.2016.00901

Han, Y., Chen, C., Yan, Z., Li, J., Wang, Y. (2019). The methyl jasmonate accelerates the strawberry fruits ripening process. Sci. Hortic., 249, 250–256. DOI: 10.1016/j.scienta.2019.01.061

Hanaka, A., Lechowski L., Mroczek-Zdyrska M., Strubińska J. (2018). Oxidative enzymes activity during abiotic and biotic stresses in *Zea mays* leaves and roots exposed to Cu, methyl jasmonate and *Trigonotylus caelestialium*. Physiol. Mol. Biol. Plants, 24(1), 1–5. DOI: 10.1007/s12298-017-0479-y

Hanaka, A., Maksymiec W., Bednarek, W. (2015). The effect of methyl jasmonate on selected physiological parameters of copper-treated *Phaseolus coccineus* plants. Plant Growth Regul., 77, 167–177. DOI: 10.1007/s10725-015-0048-8

Hanaka, A., Wójcik, M., Dresler, S., Mroczek-Zdyrska, M., Maksymiec, W. (2016). Does methyl jasmonate modify the oxidative stress response in *Phaseolus coccineus* treated with Cu? Ecotox. Environ. Saf., 124, 480–488. DOI: 10.1016/j.ecoenv.2015.11.024

Hassini, I., Martinez-Ballesta, M.C., Boughanmi, N., Diego A. Moreno, D.A., Carvajal, M. (2017). Improvement of broccoli sprouts (*Brassica oleracea* L. var. *italica*) growth and quality by KCl seed priming and methyl jasmonate under salinity stress. Sci. Hortic., 226, 141–151. DOI: 10.1016/j.scienta.2017.08.030

He, M.Y., Xu, Y., Cao, J.L., Zhu, Z.G., Jiao, Y.T., Wang, Y.J., Guan, X., Yang, Y.Z., Xu, W.R., Fu, Z.F. (2013). Subcellular localization and functional analyses of a PR10 protein gene from *Vitis pseudoreticulata* in response to *Plasmopara viticola* infection. Protoplasma, 250, 129–140. DOI: 10.1007/s00709-012-0384-8

Hong, J.K., Hwang, B.K. (2002). Temporal and subcellular localization of PR-1 proteins in tomato stem tissues infected by virulent and avirulent isolates of *Phytophthora capsici*. Protoplasma, 219, 131–139. DOI: 10.1007/s007090200014

Horbowicz, M., Chrzanowski, G., Koczkodaj, D., Mitrus, J. (2011). The effect of methyl jasmonate vapors on content of phenolic compounds in seedlings of com-

mon buckwheat (*Fagopyrum esculentum* Moench). Acta Soc. Bot. Pol., 80(1), 5–9.

Howe, G.A. (2004) Jasmonates as signals in the wound response. J. Plant Growth Regul., 23, 223–237. DOI: 10.1007/s00344-004-0030-6

Ji, J-J., Feng, Q., Sun, H.-F., Zhang, X.-J., Li, X.-X., Li, J.-K., Gao, J.-P. (2019). Response of bioactive metabolite and biosynthesis related genes to methyl jasmonate elicitation in *Codonopsis pilosula*. Molecules, 24, 533. DOI: 10.3390/molecules24030533

Ji, Y., Liu, J., Xing, D. (2016). Low concentrations of salicylic acid delay methyl jasmonate-induced leaf senescence by up-regulating nitric oxide synthase activity. J. Exp. Bot., 67(17), 5233–5245. DOI: 10.1093/jxb/erw280

Kazan, K., Manners, J. (2011). The interplay between light and jasmonate signalling during defense and development. J. Exp. Bot., 62, 4087–4100. DOI: 10.1093/jxb/err142

Koda, Y., Kikuta, Y. (2001). Effects of jasmonates on *in vitro* tuberization in several potato cultivars that differ greatly in maturity. Plant Prod. Sci., 4(1), 66–70.

Król, P., Igielski, R., Pollmann, S., Kępczyńska, E. (2015). Priming of seeds with methyl jasmonate induced resistance to hemi-biotroph *Fusarium oxysporum* f. sp. *lycopersici* in tomato *via* 12-oxo-phytodienoic acid, salicylic acid, and flavonol accumulation. J. Plant Physiol., 179, 122–132. DOI: 10.1016/j.jplph.2015.01.018

Liu, S., Qi, T.T., Ma, J.J., Ma, T., Ma, L., Lin, X. (2016). Ectopic expression of a SOC1 homolog from *Phyllostachys violascens* alters flowering time and identity of floral organs in *Arabidopsis thaliana*. Trees, 30, 2203–2215. DOI: 10.1007/s00468-016-1445-y

Lorbeth, R., Dammann, C., Ebneth, M., Amati, S., Sanchez-Serrano, J. (1992). Promoter elements involved in environmental and developmental control of potato proteinase inhibitor II expression. Plant J., 2, 477–486. DOI: 10.1046/j.1365-313X.1992.t01-21-00999.x

Lotan, T., Ori, N., Fluhr, R. (1989). Pathogenesis-related proteins are developmentally regulated in tobacco flowers. Plant Cell, 1, 881–887. DOI: 10.1105/tpc.1.9.881

Lundborg, L., Sampedro, L., Borg-Karlson, A.K., Zas, R. (2019). Effects of methyl jasmonate on the concentration of volatile terpenes in tissues of Maritime pine and Monterey pine and its relation to pine weevil feeding. Trees, 33(1), 53. DOI: 10.1007/s00468-018-1757-1

Maksymiec, W., Krupa Z. (2002). Jasmonic acid and heavy metals in Arabidopsis plants – a similar physiological response to both stressors? J. Plant Physiol., 159(5), 509–515. DOI: 10.1078/0176-1617-00610

Maksymiec, W., Krupa, Z. (2007). Effects of methyl jasmonate and excess copper on root and leaf growth. Biol. Plant., 51(2), 322–326. DOI: 10.1007/s10535-007-0062-4

Miyamoto, K., Oka, M., Uheda, E., Ueda, J. (2013). Changes in metabolism of cell wall polysaccharides in oat leaves during senescence: relevance to the senescence-promoting effect of methyl jasmonate. Acta Physiol. Plant., 35, 2675–2683. DOI: 10.1007/s11738-013-1299-5

Misra, R.C., Sandeep, Kamthan, M., Kumar, S., Ghosh, S. (2016). A thaumatin-like protein of *Ocimum basilicum* confers tolerance to fungal pathogen and abiotic stress in transgenic Arabidopsis. Sci. Rep., 6, 25340. DOI: 10.1038/srep25340

Mohamed, H.I., Latif, H.L. (2017). Improvement of drought tolerance of soybean plants by using methyl jasmonate. Physiol. Mol. Biol. Plants, 23(3), 545–556. DOI: 10.1007/s12298-017-0451-x Munemasa, S., Mori, I.C., Yoshiyuki Murata Y. (2011). Methyl jasmonate signaling and signal crosstalk between methyl jasmonate and abscisic acid in guard cells. Plant Signal. Behav., 6(7), 939–941. DOI: 10.4161/psb.6.7.15439

Munns, R., Tester, M. (2008). Mechanisms of salinity tolerance. Annu. Rev. Plant Biol., 59, 651–681. DOI: 10.1146/annurev.arplant.59.032607.092911

Natella, F., Maldini, M., Nardini, M., Azzini, E., Foddai, M.S., Giusti, A.M., Baima, S., Morelli, G., Scaccini, C. (2016). Improvement of the nutraceutical quality of broccoli sprouts by elicitation. Food Chem., 201, 101–109. DOI: 10.1016/j.foodchem.2016.01.063

Pareek, S., Benkeblia, N., Janick, J., Cao, S., Yahia, E.M. (2014). Postharvest physiology and technology of loquat (*Eriobotrya japonica* Lindl.) fruit. J. Sci. Food Agric., 94, 1495–1504. DOI: 10.1002/jsfa.6560

Peng, Q., Su, Y., Ling, H., Ahmad, W., Gao, S., Guo, J., Que, Y., Xu, L. (2017). A sugarcane pathogenesis-related protein, ScPR10, plays a positive role in defense responses under *Sporisorium scitamineum*, SrMV, SA, and MeJA stresses. Plant Cell Rep., 36(9), 1427–1440. DOI: 10.1007/s00299-017-2166-4

Pluskota, W.E., Pupel, P., Głowacka, K., Okorska, S.B., Jerzmanowski, A., Nonogaki, H., Górecki, R.J. (2019). Jasmonic acid and ethylene are involved in the accumulation of osmotin in germinating tomato seeds. J. Plant Physiol., 232, 74–81. DOI: 10.1016/j.jplph.2018.11.014

Preston, C.A., Laue, G., Baldwin, I.T. (2004). Plant-plant signaling: application of trans-orcis-methyl jasmonate sequivalent to sage brush releases does not elicit direct defenses in native tobacco. J. Chem. Ecol., 30, 2193–2214. DOI: 10.1023/B:JOEC.0000048783.64264.2a

Quintana-Rodriguez, E., Morales-Vargas, A.T., Molina-Torres, J., Adame-Alvarez, R.M., Jorge A. Acosta-Gallegos, J.A., Heil, M. (2015). Plant volatiles cause direct, induced and associational resistance in common bean to the fungal pathogen *Colletotrichum lindemuthianum*. J. Ecol., 103, 250–260. DOI: 10.1111/1365-2745.12340

Ramirez-Estrada, K., Vidal-Limon, H., Hidalgo, D., Moyano, E., Goleniowski, M., Cusidó, R.M., Palazon, J. (2016). Elicitation, an effective strategy for the biotechnological production of bioactive high-added value compounds in plant cell factories. Molecules, 21(2), 182. DOI: 10.3390/molecules21020182

Reyes-Díaz, M., Lobos, T., Cardemil, L., Nunes-Nesi, A., Retamales, J., Jaakola, L., Alberdi, M., Ribera-Fonseca, A. (2016). Methyl jasmonate: an alternative for improving the quality and health properties of fresh fruits. Molecules, 21(6), 567. DOI: 10.3390/molecules21060567

Saba, M.K., Zarei, L. (2019). Preharvest methyl jasmonate's impact on postharvest chilling sensitivity, antioxidant activity, and pomegranate fruit quality. J. Food Biochem., e12763. DOI: 10.1111/jfbc.12763

Sadeghipour, O. (2017). Amelioration of salinity tolerance in cowpea plants by seed treatment with methyl jasmonate. Legume Research, 40(6), 1100–1106. DOI: 10.18805/lr.v0i0.8394.

Saito, N., Nakamura, Y., Mori, I.C., Murata, Y. (2009). Nitric oxide functions in both methyl jasmonate signaling and abscisic acid signaling in Arabidopsis guard cells. Plant Signal. Behav., 4(2), 119–120. DOI: 10.4161/psb.4.2.7537

Santino, A., Taurino, M., De Domenico, S., Bonsegna, S., Poltronieri, P., Pastor, V., Flors, V. (2013). Jasmonate signaling in plant development and defense response to multiple (a)biotic stresses. Plant Cell Rep., 32, 1085–1098. DOI: 10.1007/s00299-013-1441-2

Scognamiglio, J., Jones, L., Letizia, C.S., Api, A.M. (2012). Fragrance material review on methyl jasmonate. Food Chem. Toxicol., 50, Suppl. 3, S572–S576. DOI: 10.1016/j.fct.2012.03.035

Scott, E.R., Li, X., Kfoury, N., Morimoto, J., Han, W.-Y., Ahmed, S., Cash, S.B., Griffin, T.S., Stepp, J.R., Robbat, A., Orians, C.M. (2019). Interactive effects of drought severity and simulated herbivory on tea (*Camellia sinensis*) volatile and non-volatile metabolites. Environ. Exp. Bot., 157, 283–292. DOI: 10.1016/j.envexpbot.2018.10.025

Selig, P., Keough, S., Nalam, V. J., Nachappa, P. (2016). Jasmonate-dependent plant defenses mediate soybean thrips and soybean aphid performance on soybean. Arthropod Plant Interact., 10(4), 273–282. DOI: 10.1007/s11829-016-9437-9

Sembdner, G., Parthier, B. (1993). The biochemistry and the physiological and molecular actions of jasmonates. Annu. Rev. Plant Physiol. Plant Mol. Biol., 44, 569–589. DOI: 10.1146/annurev.pp.44.060193.003033

Senthil-Nathan, S. (2019). Effect of methyl jasmonate (MeJA)-induced defenses in rice against the rice leaffolder *Cnaphalocrocis medinalis* (Guenèe) (Lepidoptera: Pyralidae). Pest Manag. Sci., 75, 460–465. DOI: 10.1002/ps.5139

Serrano, M., Martínez-Esplá, A., Zapata P.J., Castillo, S., Martínez-Romero, D., Guillén, F., Valverde, J.M., Valero, D. (2018). Effects of methyl jasmonate treatment on fruit quality properties. In: Emerging Postharvest Treatment of Fruits and Vegetables, Barman, K., Sharma, S., Siddiqui, M.W. (eds.). Apple Academic Press, Oakville, Canada, 85–106.

Sheteiwy, M.S., Gong, D., Gao, Y., Pan, R., Hu, J., Guan, Y. (2018). Priming with methyl jasmonate alleviates polyethylene glycol-induced osmotic stress in rice seeds by regulating the seed metabolic profile. Environ. Exp. Bot., 153, 236–248. DOI: 10.1016/j.envexpbot.2018.06.001

Sohn, H.B., Lee, H.Y., Seo, J.S., Jung, C., Jeon, J.H., Kim, J.-H., Lee, Y.W., Lee, J.S., Cheong, J.-J., Choi, Y.D. (2011). Overexpression of jasmonic acid carboxyl methyltransferase increases tuber yield and size in transgenic potato. Plant Biotechnol. Rep., 5, 27–34. DOI: 10.1007/s11816-010-0153-0

Staswick, P.E. (2008). JAZing up jasmonate signaling. Trends Plant Sci., 13(2), 66–71. DOI: 10.1016/j.tplants.2007.11.011

Stella de Freitas, T.F., Stout, M.J., Sant'Ana, J. (2019). Effects of exogenous methyl jasmonate and salicylic acid on rice resistance to *Oebalus pugnax*. Pest Manag. Sci., 75, 744–752. DOI: 10.1002/ps.5174

Talebi, M., Moghaddam, M., Pirbalouti, A.G. (2018). Methyl jasmonate effects on volatile oil compounds and antioxidant activity of leaf extract of two basil cultivars under salinity stress. Acta Physiol. Plant., 40, 34. DOI: 10.1007/s11738-018-2611-1

Tavallali, V., Karimi, S. (2019). Methyl jasmonate enhances salt tolerance of almond rootstocks by regulating endogenous phytohormones, antioxidant activity and gasexchange. J. Plant Physiol., 234–235, 98–105. DOI: 10.1016/j.jplph.2019.02.001

Van Loon, L.C., Rep, M., Pieterse, C.M.J. (2006). Significance of inducible defense-related proteins in infected plants. Annu. Rev. Phytopathol., 44, 135–162. DOI: 10.1146/annurev.phyto.44.070505.143425

Vick, B., Zimmerman, D. (1984). Biosynthesis of jasmonic acid by several plant species. Plant Physiol., 75, 458–461.

Wang, L., Guo, Z.H., Zhang, Y.B., Wang, Y.J., Yang, G., Yang, L., Wang, R.Y., Xie, Z.K. (2017). Isolation and characterization of two distinct Class II *PR4* genes from the oriental lily hybrid Sorbonne. Russ. J. Plant Physiol. 64, 707. DOI: 10.1134/S1021443717050132

Wang, S.Y., Chen, C.T., Wang, C.Y., Chen, P. (2007). Resveratrol content in strawberry fruit is affected by preharvest conditions. J. Agric. Food Chem., 55, 8269–8274. DOI: 10.1021/jf071749x

Wang, Y., Gao, L., Wang, Q., Zuo, J. (2019). Low temperature conditioning combined with methyl jasmonate can reduce chilling injury in bell pepper. Sci. Hortic., 243, 434–439. DOI: 10.1016/j.scienta.2018.08.031

Wasternack, C. (2007). Jasmonates: an update on biosynthesis, signal transduction and action in plant stress response, growth and development. Ann. Bot., 100(4), 681–97. DOI: 10.1093/aob/mcm079

Wasternack, C., Hause, B. (2013). Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in Annals of Botany. Ann. Bot., 111(6), 1021–58. DOI: 10.1093/aob/mct067

Wasternack, C., Strnad, M. (2016). Jasmonate signaling in plant stress responses and development – active and inactive compounds. N. Biotechnol., 33(5), 604–613. DOI: 10.1016/j.nbt.2015.11.001

Wilmowicz, E., Kućko, A., Frankowski, K., Świdziński, M., Marciniak, K., Kopcewicz, J. (2016). Methyl jasmonate-dependent senescence of cotyledons in *Ipomoea nil.* Acta Physiol. Plant., 38, 222. DOI: 10.1007/s11738-016-2244-1

Wu, W., Ding, C., Baerson, S.R., Lian, F., Lin, X., Zhang,

L., Wu, C., Hwang, S.-H., Zeng, R., Song, Y. (2019). The roles of jasmonate signalling in nitrogen uptake and allocation in rice (*Oryza sativa* L.). Plant Cell Environ., 42, 659–672. DOI: 10.1111/pce.13451

Xiao, Y., Chen, Y., Charnikhova, T., Mulder, P.P.J., Heijmans, J., Hoogenboom, A., Agalou, A., Michel, C., Morel, J.-B., Dreni, L., Kater, M.M., Bouwmeester, H., Wang, M., Zhu, Z., Ouwerkerk, P.B.F. (2014). *OsJAR1* is required for JA-regulated floret opening and anther dehiscence in rice. Plant Mol. Biol., 86, 19–33. DOI: 10.1007/s11103-014-0212-y

Xie, Q., Yan, F., Hu, Z., Wei, S., Lai, J., Chen, G. (2019). Accumulation of anthocyanin and its associated gene expression in purple tumorous stem mustard (*Brassica juncea* var. *tumida* Tsen et Lee) sprouts when exposed to light, dark, sugar, and methyl jasmonate. J. Agric. Food Chem., 67, 856−866. DOI: 10.1021/acs.jafc.8b04706

Xu, Q., Truong, T.T., Barrero, J.M., Jacobsen, J.V., Hocart, C.H., Gubler, F. (2016). A role for jasmonates in the release of dormancy by cold stratification in wheat. J. Exp. Bot., 67(11), 3497–3508. DOI: 10.1093/jxb/erw172

Yang, N., Guo, X., Wu, Y., Hu, X., Ma, Y., Zhang, Y., Wang, H., Tang, Z. (2018). The inhibited seed germination by ABA and MeJA is associated with the disturbance of reserve utilizations in *Astragalus membranaceus*. J. Plant Interact., 13(1), 388–397. DOI: 10.1080/17429145.2018.1483034

Yu, H., Khashaveh, A., Li, Y., Li, X., Zhang, Y. (2018). Field trapping of predaceous insects with synthetic herbivore-induced plant volatiles in cotton fields. Environ. Entomol., 47(1), 114–120. DOI: 10.1093/ee/nvx201

Zeng, X., Zhou, X., Zhang, W., Murofushi, N., Kitahara, T., Kamuro, Y. (1999). Opening of rice floret in rapid response to methyl jasmonate. J. Plant Growth Regul., 18(4), 153–158. DOI: 10.1007/PL00007063

Zhang, Y., Xie, Y., Xue, J., Peng, G., Wang, X. (2009). Effect of volatile emissions, especially α-pinene, from persimmon trees infested by Japanese wax scales or treated with methyl jasmonate on recruitment of ladybeetle predators. Environ. Entomol., 38(5), 1439–1445. DOI: 10.1603/022.038.0512