Stimulating secondary compound accumulation by elicitation: Is it a realistic tool in medicinal plants in vivo?

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Abstract Stimulating the production of secondary metabolites by elicitation seems to be an accepted tool in several in vitro cultures. In vivo application of chemical elicitation is, however, much less frequently discussed. The paper summarizes the experimental findings on the effects of jasmonic acid, methyl-jasmonate (MeJa) and salicylic acid (SA) treatments on medicinal and aromatic plants. Growth behaviour, yield, stress responses, essential oil (EO) and phenolic compounds are discussed. Exogenous application of MeJa or SA mostly by foliar spraying in concentrations between 10^{-4} and 4 mM, induced various changes in the plants. In most cases, the elicitation enhanced the volatile accumulation, although the opposite reaction was observed too. Numerous in vivo trials also demonstrated an altered EO composition. Positive effects of treatments on the concentration of phenolic type compounds were described, while in some cases the components exhibited contradictory behavior or no significant changes. Unfortunately, phenolic composition was rarely determined. There is evidence for the dose dependency of the reactions to both elicitors, but systematic studies on this issue are missing. Some results indicate that lower concentrations in replication may be at least as effective as higher ones. Changes in secondary metabolite accumulation may be induced by the elicitors directly or through other physiological processes. The in vivo results should be considered in the complex system of plant ontogenesis, environmental conditions, timing of the treatment, type of the elicitor and concentration. Research results indicate a promising aspect of chemical elicitation in vivo, but further well-designed studies are needed for the individual species.

Keywords Biomass · Essential oil · Jasmonates · Polyphenols · Salicylic acid · Stress

Abbreviations
ABA Abscisic acid
BA Benzoic acid
CA Cinnamic acid
EO Essential oil
CAA Caffeic acid
CHA Chlorogenic acid
FA Ferulic acid
GA Gibberellic acid
JA Jasmonic acid
MAP Medicinal and aromatic plant
MeJa Methyl jasmonate
NaCl Sodium chloride
RA Rosmarinic acid
Introduction

Plant secondary metabolites (SMs) have immense potential applications in the chemical-pharmaceutical industries such as pharmaceuticals, agrochemicals, perfumes, flavors, dyes, biopesticides, and food additives thanks to their biological activities (Epifano et al. 2007). However, despite many efforts, the production of SMs is still facing some limitations. In most plants, they occur in relatively low concentrations (less than 1% dry weight), accumulating in special structures or organelles; and their accumulation depends on many factors related to the producing plant and its environment (Bourgaud et al. 2001; Tohidi et al. 2017; Németh-Zámbori 2015).

Based on widespread opinion, the production of SMs by the plants may be regarded as a coping mechanism induced by unstable and changing environments like drought, high and low temperature, salinity, UV stress or pathogen infections (Edreva et al. 2008; Isah 2019; Tang and Tang 2021).

Due to the extensive demand for SM by the pharmaceutical and other industries, many strategies have been applied to enhance their synthesis and accumulation in higher plants. The most common activities are breeding and selection to improve the genetic potential of the plants. Regulating the cultivation environment as well as optimizing of technological measures and tools could contribute to larger accumulation levels of the desired compounds. A further and relatively recent possibility in the stimulation of SM production is elicitation (Isah et al. 2017; Gonçalves and Romano 2018). Elicitation has become popular due to its relatively low cost and simplicity. It is frequently mentioned as one of the most effective strategies to enhance the yield of desirable SMs and manipulate the biochemical and metabolic pathways (Narayani and Srivastava 2017; Thakur et al. 2019). It is supposed that the application of elicitors to the living target organism induces plant immune responses and triggers defense reactions. Thus, most possibly as a consequence of this, plants often increase the production of SMs (Thakur et al. 2019; Halder et al. 2019). Moreover, some authors believe that the application of elicitors may serve as a promising alternative to reduce the use of conventional biocidal pesticides since they may have a role in pest control and could protect crops from infections and diseases too (Xing et al. 2015; Pereira et al. 2019). Nevertheless, this statement is true only to some extent, because the effect of the elicitor treatment is not consistent in every plant species, and they seem to exhibit marked differences in the expression of induced resistance. The salicylic acid (SA) pathway is primarily induced by and effective in mediating resistance against biotrophic pathogens. This was detected, among others, in NahG transgenic Arabidopsis, which expresses a SA hydroxylase; hence, due to a decrease of SA in the plant, it was not able to resist the biotrophic Peronospora parasitica (Thomma et al. 1998; Thatcher et al. 2009). In parallel, the jasmonic acid (JA) pathway is primarily induced by and effective in mediating resistance against herbivores and necrotrophic pathogens (Glazebrook 2005; Wang and Wu 2013; Fu et al. 2022), as it seems that coronatine insensitive 1 (coi1) mutants of Arabidopsis showed weakened resistance to necrotrophic pathogens such as Botryris cinerea and Alternaria brassicicola.

Specific defense mechanisms that induce resistance to one attacker may render the plant more susceptible to another. JA/methyl jasmonate (MeJa) and SA may act antagonistically, as it was shown by Spoel et al. (2007), who found that infection with the biotrophic pathogen P. syringae pv. tomato (Solanum lycopersicum) strain induces SA-mediated defense, but makes plants more vulnerable to the necrotrophic pathogen, Alternaria brassicicola, by suppressing the JA signaling pathway. Therefore, using elicitors as tools for pest management is rather a complicated solution and needs to be studied more thoroughly in the future.

Despite many research papers, book chapters, and published excellent review articles on elicitation, only some of them deal at least marginally with the results obtained with in vivo plants that have been growing under agricultural circumstances (Table 1). Hence, this review has been prepared to fill this gap in focusing and providing a full overview of in vivo elicitation. It would be of interest not only to plant scientists but also for producers who are looking for efficient tools to raise yield and improve drug quality.

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Our goal was to collect and evaluate the scientific information on in vivo elicitation techniques and their results in enhancing the accumulation of biologically active compounds in plants. More specifically, we are focusing on the effects of elicitation by SA and JA along with their derivatives. We present and evaluate the references dealing with experiments where the plant material has been subjected to different dosages of the elicitor compounds. The paper discusses the effects of the treatments on growth, biomass, accumulation of SMs like volatile terpenoids and phenolic compounds, including phenolic acids and flavonoids, and finally their potential activity in mitigating the effects of abiotic stresses.

### Enhancing the biosynthesis of SMs by elicitation

Elicitation involves enhancing the biosynthesis of SMs by the application of different elicitor treatments. Elicitors can be divided into two types based on their nature: biotic and abiotic.

As for biotic elicitors, microorganisms (fungi and bacteria are the best known) and polysaccharides originated from yeast and mycelia cell walls are most frequently mentioned (e.g., chitin, pectin, and cellulose) (Narayani and Srivastava 2017). Abiotic elicitors are usually grouped as physical (light, osmotic stress, salinity, drought, and thermal stress), chemical (heavy metals), and hormonal factors, among others JA, SA, gibberellic acid (GA) usually applied in low concentrations.

In the following, we will be focusing on the chemical elicitation methods. Chemical elicitation
treatments can be applied in vitro or in vivo by different techniques.

In case of the in vitro elicitation, the elicitor molecule can be applied in cell suspension cultures where the elicitor molecule is added to the culture at a certain stage of the cell growth cycle (Keshavan et al. 2022); or by elicitation of hairy root cultures, which is a plant tissue culture mediated by *Agrobacterium rhizogenes* that infect plant roots and cause them to grow abnormally (Hashemi and Naghavi 2016).

Intensive research has been devoted to understanding the intricate mechanism of elicitation in many plants. However, most studies on elicitation have been focusing on in vitro application. Numerous authors believe that it has more advantages than open field application due to the lack of interferences, like climatic and geographical conditions (Hussain et al. 2012).

According to various publications, in vitro elicitation was proven to be indeed an effective tool in promoting the production of SMs. Reports about this type of treatment are numerous. Examples include the induction of the accumulation of glycyrrhizin acid; a triterpenoid saponin and the major active constituent of liquorice (*Glycyrrhiza glabra*) by MeJa and SA in root cultures (Shabani et al. 2009). Similarly, cell culture elicitation by SA increased not only phenolic content, but also antioxidant activity in red sage (*Salvia miltiorrhiza*) and callus cultures of roselle (*Hibicus sabdariffa* Linn) (Dong et al. 2010; Jirakit-tikul et al. 2021). Biotic elicitation by two bacterial strains, *Bacillus cereus* and *Staphylococcus aureus*, resulted in an enhanced production of scopalamine, a tropane alkaloid accumulating in Indian thornapple (*Datura metel*) hairy roots (Shakeran et al. 2017). It has been demonstrated that different types of elicitors show synergic or antagonistic effects when applied together. Thus, the combined application of ultraviolet-C irradiation with MeJa or SA significantly stimulated the biosynthesis of stilbene and flavonoids in grape vine (*Vitis. vinifera*) cell cultures (Xu et al. 2015).

Scientific results on in vivo elicitation are less numerous, however. This method most frequently involves foliar application by spraying the living plant at selected times in the vegetation period with a dilution of the elicitor molecule prepared with plain water or dissolved first in other solvents such as ethanol or mixed with additives like Tween-20 (Polyoxyethylenesorbitan monolaurate) (Wang et al. 2008; Złotek et al. 2016a). As an alternative, elicitor molecules are provided in the form of solutions absorbed by the root system (Fard et al. 2012). In addition, soaking can be used as well for seeds (Cho et al. 2008).

The trials are also heterogeneous concerning the number and frequency of the applied treatments. Depending on the study, cumin (*Cuminum ciminum*) was sprayed with the elicitor twice in one-week intervals (Rahimi et al. 2013), the spraying of yarrow (*Achillea millefolium*) was done for three consecutive days (Gorni et al. 2019), while in the case of marjoram (*Origanum majorana*) the plant was treated only once (Złotek 2017). In the hydroponic system, where the roots of the plants are soaked in a nutrient solution containing the elicitor, treatment may last from a few hours to a couple of days (Fard et al. 2012).

### Methodology and search strategy

129 published references have been cited in this review, mainly dated over the past 20 years. The evaluated studies were acquired from electronic databases following a search strategy planned to retrieve new and rich data for our review. We used such databases as Google Scholar, PubMed, Science Direct, SciFinder, Web of Science, etc. Additionally, other online sources (ResearchGate, National Center for Biotechnology Information (NCBI), Springer Nature Open Access, Wiley Online Library, JSTOR etc.) were used. The following search terms were used to find articles relevant to this review: *elicitation*, *jasmonate*, *SA*, *phytohormones*, *effect of MeJa and SA on SMs*, etc. Other alternatives to these terms were used as well to ensure a full search result. Besides, the bibliographies of the available publications were checked for additional references like available reports, dissertations, and monographs located in the library of the Hungarian University of Agriculture and Life Sciences and websites of other universities.

The data obtained from different sources were evaluated to determine which facts and results have been confirmed, put into practice, improved or corrected. In order to obtain a better comparison, the dosages of the applied chemicals in the different publications—if necessary and possible—were recalculated and given in the text in mM (millimol) unit.
Jasmonates

Plants produce volatile and non-volatile compounds, including phytohormones, that help them withstand and manage biotic and abiotic stresses (Bücker-Neto et al. 2017; Alhaithloul et al. 2021). JA, its methyl ester MeJa and other derivatives, collectively referred to as jasmonates, are considered some of the most prominent phytohormones (Fig. 1). One of the first identified jasmonate type compounds was MeJa, as a component in the essential oil (EO) of Spanish jasmine (Jasminium grandiflorum) flowers, while JA was first isolated from the cultures of the fungus Lasiodiplodia theobromae (Demole et al. 1962). Jasmonates are derived from polyunsaturated fatty acids via the octadecanoid pathway (Küpfer et al. 2009; Kombrink and Wasternack 2010). The biosynthesis of jasmonates is initiated with the formation of \( \alpha \)-linolenic acid from galactolipids of the chloroplast membranes, which is converted to 12-oxophytodienoic acid (OPDA) with the help of the enzymes phospholipase A1, 13-lipoxygenase (LOX), allene oxide synthase (AOS) and allene oxide cyclase (AOC). The remaining stages of JA biosynthesis take place in peroxisomes. OPDA is exported from the chloroplast and enters the peroxisomes, undergoes a reductase reaction and several \( \beta \)-oxidations, and eventually produces JA (Wasternack and Song 2017).

Although it was proven that the peroxisomal membrane transporter COMATOSE (CTS) is responsible for importing the OPDA inside the peroxisome (Footitt et al. 2002), for a long time it was a mystery, how the OPDA travels from the chloroplast to the peroxisome. However, recently, Guan and coworkers (2019) revealed a protein called JASSY localized to the outer chloroplast envelope, which seems to be involved in this transport mechanism. Following the production of JA, several metabolic pathways can convert the hormone into more active, partially active, or inactive forms. These include conjugation (JA-Ile) for gene expression, hydroxylation and carboxylation (12-OH-JA) in order to maintain homeostasis among the active and inactive forms of derivatives, decarboxylation (cis-jasmone) for the pollination process, methylation and esterification (MeJa) for pollination and signaling (Koo and Howe 2012).

Although JA and MeJa—the latter obtained by methylation and esterification with the help of MeJa methyltransferases—are the most prominent signaling compounds, clear evidence has recently shown that the most biologically active derivative of jasmonates is jasmonoyl-L-isoleucine (JA-Ile) (Wasternack and Song 2017), JA-Ile occurs after a triple \( \beta \)-oxidation of the JA in the cytosol, after which it is transported into the nucleus where it binds to receptor complexes to activate gene expression. Additionally, to JA-Ile, other amino acid conjugates of JA like \((\pm)-7\text{-iso-JA-Ala}\), \((\pm)-7\text{-iso-JA-Val}\), \((\pm)-7\text{-iso-JA-Leu}\) and \((\pm)-7\text{-iso-JA Met}\) were recognized to be endogenous bioactive molecules (Wasternack and Strnad 2018).

Jasmonates have dual tasks in plants. They play a crucial role in defense and regulation of biotic/abiotic stress responses, as well as in activities related to plant growth and development (Huang et al. 2017). Healthy, non-stressed plants are also able to produce endogenous JA or its derivates, which affect several

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**Fig. 1** Structure of jasmonates
developmental processes such as root growth, germination of seeds, tuber formation, tendril coiling, trichome initiation, flower development, and senescence (Wasternack 2007; Browse and Howe 2008; Santino et al. 2013). Moreover, they are also considered important factors in signal transduction processes that trigger defense responses in plants (Ahmad et al. 2016).

Morphological responses

In vivo application of jasmonates is most often carried out by spraying the aboveground parts (leaves, shoots) with a solution of the elicitor. Experimental data refers to both positive and negative impacts of treatments or even ineffectiveness. Nevertheless, in these studies, the target species, the applied dosages, duration of exposure, the age of the plant, and the number of replications vary on a large scale, which makes a reliable general conclusion very difficult.

Concerning the morphological traits and biomass production, the application of exogenous MeJa twice with an interval of 23 days before the blooming stage has revealed no significant differences in the case of St John’s wort (*Hypericum perforatum*). Little variation in height, dry weight, and number of branches appeared even as a consequence of the highest concentration of MeJa (1.78 mM) (Hamedi et al. 2012). Another study also reported no significant effect on growth indices of thyme (*Thymus daenensis*) by foliar application of JA three times from vegetative stage until 25% blooming stage (Alavi-Samani et al. 2015). This is also in accordance with the results of Złotek et al. (2016a, b) who noted no retardant effects in basil (*Ocimum basilicum*) up to 0.1 mM concentration of MeJa. In parallel, 0.1 mM MeJa elicitation performed once on potato (*Solanum tuberosum* L. var. Granola) did not cause significant changes in the plant’s height (Rohmawati et al. 2019).

Contrary to the previously cited findings, elicitor treatments resulted in most cases in retardant effects on the growth behavior of tomato, soybean (*Glycine max*) and sunflower (*Helianthus annuus*) (Li et al. 2018). Spraying the leaves of soybean with 1 mM MeJa resulted in a 26% decrease in root length, whereas the dry shoot mass of sunflower was reduced remarkably—threefold—due to MeJA in all applied concentrations (0.1, 0.5, 1.0, and 2.5 mM). This is in accordance with another study that found the exogenous application of MeJa twice, 27 days and 13 days before sampling on 8-month-old seedlings of Monterey pine (*Pinus radiata*) led to a remarkable reduction in growth. The treatments decreased seedling height by 45% when 25 mM of the elicitor was applied (Lundborg et al. 2019). About 0.5 mM of MeJa significantly decreased the fresh mass of spearmint (*Mentha spicata*) too, however in this case, the foliar spraying was repeated 3 times (Zheljazkov et al. 2013). The dose dependent reaction and retarding effects of higher dosages in the case of MeJa were demonstrated clearly by the same author in another study (Zheljazkov and Astatkie 2011).

On the other hand, positive results are also reported. Abdi and Coworkers (2019) showed that the growth of peppermint (*Mentha piperita*) was slightly improved in the case of foliar application of 0.05 mM of MeJa three times at an interval of approximately 10 days. The shoot length was enhanced by 4 cm on average. In addition, 0.05 mM of MeJa was able to induce 1–2 day of earlier flowering in six oilseed rape (*Brassica napus*) cultivars from China with different life cycle lengths. This was in comparison to the non-treated plants (Pak et al. 2009).

Based on these data, it seems that the effect of jasmonates on growth behavior may be influenced by the plant species and/or the dosage of the elicitor. Most likely, the time of application is also of great importance, as in different phenological phases the sensitivity and reaction of the target plant individual might be different.

Effect of MeJa/JA on the accumulation of volatiles

The effect of MeJa has been examined on the accumulation of different metabolites. The highest number of references deals with plant species containing volatile compounds. The results include data on the chemical composition of the EO, on the concentration of volatile components and in connection with the biomass; in some cases, EO yield is mentioned also.

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In numerous cases, exogenous application of MeJa was found to have a significant effect on the quantity of volatile organic compounds. Spraying 0.1 mM of MeJa four times on marjoram failed to increase the yield of EO; in fact, it dropped significantly, by 11% compared to the control. Nevertheless, this result may presumably be explained by the negative effect of the
elicitor on the fresh and dry mass, where the fresh weight slightly dropped from 7.66 g/plant to 7.36 g/plant, while the percentage of EO was not significantly affected (Farsi et al. 2019).

Conversely, when $10^{-4}$, $10^{-3}$, and $10^{-1}$ mM of JA were applied by foliar spraying in the case of basil, the results revealed that the highest oil yield was achieved by the application of $10^{-3}$ mM of JA, which represented a value greater by 0.21 ml/100 g dry weight compared to the control (Zlotek et al. 2016a). In peppermint, Khanam and Mohammad (2016) demonstrated that even a concentration of $5 \times 10^{-6}$ mM of MeJa was able to enhance the EO content by 37% and the yield of the oil per plant by 98% when the treatment was repeated five times.

The study on anise hyssop (Agastache foeniculum) was carried out in a hydroponic system, in boxes with liquid medium containing both the nutrients and the elicitor. The results showed that $10^{-1}$ mM of MeJa was more efficient in stimulating the accumulation of EO compounds than the higher concentration of 1 mM. Already, after 24 h this treatment enhanced the volatile concentration by 22%, and during a 48 h-treatment, the increase reached 26% compared to the control (Fard et al. 2012).

Based on these studies, the dose of $10^{-1}$ mM of JA/MeJa seems to be efficient in inducing the accumulation of volatile compounds in different species. Furthermore, it has been suggested that the concentration of the elicitor can make a difference, as well as the application method and the elicitation period. On the other hand, it should be noted that the actual real yield of EO is the result both of the concentration of volatiles in the tissues and of the plant biomass, thus optimization of both factors would be necessary.

The elicitation treatments with jasmonates frequently affected the composition of the EO also. In basil, $10^{-1}$ mM JA elicitation induced an increase in the ratio of EO components linalool (from 4.98% in the control sample to 20.88% in the treated one), eugenol (from 17.59 to 24.88%), and limonene (from 0.64 to 0.88%). In parallel, some other components showed a lower concentration compared to the control, such as (Z)-caryophyllene (from 9.53 to 4.53%), 1,8-cineole (from 16.68 to 9.05%), and methyl eugenol (from 25.81 to 10.84%). Additionally, the composition of EO in treated plants included some compounds that were not detected in the control samples, like bornyl acetate, camphene, camphor (Zlotek et al. 2016a). The same concentration ($10^{-1}$ mM) of MeJa induced changes in hyssop oil (Hyssopus officinalis), increasing significantly the ratio of monoterpenes and decreasing the sesquiterpenes (Kandoudi et al. 2021). Pirbalouti et al. (2013) indicated that, based on the results of a trial where 50, 100, and 200 μL levels of JA were applied foliarly once, 10 days before harvest, the treatment had a significant impact on the major components in the EO of hyssop. Thus, under 200 μL MeJa treatment, a decrease was observed in the proportions of monoterpenes like α-pinene, β-phellandrene, β-pinene, myrtenol, cis-3-pinanone, and trans-3-pinanone (from 20 to 5%). On the other hand, the ratio of the sesquiterpene group increased, including bicyclogermacrene and germacrene D four-fold. In addition, elemol was absent in samples sprayed with only water, unlike the ones treated with MeJa, which was able to synthesize the volatile compound up to 17.26% of the oil.

MeJa increased the concentration of l-carvone, the main constituent in the EO of Scotch spearmint (Mentha x gracilis Sole). Interestingly, even though there is a 100-fold difference between the two applied elicitor concentrations, the rise of carvone content was only slightly different (74.8% and 75.5% due to 4.58 × $10^{-2}$ and 4.46 mM of MeJa, respectively) (Zheljazkov and Astatkie 2011). In addition, MeJa was also able to elevate the menthol ratio in the EO of Mentha x piperita (Khanam and Mohammad 2016).

It seems that JA and MeJa elicitor treatments could lead to significant changes in the ratio of the EO components, thus affecting the quality of the drug or product. However, as authors always provide GC area percentage data, unfortunately it is not clear in which biosynthetic processes the elicitor might have been involved. Therefore, the background of the changes needs further clarification in all these studies.

Effect of MeJa on the accumulation of phenolic compounds

The accumulation of phenolic compounds induced by elicitation has been documented in many MAP and vegetable species.

Sweet basil is a rich source of polyphenols with high antioxidant potential, in particular, caffeic acid (CAA) and its ester rosmarinic acid (RA). A study revealed that the elicitation by 0.1 mM and 0.5 mM MeJa significantly increased the total phenolic content
(TPC) of the sweet basil after treatments, compared with the untreated control, including the above-mentioned two main phenolic compounds. The higher dosage was more effective in improving these compounds: TPC, RA, and CAA were enhanced by 57, 47 and 220%, respectively (Kim et al. 2006). This study largely corresponds to the results obtained by Złotek et al. (2016b). The application of $10^{-3}$ mM JA on basil induced the accumulation of TPC by 47% and the phenolic acid RA by 30%, but no significant difference was observed in CAA content.

In butter lettuce (Lactuca sativa L.), the application of $10^{-3}$ mM JA resulted in a threefold increase of TPC followed by a marked elevation of the phenolic acids, ferulic acid (FA), CAA, and chlorogenic acid (CHA) by 319%, 472%, and 85%, respectively. On the other hand, the flavonoids reacted specifically to the elicitor, as the quercetin concentration was doubled while the kaempferol content decreased significantly, by 20% (Złotek et al. 2014).

It seems that in the majority of cases, the concentration of different phenolic compounds and the total accumulation rate of phenolics were affected by elicitation. However, the comparison of the levels of phenolic compounds in plants in vivo seems to be even more difficult than in the case of, for example, the volatile, mostly terpenoid type compounds. The phenolics are definitely more influenced by environmental factors and the plant’s exposure to biotic or/and abiotic stresses.

**Salicylic acid**

SA or 2-hydroxy benzoic acid (Fig. 2) is a phenolic derivative classified under the group of plant hormones. It can be synthesized via the phenylpropanoid pathway in the cytoplasm initiated from phenylalanine (Phe) or isochorismate (IC) routes in the chloroplast. SA is ubiquitously distributed in the whole plant kingdom; however, its concentration may fluctuate depending on the species, even within the same plant family (Peng et al. 2021).

SA and its salts and esters, such as acetylsalicylic acid (aspirin), methyl salicylate, salicilin, and 4-aminosalicylic acid are known as salicylates (Ekinci et al. 2011).

Salicylates play a pivotal role in the activation and regulation of multiple responses to biotic and abiotic stresses and are involved either directly or indirectly in the defense responses of plants (Hara et al. 2012; Wani et al. 2016). Ryals et al. (1995) declare that species that cannot produce SA anymore due to some genetic modification, are more susceptible to pathogen infection. In addition, SA takes part in signaling processes during photosynthesis, in the biogenesis of chloroplasts, water use efficiency, stimulation of nitrogen metabolism, inhibition of fruit ripening or gravitropism (Hayat et al. 2010).

Studies have found evidence that SA can be synthesized via two distinct pathways: the IC pathway in the chloroplast and the phenylalanine ammonia-lyase (PAL) pathway that takes place in the cytosol. However, both of them share the same origin: they start from chorismate (Lefevere et al. 2020). In the IC pathway, chorismic acid is converted into IC by the action of isochorismate synthase, then isochorismate pyruvate lyase (IPL) catalyzes the transformation to SA in the chloroplast, and afterward it is exported to the cytosol. On the other hand, in the PAL route, Phe is produced by the action of chorismate mutase (CM) on the chorismic acid, followed by a reduction. Phe is later converted into trans-cinnamic acid (t-CA) by PAL and can be transformed into ortho-coumaric acid (o-CA) or benzaldehyde. SA can be synthesized directly from o-CA while aldehyde oxidase (AO) transforms benzaldehyde into benzoic acid (BA) and then to SA by benzoic acid 2-hydroxylase (BA2H) (Maruri-López et al. 2019; Peng et al. 2021). Once SA is synthesized, it undergoes a few biochemical modifications like glycosylation to render the acid inactive, then it is stored inside the vacuole to maintain cytoplasmic SA levels low until the plant is subjected to stress (Fu and Dong 2013).

Accumulation of SA has been detected right at the site of infection during a pathogen attack. SA usually triggers a hypersensitive response, then it spreads to distant tissues of the plant to induce a wide range of defense reactions (Figueroa-Pérez et al. 2018;
Papadopoulou et al. 2018). In addition to improving the plant’s abiotic stress tolerance, SA is able to induce the expression of genes regulating several biosynthetic processes of SMs. It is well documented that the application of SA affects multiple aspects of plant growth and development, from seed germination and vegetative growth to flowering and senescence (Khan et al. 2015; Wani et al. 2016; Klessig et al. 2018).

Morphological and production responses

Exogenous application of SA has been shown in multiple studies to stimulate plant growth. Gharib (2006) indicated that two foliar applications of SA on marjoram and basil (three and a half months after sowing) increased plant height, number of branches, spikes, and leaves per plant, as well as leaf area in three different cuts. When compared to the control, the treatment in three different concentrations of SA (10⁻², 10⁻¹ and 1 mM) improved fresh and dry weights. This promoting effect was maximal in the first cut of basil at 10⁻¹ mM SA for all growth parameters, where the fresh weight increased twofold, except for leaf area (30% increase), showing maximum values at 10⁻² mM concentration.

Similarly, both concentrations of SA (10⁻¹ mM and 10⁻² mM) when sprayed at the flowering stage twice in one-week intervals, resulted in significant stimulation of plant growth in cumin, where the highest plant height and the largest number of branches and umbels per plant were recorded. Besides, the highest seed yield was obtained as the result of SA application in 10⁻¹ mM concentration, showing a significant increase of about 77% compared with control (Rahimi et al. 2013).

The growth and production promoting effects of SA were ascertained in several other references, too. SA at both 0.724 and 1.448 mM applications significantly increased all studied production parameters of marjoram. Plant height and fresh yield per plant, as well as dry yield per plant improved, compared to control. The highest elevation was recorded at a concentration of 1.448 mM, with a growth of fresh yield increasing by approximately 62% (Hashem 2018). In addition, 0.724 and 1.086 mM of SA enhanced the shoot dry weight in four ecotypes of thyme (Thymus kotschyanus) from different regions in Iran, reaching the highest increase of 74% by 1.086 mM SA in the case of the Kerman region ecotype (Mohammadi et al. 2019). Thus, in this latter experiment, a definite intraspecific genotype-dependent reaction was also justified.

Lower dosages may also be effective. In soybean, foliar spraying of different dosages of SA (0.181, 0.362, 0.543, 0.724, 0.905, and 1.086 mM) was applied at 12, 24, and 36 days after sowing. The results demonstrated a 2–5 day earlier appearance of floral buds and a higher number of them per plant due to treatments with 0.362 and 0.543 mM SA on the 24th day. Moreover, a significant increase was observed in pod weight and grain yield in SA treated plants over the control, reaching a maximum when plants were treated with 0.362 mM SA at the 24th day (Kumar et al. 1999). After this and several other studies, some authors believe that SA may also have flowering-inducing effects (Raskin 1992; Hegazi and El-shraiy 2007).

Effect of SA on the volatile compounds

Foliar applications of SA (0.724 and 1.448 mM) significantly improved the EO percentage and EO yield per plant in marjoram. The statistical analysis indicated that there was a 100% increase in oil yield when 1.448 mM was applied. At the same time, the predominant compounds of the EO obtained from treated and control plants were qualitatively similar, although differences in their ratios were observed. The elicitation by the concentration of 0.724 mM increased α-terpinene, γ-terpinene, α-terpinolene, and terpinen-4-ol percentages but decreased those of sabinene and 4-thujanol by 26% and 57%, respectively (Hashem 2018). Previous experiments with marjoram showed similar tendencies; the plants treated with 10⁻², 10⁻¹, and 1 mM SA all showed an increase in the yield of EO, the highest one registering a 50% increase with application of the 10⁻¹ mM concentration. The treated samples exhibited the same spectrum of major components of EO as the control with some quantitative changes in their proportions. Cis-sabinene hydrate elevated from 37.5% of control samples to 40.6% in the treated ones. Similarly, the ratio of ρ-cymene, α-pinene, α-myrcene, α-terpinene, and γ-terpinene, as well as of the sesquiterpenes caryophyllene and α-humulene, also increased (Gharib 2006). Conversely, foliar application of SA (10⁻¹ mM and 2 mM), applied twice with an interval of one week did not have any significant effects on the EO content of marjoram, peppermint, and hyssop. However, the
dosage of $10^{-1}$ mM was able to increase the ratio of isopinocamphone significantly in hyssop by 60% (Kandoudi et al. 2021).

In another trial of cumin (*Cuminum cyminum*) a significant increase occurred. The EO yield doubled after the application of 0.1 mM of SA, although it might be the consequence of the increased mass (by 76%) of cumin seeds. As for the EO components, they were not drastically changed by the SA treatment (Rahimi et al. 2013).

The study conducted by Mohammadi et al. (2019) proved that the reaction of even a single species is not always uniform, but there might be intraspecific differences. Different ecotypes of the same species may react differently to the same dosage of elicitor concerning growth parameters (see the subchapter above) and physiological traits like photosynthetic pigments, relative water content, and the accumulation of SMs. The four ecotypes of *Thymus kotschyanus* from different provinces in Iran sprayed with 0.724 and 1.086 mM of SA on their leaves at early stages of flowering showed different changes in their EO content. The concentration of 1.086 mM failed to increase the percentage of the EO in all cases, in contrast to the lower dosage, which was able to increase the concentration of volatiles in the accession originating from Zanjan and west Azerbaijan by 10 and 16%, respectively. Yet the treatment decreased it in the case of the accessions, from Kerman and Ghazvin by 162% and 18%, respectively. Furthermore, in two accessions the oil composition was studied, and researchers established that, as a consequence of 0.724 mM SA spraying, a significant increase in oxygenated monoterpenes and a parallel reduction in the ratio of monoterpene hydrocarbons were found.

While comparing 6 different plant growth regulators for stimulating peppermint field performance and drug quality, SA proved to be the best for increasing oil content, oil yield, menthol concentration, and menthol yield (Khanam and Mohammad 2016).

**Effect of SA application on the accumulation of phenolic compounds**

SA treatment of peppermint showed an increase in TPC and flavonoids for all concentrations of 0.5, 1, and 2 mM when compared with the control. The highest value of TPC recorded in mint infusion was 48.63 μg/ml with the concentration of 0.5 mM SA, compared to 29.42 μg/ml in the untreated samples, while in terms of flavonoids, the content doubled with both concentrations 0.5 and 1 mM. As for the phenolic composition, the main compounds remained the same but with a significant increase. Hesperidine and RA production was raised by 145 and 65%, respectively, when 1 mM of SA was applied. Furthermore, naringin, rutin, and sinapic acid were found in treated peppermint leaves but not in the controls, which might be explained by the stimulation of the pathway, or the enzymes involved in the synthesis of these compounds (Figueroa Pérez et al. 2014).

Spraying spearmint (*Mentha spicata*) with 0.724, 1.448, and 2.172 mM of aqueous solutions of SA on the plants twice after 30 days and 60 days of planting, was accompanied by statistically proven differences. The 60 day old SA-treated plants showed significantly higher TPC and flavonoid contents. Among all the treatments of SA, the 1.448 mM concentration showed maximum efficacy: TPC was higher by almost 55% and flavonoid content was about 90% higher than in non-treated plants (Kundu et al. 2018). Therefore, elicitation of *Mentha* species might be useful in improving some of their physiological properties, since TPC frequently has a close relationship with the antioxidant activity of the drug or extract (Shahidi 2000).

Higher concentrations of SA had some interesting effects on table grapes (*Vitis vinifera*) as well when applied at the beginning of ripening. TPC was increased by nearly 140% and 180% with the application of 0.724 and 3.62 mM of SA. All studied phenolic acids were improved quantitively due to both concentrations of SA, although not significantly despite the five-fold change, with the exception of the trans-ferulic acid, which was also increased by 120 and 360% at 0.724 and 3.62 mM, respectively. However, other phenolic compounds reacted specifically to the two different dosages of SA. The flavonols myricetin and trans-resveratrol were increased by 290 and 215%, respectively with the 3.62 mM SA application, while the other two flavonols, quercetin and quercetin-3-glucoside, decreased by 490% and 113% in plants treated with 0.724 mM SA. The anthocyanin content decreased significantly as a result of the application of the lower dosage of SA, and especially the main compound, malvidin-3-glucoside, was drastically reduced (by 440%). Since the anthocyanins
start to accumulate in berry skins during the ripening and the treatment was applied at veraison, it was supposed that SA might have retarded the ripening process, and in consequence, the accumulation of anthocyanins (Blanch et al. 2020). This hypothesis is in accordance with the statement of Ranjbaran and Coworkers (2011) on the antagonistic effect of SA and abscisic acid (ABA), the latter being responsible for the grape berry ripening.

Effect of hormonal elicitors on plant tolerance against abiotic stress conditions (MeJa and SA)

Abiotic stresses are one of the most important conditions that adversely affect crop production due to reduced or missing essential resources, excess amounts of toxic substances such as salts and heavy metals, or to other changes in the environment. Plants, when reacting to abiotic stresses, exhibit a series of morphological, physiological, and biochemical changes to reduce detrimental effects (Potters et al. 2007; Ghorbanpour et al. 2013). Based on several references, it seems that plant tolerance to external stress conditions could be developed by the application of hormones such as MeJa and SA (Overmyer et al. 2003; Khan et al. 2015). In this chapter, we are going to deal with drought and hypersalinity, the primary causes of crop loss worldwide.

Water deficit

Drought stress, or water deficit, is among the abiotic stresses that exert a great effect on plant growth and development. It is a restrictive factor for agricultural production around the world (Doupis et al. 2011; Aghdam et al. 2016). The negative effects of drought on yield have been discussed several times, and in vivo studies were carried out to examine the recovering effects of elicitors under these circumstances. Kleinwächter et al. (2015) showed that the retarding effect of drought is highly dependent on the species and the duration of the unfavorable circumstances. MeJa and SA treatments were able to compensate the biomass reduction only partially, but at the same time both treatments induced increased concentrations of volatiles and flavonoids in thyme and parsley.

In a pot experiment of wheat (Triticum aestivum L.) it was observed that shoot length was significantly reduced under drought conditions. However, JA enhanced the shoot length by 23% in the same induced drought treatment as compared to control (Ilyas et al. 2017).

Additionally, MeJa was able to mitigate the drought stress damage over the production of EO in summer savory (Satureja hortensis). Under mild and severe water stress, the concentration of 0.15 mM was able to stimulate the percentage of EO, reaching 3.5% compared to 2.9% in plants under stress free conditions (Miranshahi and Sayyari 2016).

Both quantitative and qualitative changes in the EO composition were registered in common rue (Ruta graveolens) when the plants received a reduced irrigation (50% field capacity) but were treated with 1.5 mM SA as a foliar spray. The percentage of EOs in the leaves and flowers increased by 44 and 40%, respectively. Moreover, the ratios of long chain methyl ketones accumulated from 84.76 to 94.20% in EOs of flowers compared to the control under the same irrigation conditions (50% field capacity) (Attia et al. 2018).

To the contrary, Mohammadi et al. (2019) showed that foliar spraying of SA negatively affected the EO content and composition of drought stressed thyme plants. The reaction of both investigated ecotypes was the same. The EO content varied from almost 3.0% under a drought stressed condition to 1.4 and 1.0% in the same water deficit condition with the application of 0.724 and 1.086 mM of SA, respectively, in the Urmia ecotype. In parallel, it decreased in the Ghazvin ecotype by 63 and 100% with 0.724 and 1.086 mM SA applications, respectively.

Phenolics and total flavonoids levels were also altered in case of basil under severe water stress (25% of field capacity), following a treatment with 0.1 mM of SA. The phytohormone countered the harmful effects that might be associated with drought and increased both parameters significantly (Kulak et al. 2021).

Salt stress

In many regions of the world, soil salinity is one of the major global problems constraining food production because it limits crop yield and impairs crop growth and development. Despite the importance of mineral salts in the soil, excessive amounts may cause cytotoxicity due to extreme intake of ions, especially...
those of sodium (Na\(^+\)) and chloride (Cl\(^-\)), which lead to toxicity (Tester and Davenport 2003; Shabala et al. 2015). Additionally, they may generate a disproportion between antioxidant defense mechanisms and reactive oxygen species (ROS), which results in oxidative stress (Hernández et al. 2001; Isayenkov 2012).

A study showed that *Catharanthus roseus* seedlings grown under four different treatments (non-saline control, 100 mM NaCl, 0.05 mM SA, and a combination of 100 mM NaCl + 0.05 mM SA) accumulated lower biomass of both leaves and roots in the presence of salinity, but when SA was added, it mitigated the negative effect. The fresh and dry weight of the roots was elevated from 31 mg to 17.1 mg/plant in non-stressed individuals to 49.4 mg and 23.8 mg in plants exposed to salinity and treated with SA, respectively (Misra et al. 2014).

Different treatments of SA, ranging from 50 to 100 mM of SA significantly increased the height of valencia trees (*Citrus sinensis* L. Osbeck) under salinity stress (60 mM NaCl) compared to the control. This study showed a promising alternative to the salinity problem in citriculture (Mahmoud et al. 2021).

Intraspecific differences in stress reactions have also been described. Two cultivars of basil showed different responses when they were treated with MeJa under salt stress conditions. However, the 0.5 mM phytohormone was able to increase the yield of EO only under 30 mM salinity, while under 60 and 90 mM conditions, the same treatment did not have any significant effect. Moreover, at the higher salinity levels the EO yield decreased by 18–60% in spite of the MeJa elicitation. The two examined varieties showed only a slightly different magnitude of the reaction (Talebi et al. 2018).

Similarly, in scarlet sage (*Salvia coccinea*), the concentration of 0.5 mM of SA was able to alleviate the salinity stress due to the exposition of NaCl solution of 100 and 200 mM, resulting in a significant increase of TPC by 50 and 26%, respectively. On the other hand, samples under 300 mM salinity needed a higher concentration of SA to show an increase in TPC (20% increase) (Grzeszczuk et al. 2018).

**Conclusion**

This review deals with the exogenous application of jasmonates and SA to in vivo plants, mainly in the form of foliar spraying. The applied elicitor concentrations ranged between \(10^{-4}\) and 100 mM and induced various changes in the treated plants.

The inhibitory impact of jasmonates on root and shoot growth has been described earlier (Wasternack and Hause 2013). Data on enhancing and retarding effects, as well as no effect on growth, are available in the studies cited in this paper. Effects of MeJa treatments were also formerly proved to act differently on different species even within the same experiment (Kleinwächter et al. 2015). Concerning the referenced publications, not only the species but also the concentration of the elicitor, the time/phenophase, and the number of applications is different. The effects of the elicitors are tightly connected with other hormonal signaling processes; thus, the detected antagonistic responses may also be the result of an imbalance between GA and Ja (Wasternack and Hause 2013), for example.

Jasmonate treatments frequently induced a retarding growth and decreased biomass in the plants, especially when applied at higher (above 0.1 mM) dosages or several times. Nevertheless, a clear statement on the negative effect of this elicitor on growth parameters cannot be established as there are also contradictory results depending on the circumstances and target species. Not rarely, under stress conditions, JA or MeJa could even mitigate the negative effects to some extent.

According to the cited papers, 0.01–1.5 mM of SA treatment resulted in slight or even significant growth enhancement of several species. In some cases, the fresh or dry weight could be doubled. SA was also effective in inducing earlier flowering and promoting root growth. Earlier literature also mentioned numerous positive examples of yield promotion in larger crops as effects of exogenous SA in vivo, while interestingly, negative findings have hardly been documented (Hayat et al. 2010).

There is evidence for the dose dependency of the reactions to both elicitors, but systematic studies on this aspect could not be found.

Unfortunately, the results on elicitation under stress conditions and the eventual close relationship between the conditions and the induced changes lead one to
consider if any of the experimental environments were really the optimal ones for the target plants or if some level of stress—even unintended—also contributed to the established results in any of the other trials.

MeJa spraying treatment was able to elevate the EO accumulation of different species. At the same time, higher dosages or repeated application frequently have shown a retarding effect. The reaction of volatile terpenoid compounds on SA treatments also proved to be variable. In the majority of papers, SA spraying enhanced the volatile accumulation, although more rarely, the opposite was observed, too.

Numerous in vivo trials demonstrated not only the overall change in accumulation but also the altered EO composition due to jasmonate or SA treatments. Both the ratio of the determined compounds and the qualitative spectrum were influenced (the latter in several cases). Interestingly, the changed oil components do not seem to be in any relevant chemical connection with each other. Mono- and sesquiterpenes of different skeleton types, both hydrocarbons and oxygenated ones, were targets of either elevation or reduction in the EOs of variable species.

Unfortunately, in almost all the papers, EO content has been determined as a percentage of the dry mass. Therefore, the absolute accumulation of the compounds by the treated plants cannot be ascertained without a parallel comparison of their biomass production. This is, however, almost never discussed. Kleinwächter et al. (2015) demonstrated that the stimulation of volatile accumulation by MeJa or SA was able to compensate for the loss of biomass and, thus, the yield of EO in consequence of drought only for some weeks. Martin et al. (2002) described increased amounts in μg/g of total monoterpenes after MeJa treatment in Norway spruce, but the changes of the individual compounds were variable (+ or −), indicating differential enzymatic responses to the elicitation.

Based on the available information, it could be assumed that the background of the described qualitative and quantitative changes in volatiles may be varied. As the discussed plant hormones are able to influence complex physiological and metabolomic processes, any changes, among others, in plant growth, photosynthetic activity, leaf senescence, flowering induction, enhancement of competitive pathways etc. are affected. These processes may also have an indirect influence on volatile accumulation. The formation of glandular trichomes, the sites of volatile accumulation, is also influenced by Ja (Wasternack and Hause 2013). At the same time, the elicitor induced changes in terpenoids may also be affected by the elicitors directly through modifying their biosynthetic pathways. Li et al. (2007) demonstrated that the total amount of terpenoids, especially those of linalool and eugenol, significantly increased in O. basilicum cell suspension cultures due to up-regulation of genes. Exact biochemical and genetic studies on these topics are, however, not numerous; results originate mostly from in vitro trials. It was established that JA may be responsible for the regulation of transcription factors in the synthesis of the sesquiterpene artemisinin (Yu et al. 2012). According to Deschamps and Simon (2006), the activity of 3-hydroxy-3-methylglutaryl reductase, the first rate-limiting step of terpenoid pathway, may be induced by elicitor treatment in a range of plant species. Besides, it was proved that the MeJa treatment also influences the enzymes taking part in the synthesis of mono-, sesqui-, and diterpenes, thus, in the later steps of the pathway. Moreover, it seems that this influencing effect is characteristically different to the individual enzymes and depends as well on the specific tissues within the plant (Martin et al. 2002).

Numerous positive findings have been published concerning the effect of jasmonates on the accumulation ratio and composition of phenolic type compounds. Elevated levels of TPC, TFC, RA, CAA and other phenolic acids were demonstrated, while in some cases the components showed contradictory behavior, or the treatments did not result in significant changes. Dose dependency was also recorded.

SA treatment (in the range of 0.5–1.5 mM) in most cases accelerated the accumulation of total phenolic content in several taxonomically not closely related plant species. Besides, in the described experiments, increased concentrations of total flavonoids, phenolic acids, and anthocyanines in the plant material were also demonstrated. Unfortunately, phenolic composition was relatively rarely determined, but a restricted number of results showed that SA may also alter the ratio of individual flavonoid or phenolic acid components compared to control. Inhibition in SM production due to this elicitor has rarely been documented, just like a decrease in anthocyanines in grapes (Blanch et al. 2020). On the other hand, it seems that both SA and MeJa may play an important role in anthocyanin
biosynthesis, inducing the late-biosynthesis genes through several transcription factors (Shan et al. 2009). The suggestion by Blanch et al. (2020) about the connection of anthocyanin decrease and retarded ripening of the berries shows that changes in the levels of SMs might also be indirectly influenced by the elicitors. As there are a lot of indigenous and endogenous factors which influence the accumulation of the SM molecules, including ontogenetic phase, organic differentiation, growing conditions, health status, etc., the background of the changes due to elicitor treatment must be investigated in a complex system. As many of the changes in consequence of the elicitation seem to occur as stress reactions, the time factor is of great significance, too. Any response may vary during the time specifically for the chemical compound, as Kim et al. (2006) demonstrated for different phenolic acids in basil. The period between treatments and sampling varies between 2 and 60 days in the cited papers. Thus, the influence of this element needs to be considered in any evaluation, too.

Elicitation responses in the context of biochemical processes and molecular genetic mechanisms have been investigated almost exclusively in in vitro systems under very diverse conditions and objects. Therefore, although these results may give some information, there is no direct explanation for the in vivo findings cited in the present paper. Thakur et al. (2019) demonstrated elevated concentrations of stilbenes and trans-resveratrol together with the contents of total phenolics and flavonoids in grape cell suspension culture due to MeJa or SA treatments. At the same time, an up-regulation of the expression of genes responsible for stilbene and flavonoid synthesis was detected.

In parallel with elevated concentrations of total phenols and some phenolic acids due to MeJa treatment of sweet basil, overexpression of several genes has been observed, among others, that of the LOX (lipoxygenase) enzyme, which is one of the key enzymes in the synthesis of jasmonates (Li et al. 2007). This suggests that due to an elicitor treatment, both the syntheses of the corresponding SMs are regulated; however, the formation of further amounts of this elicitor itself may be stimulated as positive feedback (Sasaki et al. 2001), as well. Unfortunately, very few papers present data on the concentration of jasmonates in in vivo elicitor treated and untreated tissues.

Based on the wide scale literature search, we conclude, that there has been much less research conducted concerning in vivo elicitation compared to studies on cells and hairy roots in vitro cultures. It is not surprising, as obviously for interpretation of the in vivo results, as well as for comparison and conclusion, a much more complex context should be considered: developmental phase, growing conditions, environmental factors, along with the plant’s exposure to biotic or/and abiotic stresses, beside the method, the timing of the treatment, and type and concentration of the elicitor.

Overall, the research results on jasmonates and SA elicitation in vivo indicate a promising aspect of the developments. In particular situations, the positive effects of the elicitors on SMs might be practically useful on an industrial scale. Some results indicate that lower concentrations, when replicated treatments are applied, may be at least as effective as higher ones. However, in order to realize the knowledge on this topic collected until now, further well-designed, systematic studies are required on individual target crops.

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**Declarations**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** The manuscript is original, has not been published before and is not currently being considered for publication elsewhere. Its publication is approved by all authors.

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