The role of methyl salicylate in plant growth under stress conditions

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A B S T R A C T

Methyl salicylate is a volatile compound, the synthesis of which takes place *via* the salicylic acid pathway in plants. Both compounds can be involved in the development of systemic acquired resistance and they play their role partly independently. Salicylic acid transport has an important role in long-distance signalling, but methyl salicylate has also been suggested as a phloem-based mobile signal, which can be demethylated to form salicylic acid, inducing the *de-novo* synthesis of salicylic acid in distal tissue. Despite the fact that salicylic acid has a protective role in abiotic stress responses and tolerance, very few investigations have been reported on the similar effects of methyl salicylate. In addition, as salicylic acid and methyl salicylate are often treated simply as the volatile and non-volatile forms of the same compound, and in several cases they also act in the same way, it is hard to highlight the differences in their mode of action. The main aim of the present review is to reveal the individual role and action mechanism of methyl salicylate in systemic acquired resistance, plant-plant communication and various stress conditions in fruits and plants.

1. Introduction

Salicylic acid (SA) has an important role at several levels of plant development and physiological processes, such as seed germination, flowering, fruit yield, cell growth, nodulation in legumes, stomatal closure and in regulating the induction of biotic resistance and abiotic stress tolerance (Dempsey and Klessig, 2017; Gondor et al., 2016; Janda et al., 2012; Koo et al., 2020; Kovács et al., 2014; Sharma et al., 2020). As a signal molecule, it induces the antioxidant enzyme system to protect the plants against oxidative damage (Miura and Tada, 2014); in addition it has an important role in signal-transduction pathways and in cross-communication between them, which could regulate the physiological processes (Mohsenzadeh et al., 2011). Several derivatives and conjugated form of SA are present in plants, like methyl salicylate (MeSA), which is a volatile form, that can be also partly transported (Attaran et al., 2009), or storage forms like salicylic acid 2-O-β-d-glucoside (SAG) (George Thompson et al., 2017; reviewed in Pokotylo et al., 2019).

MeSA is the methyl ester form of SA and it is a volatile organic compound (VOC). MeSA was first isolated in 1843. It is also called oil of wintergreen, because it is the most abundant component in wintergreen oil and was traditionally isolated from wintergreen plants. This ester is colourless and has a sweet odour, low molecular weight (152.149 g/mol) and a high boiling point (223 °C). Its role is not as well known as

that of salicylic acid. Experiments involving various modes of application or the use of SA mutant or transgenic plants have proved that SA induces several plant responses during biotic and abiotic stress, but very few studies have focused on MeSA, and these mainly reported its role in biotic stress. For example, *Nicotiana benthamiana* seedlings treated with MeSA exhibited higher resistance against *Pseudomonas syringae* pv. tabaci and *Pectobacterium carotovorum* subsp. carotovorum, than the control (Song and Ryu, 2018). Transgenic benzoic acid/SA carboxyl methyltransferase 1 knockout mutant (*Atbsmt1*) Arabidopsis plants failed to accumulate MeSA, SA or its glucoside in the uninoculated leaves and did not develop systemic acquired resistance (SAR) during pathogen infection(Liu et al., 2010). However, recent findings suggest that MeSA is also an important signal molecule, so the present review would like to highlight the fact that MeSA is not only a VOC but can also induce defence mechanisms under various stress conditions. The main aim was to summarize the effects of different MeSA treatments on plants, especially on crop species, with the additional goal of revealing the differences in the mode of action of SA and MeSA.
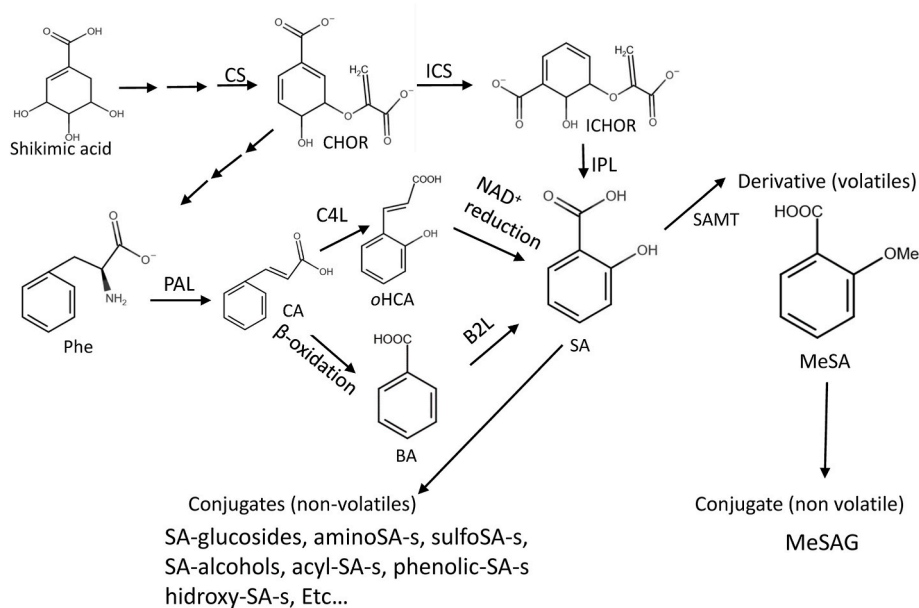
2. SA-related synthesis of MeSA in plants

Plants synthesize MeSA from SA (Fig. 1.) and the shikimate pathway plays an important role in the synthesis of SA (Maruri-López et al., 2019). Shikimate (3,4,5-trihydroxy-1-cyclohexene-1-carboxylic acid) is transformed into chorismate (CHOR) in a two-step reaction (Brown and

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Abbreviations

4Cl	p-coumarate-CoA ligase
ABA	abscisic acid
ACC	1-aminocyclopropane-1-carboxylic acid
ADT	arogenate dehydratase
ANS	anthocyanidin synthase
AOX	antioxidant enzymes
APX	ascorbate peroxidase
Asc-GSH cycle	Ascorbate-glutathione cycle
B2L	benzoic acid 2-hydroxylase
BA	benzoic acid
BAMT	benzoic acid carboxyl methyltransferase
C4H	cinnamate 4-hydroxylase
C4L	cinnamate 4-monooxygenase
CA	cinnamic acid
CAD	cinnamyl-alcohol dehydrogenase
CAT	catalase
CHI	chalcone isomerase
CHOR	chorismate
CHS	chalcone synthase
CLas	Candidatus Liberibacter asiaticus
CM	chorismate mutase
CS	chorismate synthase
DFR	dihydroflavonol
DHAR	dehydroascorbate peroxidase
eds	enhanced disease susceptibility
ESPS	3-phoshoshikimate 1-carboxyvinyl transferase
F3H	flavanone 3-hydroxylase
FUM	fumaric acid
GPX	guaiacol peroxidase
GR	glutathione reductase
HIPVs	herbivore-induced plant volatiles
ICHOR	isochorismate
ICS	isochorismate synthase
IPL	isochorismate pyruvate lyase
JA	jasmonic acid
MeJA	methyl jasmonate
MeSA	methyl salicylate
MeSAG	MeSA 2-O-β-d-glucoside
NPR1	nonexpressor of pathogenic related gene1
oHCA	ortho-hydroxy cinnamic acid
Phe	phenylalanine
PAL	phenyalalanine ammonia-lysase
PAT	phenylpyruvate transaminase
PDT	prephenate dehydratase
POD	peroxidase
PPO	polyphenol oxidase
PR	pathogenesis-related
PTA	prephenate transaminase
PTAL	phenylalanine/tyrosine ammonia-lyase
ROS	reactive oxygen species
SA	salicylic acid
SABATH	salicylic acid benzoic acid theobromine
SABP	salicylic acid binding protein
SAG	salicylic acid 2-O-β-d-glucoside
SAGC	salicylic acid glucosylated conjugates
SAMT	salicylic acid carboxyl methyltransferase
SAR	systemic acquired resistance
SOD	superoxide dismutase
SPX	syringaldazine peroxidase
SUCC	succinic acid
TF	transcription factor
TISR	Trichoderma atroviride-induced resistance
UFGT	udp-glucose flavonoid 3-o-transferase
UGT71C3	uridine diphosphate-glycosyltransferase
UGT74F1	uridine diphosphate-glycosyltransferase
VOC	volatile organic compound

Fig. 1. SA-related synthesis of MeSA in plants. (CS: chorismate synthase, CHOR: chorismate, ICS: isochorismate synthase, ICHOR: isochorismate, IPL: isochorismate pyruvate lyase, Phe: phenylalanine, PAL: phenylalanine ammonia-lysase, CA: cinnamic acid, C4L: cinnamate 4-monooxygenase, *o*HCA: *ortho*-hydroxycinnamic acid, SA: salicylic acid, BA: benzoic acid, B2L: benzoic acid 2-hydroxylase, SAMT: salicylic acid carboxyl methyltransferase.)

Neish, 1955 reviewed in Rehan, 2021). First, shikimate kinase transforms shikimate into shikimate-3-phosphate, after which 3-phosphoshikimate 1-carboxyvinyl transferase converts this into 5-enolpyruvylshikimate 3-phosphate. Chorismate synthase (CS) catalyses the formation of CHOR, which is a branching point on this pathway, being the starting point for the isochorismate synthase (ICS) and phenylalanine ammonia-lyase (PAL) routes. CHOR is transformed into isochorismate (ICHOR) by ICS in the chloroplasts, after which isochorismate pyruvate lyase forms SA in the cytosol (Dempsey et al., 2011; Fragnière et al., 2011; Maruri-López et al., 2019).

In case of *Arabidopsis*, only 10% of the defence-related SA is produced *via* the PAL pathway, thus the major part is derived by the isochorismate synthase1 in the plastid (Garcion et al., 2008). The synthetised ICHOR is exported from plastid to cytosol *via* the Enhanced Disease Susceptibility 5 (EDS5) protein (Rekhter et al., 2019). The PBS3, which is an avrPphB susceptible enzyme, catalyses the conjugation of ICHOR into ICHOR-glutamate; and after all, the EPS1 (Enhanced Pseudomonas Susceptibility 1, which is an acyltransferase-family protein) forms the SA (Torrens-Spence et al., 2019). The overexpression of *ICS* gene during the pathogen infection or acclimation to drought conditions (Rekhter et al., 2019; Wang et al., 2021) suggest that the PAL pathways is less predominant than the ICS pathway.

In contrast to *Arabidopsis*, where the SA accumulation was parallel with the stress-induced *AtICS1* expression, in *Nicotiana tabacum* L. *ICS* expression was not induced, thus the *NtICS* gene is probably not the main production route responsible for the stress induced SA accumulation (Yokoo et al., 2018). The involvement of PAL in stress responses has been characterised in various plant species, such as *Brachypodium* (Pant et al., 2021), rice (Gho et al., 2020), wheat (Feduraev et al., 2020), pea (Dukare and Paul, 2021) and tomato (Lu et al., 2020). In soybean, the PAL and ICS pathways play equally important role in the pathogen-induced SA production (Shine et al., 2016). Compared to this, in rice the PAL pathway seems to be more important for SA accumulation (Duan et al., 2014), but it should also be taken into consideration that the regulation/contribution of SA biosynthesis pathways can be different even in the different organs within the same plant (Lefevere et al., 2020)

The PAL pathway starts from CHOR, which is isomerized into prephenate by chorismate mutase. Then either prephenate dehydratase (PDT) transforms it into phenylpyruvate or prephenate transaminase induces the formation of L-arogenate, which can be transformed by arogenate dehydratase into phenylalanine. Phenylpyruvate is transaminated by phenylalanine aminotransferase to form phenylalanine (Tzin and Galili, 2010). PAL and phenylalanine/tyrosine ammonia-lyase (PTAL) deaminate phenylalanine to form cinnamic acid (CA). The PTAL enzyme, which is well known in maize (Rosler et al., 1997), *Arabidopsis* (Barros and Dixon, 2020) and bean (Scott et al., 1992), eliminate the ammonium and form *para*-hydroxy cinnamic acid from tyrosine (Barros and Dixon, 2020). SA can be synthesised from CA in two ways. One involves transformation *via* CoA-dependent β-oxidation (Qualley et al., 2012), where the intermediate product is benzoic acid (BA), after which the BA 2-hydroxylase enzyme produces SA (León et al., 1995). In the other pathway *trans*-cinnamate 4-monooxygenase enzyme first transforms CA into *ortho*-hydroxy CA, from which SA is formed by NAD^+ reduction (Tohge et al., 2013). SA carboxyl methyltransferase (SAMT) then methylates SA into MeSA using the methyl group of S-adenosyl-L-methionine (Negre et al., 2002). SAMT has been described in *Lycium chinense, Atropa belladonna* (Wang et al., 2019b), rice (Zhao et al., 2010), wheat (Allamong and Abrahamson, 1977), maize (Köllner et al., 2010), tomato (Sánchez-Aguayo et al., 2004) and pea (Aarnes, 1977) and in Arabidopsis (Chen et al., 2003).

3. Fine-tuning of MeSA and SA

Salicylic Acid Binding Proteins (SABP) were identified and isolated from tobacco (Du and Klessig, 1997), cucumber, tomato, *Arabidopsis*,

soybean, maize and rice (Sánchez-Casas and Klessig, 1994). Nearly 30 SABPs have been identified and almost 100 putative SABPs have been suggested (Manohar et al., 2015). These proteins exhibit a range of affinities for SA and all of them have enzyme function, which can be are altered by SA binding, and most of them play a role in plant immunity (Klessig et al., 2016; Kumar, 2014). However the physiological result of the interaction between most of these SABPs and SA is still unclear, in addition their receptor role is also questionable. Although, Non-expressor of Pathogenesis-related protein 1 (NPR1) a key transcriptional regulator of SA signalling, which is one of currently known SA receptors (Wu et al., 2012) has been also characterised as SABP (Manohar et al., 2015). Furthermore, NPR3 and NPR4 may also bind SA and they have also been suggested as potential receptors for SA signalling in Arabidopsis (Fu et al., 2012)

As some examples, SABP1 exhibits SA-inhibitable catalase activity, and can be inhibited also by 2,6-dihydroxy benzoic acid or acetyl-SA (Du and Klessig, 1997; Sánchez-Casas and Klessig, 1994), but not by SA conjugates (Chen et al., 1993). The SABP2 is a low abundance protein with high affinity for SA (Du and Klessig, 1997) and MeSA. It is localized in the cell membrane, as shown in tobacco plants (Forouhar et al., 2005). SABP2 belongs to the α/β hydrolase family with esterase activity and it may also hydrolase MeSA into SA (Forouhar et al., 2005; Park et al., 2007; Vlot et al., 2008). It also shows some, although low affinity for both methyl jasmonate (MeJA) and methyl indole acetic acid. However, these methylated forms failed to compete with SA for binding, even when present in a 1,000-fold molar excess (Forouhar et al., 2005; Kumar and Klessig, 2003; Tripathi et al., 2010). In poplar plants, SABP2 is encoded by the *PtSABP2-1* and *PtSABP2-2* genes. In poplar leaves *PtSABP2-1* exhibited a higher level of expression, while in the roots transcript level of *PtSABP2-2* was dominant (Zhao et al., 2009). The transgenic overexpression of a *SABP2*-like gene, *LcSABP* (*SABP2* ortholog from *Lycium chinense*) in tobacco had a positive effect on drought stress tolerance, increasing not only the endogenous SA content (due to the promoted conversion of MeSA to SA), but inducing the antioxidant enzyme system and the expression of stress-related transcription factors (TF) (Li et al., 2019). SABP3, also known as β-carbonic anhydrase (Slaymaker et al., 2002) having antioxidant activity, and it functions in the HR in plant disease resistance (Slaymaker et al., 2002). It is present in the chloroplasts, where it catalyses the interconversion of CO_2 and bicarbonate (HCO_3^-) (Hewett-Emmett and Tashian, 1996, reviewed in Pokotylo et al., 2019). This enzyme is needed for positive regulation of defense responses in plants. SABP3 is a target for modification via S-nitrosylation during later stages of R-gene mediated protection against avirulent plant pathogens (Feechan et al., 2005). Upon pathogen infection, during the nitrosative burst, NO accumulation promotes S-nitrosylation of the AtSABP3 at Cys280. It supresses both its binding to SA and the carbonic anhydrase activity leading to decreased plant immunity (Wang et al., 2009).

Similarly to SA, MeSA also has glucosylated conjugated form, MeSA 2-O-β-d-glucoside (MeSAG). A uridine diphosphate-glycosyltransferase (UGT71C3), which has been characterised in Arabidopsis, was found to be responsible for the glycosylation of form MeSA glucosides. This enzyme acts specifically on MeSA, and not on SA, thus has main role in the controlling of the active MeSA level (Chen et al., 2019). UGT71C3 is up-regulated in response to pathogens and MeSA accumulation, and in turn accelerates the glycosylation of MeSA (M'Hamdi, 2019). This glycolysation is negative regulator in the plant defence, because MeSA that reaches the systemic tissue is further glycosylated by UGT71C3, thus preventing the accumulation of MeSA. Overexpression of *UGT71C3* led to more severe disease symptoms and deficiency in SAR (Chen et al., 2019), while loss of function mutants showed reduced symptoms and higher accumulation of SA and MeSA (M'Hamdi, 2019). Thus, the glycolysation has role in the optimum homeostasis of MeSA and proper development of SAR.

MeSAG is a non-volatile storage form of MeSA which formed under pathogenic attack (Song et al., 2008), but the role of this compound is unclear. In the same way, SA is transformed into the inactivated form

SAG by uridine diphosphate-glycosyltransferase (UGT74F1). In *Arabidopsis thaliana* UGT74F1 was found to transform free SA into SAG, while UGT74F2, an enzyme homologous to UGT74F1, is responsible for the development of the SA glucose ester (Fig. 2) (Thompson et al., 2017).

The SABATH enzyme family (catalysing methylations in plants), was named after the first discovered members, namely <u>SA</u> carboxyl methyltransferase (SAMT), <u>BA</u> (benzoic acid) carboxyl methyltransferase (BAMT) and <u>T</u>heobromine synthase (D'Auria et al., 2002). The *SAMT* gene has been isolated from *Atropa belladonna,* cucumber, *maize* and *Arabidopsis* (Köllner et al., 2010; Zhao et al., 2010). SAMT catalyze transfer of the reactive methyl group from S-adenosyl-l-methionine (SAM) to the carboxyl forming S-adenosyl-l-homocysteine and MeSA (Ross et al., 1999). In Arabidopsis leaves, the expression of *AtBSMT1* was induced by *Plutella xylostella* herbivory, uprooting, physical wounding, and methyl jasmonate, with the maximal emission of MeSA following alamethicin treatment,and it was suggested that AtBSMT1 responsible for MeSA production mainly during pathogen infection (Chen et al., 2003). When rice SAMT gene *OsBSMT1* was transformed into Arabidopsis, overproduction of MeSA and MeBA and depletion in SA accumulation was observed, which resulted in more susceptible plants and little induction of PR1. However, due to the vaporised MeSA, which serves as an airborne signal for plant to plant communication, SAR was activated in neighbouring plants in an ICS-independent way (Koo et al., 2007). However, the knockout Arabidopsis mutant (*Atbsmt1*) failed to accumulate MeSA after pathogen infection and it did not develop SAR (Liu et al., 2010). In tobacco, when SAMT gene was silenced, SAR was also impaired in virus infected plants (Zhu et al., 2014)

The *SAMT* gene expression in *Citrus sinensis* (*CsSAMT*) was upregulated by *Candidatus* Liberibacter asiaticus (*C*Las) infection in the early stage of infection, but the MeSA level and *SAMT* expression decreased after a long period of infection compared to the uninfected control. This results was in parallel with changes in the citrus odour during *C*Las infection (Martini et al., 2018). Overexpression of citrus *SAMT* gene (*CsSAMT1*) in Wanjincheng orange plants susceptible for Citrus Huanglongbing (HLB) disease, conferred increased tolerance to *Candidatus* Liberibacter asiaticus (*C*Las), which was accompanied with increased MeSA and SA levels, induced transcription of defence genes and decreased phloemic cell over-proliferation, starch over-accumulation and callose over-deposition during infection compared with the wild type.

CsSAMT1 overexpression elevated the transcription activity of disease resistance genes, thus enhancing HLB tolerance (Zou et al., 2021).
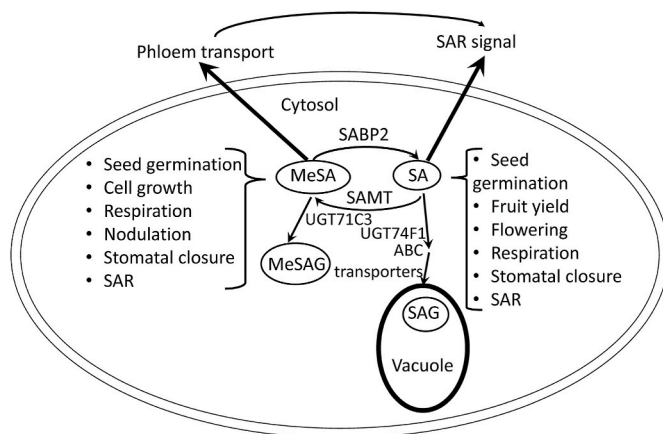
Fig. 2. Schematic diagram of the fine-tuning of MeSA and SA in plants. (MeSA: methyl salicylate, SA: salicylic acid, SABP2: SA binding protein 2, SAMT: salicylic acid carboxyl methyltransferase, UGT71C3: *uridine diphosphate-glycosyltransferase,* UGT74F1: *uridine diphosphate-glycosyltransferase,* MeSAG: MeSA 2-O-β-d-glucoside, SAG: SA 2-O-β-d-glucoside, SAR: Systemic acquired resistance, ABC transporters: ATP-binding cassette transporters, bold arrows show mobile sign of the SAR.

The *SABP2* expression in *Populus tomentose* increased rapidly after *B. dothidea* infection, peaking after 48 h, but decreased after 72 h. In contrast, *SAMT* expression peaked 12 h after the infection and decreased after 72 h (Li et al., 2018). *Pseudomonas syringae* can change the SA-mediated plant defense responses (Attaran et al., 2009) as the pathogen produces Coronatine, a virulence factor, which enhances the production of MeSA (by activating SAMT activity), thereby reducing levels of SA (by inhibition of ICS) (Zheng et al., 2012). This could also be a strategy of *P. syringae* for protecting the host plant against potential damage caused by accumulation of SA to high concentrations (Attaran et al., 2009). These results indicate that the SA homeostasis modulated by SAMT and SABP2 plays an important role in the development of resistance against various pathogen attacks.

4. Endogenous MeSA under biotic stress

Since plants are rooted and unable to move, different defence systems are needed than in the case of animals. Plants have developed direct and indirect defence mechanisms to protect themselves. Direct defence methods involve protecting themselves from herbivores with mechanical strategies such as hairs, trichomes, thorns, spines and thick leaves, or with chemical strategies, by producing toxic components, like terpenoids, alkaloids, anthocyanins, phenols, and quinones. In indirect defence mechanisms plants may use VOCs to attract the enemies of herbivores (Hanley et al., 2007).

In the presence of biotic stressors, volatile plant hormones such as MeSA, ethylene and MeJA also play an important role in plant signalling. These volatile components may specifically indicate biotic stress, i. e. the presence of pathogenic or herbivorous animals (Rowen et al., 2017). Tomato plants were reported to induce the emission of VOCs, especially MeSA, in the case of aphid infestation and water deficit, both separately and in combination (Catola et al., 2018). Under aphid attack, the emitted MeSA increased the expression of the *PAL* gene (*LePAL5*), the MeSA transferase gene (*LeSAMT*) and one isoform of the lipoxygenase coding gene (*LeLOXD*), but no changes were observed in the expression of the another isoform of lipoxygenase coding gene (*LeLOXC*), or of the dehydrin coding *LeTAS14*, germacrene C synthase (*LeGCS*) and hydro peroxide lysase (*LeHPL*) genes. However, combined stress led to the expression of different defence genes and had an impact on different defence pathways than in the case of single stress, whether biotic or abiotic (Catola et al., 2018). Furthermore, it was also found in grapes and hops that exogenously applied MeSA recruits and retains the local population of beneficial, predator insects, leading to the reduction of the major arthropod pests, resulting better biological pest control management (James and Price, 2004).

5. Systemic acquired resistance

Systemic acquired resistance (SAR) is a plant defence system against a broad range of biotic stressors. The most important routes of SAR are the SA-mediated and the pipecolic acid dependent pathways. These are two parallel and interconnected branches, which can act both independently and synergistically (Bernsdorff et al., 2016; Wang et al., 2018). The findings that accumulation of SA has been detected both locally and systemically during the development of SAR, and that the degradation of SA in *NahG* transgenic plants compromised both the local immunity and SAR (Vernooij et al., 1994, reviewed in Vlot et al., 2009), suggested that SA is a central component of SAR, and can be a long-distance signal. However, when wild-type tobacco scions grafted to *NahG* rootstocks, the wild-type scion could establish SAR despite of the SA synthesis deficiency of the rootstock, demonstrating that long-distance signals might be others than SA (Vernooij et al., 1994).

MeSA was one of the first confirmed VOC signal molecules in SAR (Park et al., 2007), which also serves as a plant-plant signal (Shulaev et al., 1997, reviewed in Singewar et al., 2021). It has been reported that the first step in SAR induction could be that the pathogen induces SA

synthesis, part of which is methylated to MeSA by SAMT (Park et al., 2007). SA is transported *via* apoplast (Lim et al., 2016, reviewed in Kachroo et al., 2020). In the target part of the plant SA may induce the transcription of nonexpressor of pathogenic-related genes1 (*NPR1*), which is the main regulator of SA branch of SAR (Ding et al., 2020; Zavaliev et al., 2020) MeSA is more hydrophobic than SA, thus MeSA is less phloem mobile than SA (Lim et al., 2020). Although MeSA can be transported through the phloem, it is highly volatile, this fact make it possible to function not only as a long distance signal for distal tissues of the infected plant, but as a signal for plant to plant communication (Oelmüller, 2021).

As, it was mentioned, MeSA can be converted into SA by the SABP2 methyl esterase enzyme, (Fig. 2), according to this, the actual MeSA concentration in the cell could be fine-tuned *via* the inhibition of the activity of SABP2 (Farhad et al., 2005 reviewed in Pokotylo et al., 2019). On the other hand, MeSA can be also glucosylated to its inactive conjugated form (MeSAG) by UGT71C3, (Chen et al., 2019). It has been demonstrated that knockout mutation of *UGT71C3* resulted in stronger expression of SAR, while its overexpression led to more severe disease symptoms and SAR deficiency (Chen et al., 2019; reviewed in M'Hamdi, 2019). According to these, as it is summarised on Fig. 2., the proper development of SAR requires optimal, fine-tuned balance in the accumulation of both MeSA, SA and their glycosylated forms.

However, information on the essential role of MeSA in SAR is contradictory. For example, in *bsmt1-3* mutant *Arabidopsis* plants, due to a knockout mutation of the SAMT1 ortholog benzoic acid/SA methyl transferase1 (*BSMT1*), very little MeSA accumulation was observed after pathogen infection and they were defective for SAR (Liu et al., 2010). While investigations made on *bstm1-1* and *bstm1-2* mutant *Arabidopsis* lines revealed that despite of the impaired MeSA accumulation after pathogen infection, the accumulation of SA and *PR-1* transcripts together with the development of SAR was observed (Attaran et al., 2009). Contradictory results can be explained with the differences in the experimental designs, including the developmental age of the plants, the virulence of the pathogen, or even the light conditions (Liu et al., 2010). The influence of light on SAR was supported by the facts that *phytochromeAphytochromeB* (*phyAphyB*) double mutant *Arabidopsis* plants showed SAR-defective phenotype (Griebel and Zeier, 2008). In addition, also in *Arabidopsis* it has been reported that the length of light exposure after the infection determines the extent to which MeSA is required for SAR development, as in case of very little light exposure the MeSA was essential, while longer light exposures reduce the importance of MeSA for SAR development (Liu et al., 2010). In tobacco, it was found that different light intensities influenced the SAR induction capacity and the involvement of signalling compounds. SAR is induced without SA accumulation under high light conditions, but depended on the expression of *FLAVIN-DEPENDENT-MONOOXYGENASE1* (*FMO1*), which has role in the conversion of pipecolic acid to N-hydroxypipecolic acid. While MeSA, DIR1 and G3P are activated only when SAR is induced under darkness. Studies on SAR-deficient mutants and silenced lines suggested that MeSA-induced SAR operates in Arabidopsis under darkness (Ádám et al., 2018), and in tomato plants it was also observed that the plant defence responses are different in the daytime and at night (Czékus et al., 2021).

Putative SAR signal molecules or important factors for movement of long distance SAR signals are collection of diverse mobile molecules (Ádám et al., 2018). It included the SA (Gaffney et al., 1993; Shulaev et al., 1995; reviewed in Vlot et al., 2009), MeSA (Park et al., 2007), azelaic acid (G.-H. Lim et al., 2016), glycerol-3-phosphate (Chanda et al., 2011; G. H. Lim et al., 2016), dehydroabietinal (Chaturvedi et al., 2012; Chowdhury et al., 2020), free radicals such as nitric oxide and reactive oxygen species (Chen et al., 1993; reviewed in Gao et al., 2021; Wang et al., 2014), and pipecolic acid, N-hydroxy Pip (Caixia et al., 2022; Návarová et al., 2012), pinene volatiles (Chen et al., 1993; reviewed in Gao et al., 2021) and extracellular (e)NAD(P) (Wang et al., 2019a; reviewed in Kachroo and Kachroo, 2020) could also induce the

SAR in distal tissues. Ca, ROS, NO are necessary for cell-to cell signal propagation during SAR and show emergent roles in the mediation of other SAR metabolites (Eccleston et al., 2022).

Based on the above listed findings, SAR can be also established at least partly independently from MeSA production. In NahG Arabidopsis plants, which is a non-host plant for *Pseudomonas syringae* pv. phaseolicola 3121 (*Psp*) (Ham et al., 2007) the loss of resistance to this strain, was not due to the low level of SA, but rather to the catabolism of SA by NAHG (Van Wees and Glazebrook, 2003). Interestingly, although SA synthesis was blocked in *sid2NahG* double mutants, the resistance to *Psp* is retained, leading to the conclusion that catechol may be responsible for susceptibility of *NahG* plants to *Psp*. (Van Wees and Glazebrook, 2003). However, the exact role of catechol is still unclear.

Investigations on *Arabidopsis* and tobacco *dir1* (defective in induced resistance1) mutants, which are unable to develop SAR, revealed that under certain conditions, including the developmental stage of the plants, the type and the concentration of the pathogen inoculum, SAR could activated due to the interplay between MeSA and a lipid signal complex, but this is still unconfirmed (Liu et al., 2011). Several candidate SAR signals that are linked to lipid metabolism and their translocation have been also described, like DIR1 (defective in induced resistance), a protein that shows homology to the lipid transfer protein (LTP) family (Fernandez-Maldonado et al., 2002). Previously it was only hypothesized that DIR1 moves down the leaf petiole to distant leaves (Fernandez-Maldonado et al., 2002, but later it was demonstrated that DIR1 can be a long distance signal and translocated to distant tissues during SAR (Champigny et al., 2013).

6. Plant-plant communication

VOCs are able to act as external signals in within-plant communication and may also induce defence reactions in nearby plants (Heil and Bueno, 2007). Some VOCs, like isoprene, methanol, the phytohormone ethylene, and some monoterpenes are limited to plant interactions at shorter distances, because they are highly volatile. Less volatile VOCs such as terpene, MeJA, MeSA, or green leaf volatiles (C_6 aldehydes, alcohols, and their esters) are able to act over longer distances (Hatanaka, 1993, reviewed in Matsui, 2006, reviewed in War et al., 2011). As a volatile compound, MeSA could serve as a signal not only inside the plant but also between plants. It has been identified as a member in the herbivore-induced plant volatiles (HIPVs) emitted by various crop species, including hops (*Humulus lupulus* L.), tomato and cucumber (Van Den Boom et al., 2004). Furthermore, exposure of sweet pepper to HIPVs, including MeSA activates the immune defence system, by upregulating the JA and SA signalling pathways in healthy plants (Riahi et al., 2022).

Interconnection, either underground or on the surface, is important not only in the case of herbivore attack or pathogen infection, but also under various other stress conditions, including nutrient deficiency. This type of communication has been described in natural plant communities like tomato plants, where SA and jasmonic acid (JA) also play an important role as a signal (Song et al., 2010). Phenolic acids like rosmarinic acid in sweet basil or CA in barley have been also detected in the root exudates as antimicrobial compounds (Bais et al., 2002; Lanoue et al., 2010). Besides these, bioactive secondary metabolites, such as indole, terpenoid, benzoxazinone and natural flavonoids/isoflavonoids products are also isolated from plant-root exudates of various plant species (Bais et al., 2002; reviewed in Bais et al., 2004).

On the surface, the above-ground communication may involve VOCs. Different types of stress could affect the quality of the VOCs, and could induce genetically encoded programs and pathways to prepare defence against different stresses (Conrath et al., 2015, reviewed in Ninkovic et al., 2021). Whiteflies (*Bemisia tabaci*) were found to produce VOCs similar to those in plants. These may inhibit SA-related defence in neighbouring plants, preparing a safe environment for their progeny (H. Zhang et al., 2019). Abiotic stress can also induce the production of

VOCs, which could be detected by neighbouring plants, and VOCs may induce SA-related pathways leading to defence in neighbouring plants against abiotic stress. Tea plants have been, reported to emit geraniol, linalool and MeSA under cold stress, and these VOCs were able to induce cold tolerance (Zhao et al., 2020). Although plant VOCs have been studied mostly as above-ground chemical signals, recently it was suggested that VOCs also take part in below-ground plant–plant interactions (Gfeller et al., 2019).

MeSA affects not only plants: it was shown to be an attractive signal for various bugs, such as western big-eyed bug (*Geocoris pallens* Stal.), ladybird beetle, spider mite destroyer (*Stethorus punctum picipes* Casey) and Colorado potato beetle (*Leptinotarsa decemlineata* Say) (Dickens, 2006; James and Price, 2004, reviewed in War et al., 2012). Insect herbivores prefer HIPVs such as terpenoids, volatile fatty acid derivatives, aldehydes, alcohols, esters and acids, and also MeSA. MeSA can be a trigger for the induction of defence signalling in plants (War et al., 2011, reviewed in War et al., 2012.). The *Diaphorina citri* Kuwayama bug is the vector of the *C*Las bacterium, which causes citrus greening. The bug was attracted to *C*Las-infected citrus, which emitted MeSA, thus protecting other fruit from infection (Martini et al., 2018). MeSA induces resistance in lima bean attacked by bacterial pathogens by increasing the content of an antimicrobial VOC, nonanal, after 24 h (Girón-Calva et al., 2012, reviewed in Ninkovic et al., 2019). MeSA also serves as one of the attraction-aggregation-attachment pheromones produced by South African bont tick (*Amblyomma hebraeum* Koch) (Norval et al., 1996). The green-veined white male butterfly (*Pieris napi* Linnaeus) transfers MeSA to the female during mating as an anti-aphrodisiac pheromone (Andersson et al., 2000). Mated females of the cabbage moth (Mamestra brassicae L.) avoid MeSA-emitting plants, thus reducing egg-laying on these plants (Ulland et al., 2008).

7. Application of MeSA to improve stress tolerance in plants

7.1. Biotic stress

Exogenous MeSA treatment in rice plants induced peroxidase (POD) activity, leading to increased herbivore resistance against the rice leafroller (Cnaphalocrocis medinalis Guenée). MeSA spraying induced the accumulation of VOCs, ROS and SA and elevated the expression of defence-related genes and PR genes (Kalaivani et al., 2018, 2016). When the developmental characteristics of *C. medinalis* were monitored after spraying rice plants with various concentrations of MeSA, decreased feeding activity was found, which led to nutrition loss and disturbances in the metabolic activities of the larvae (Indhumathi et al., 2019). Similarly, when rice seedlings were inoculated with Xanthomonas oryzae and sprayed with MeSA solution, the application of MeSA regulated the expression of POD genes, and increased the activity of the antioxidant enzyme system (Kalaivani et al., 2021). Repeated application of MeSA in tobacco seedlings induced stronger SAR capacity and expression levels of the N. benthamiana Pathogenesis-Related 1a (NbPR1a) and NbPR2 genes during Pectobacterium carotovorum subsp. carotovorum (Pcc) and *Pseudomonas syringae* pv. tabaci infection, suggesting that plants may remember to volatile priming (Song and Ryu, 2018). When cucumber plants were treated with MeSA, no direct effect on cotton aphids was detected (Fig. 4). However, MeSA accelerated Scymnus (Pullus) sodalis bug visiting, which suppressed the aphid population, reducing crop yield losses (Dong and Hwang, 2017). In cucumber plants, pre-treatment with *Trichoderma atroviride* TRS25 reduced the incidence of *Rhizoctonia solani*-induced disease, a phenomenon known as TRS25-induced resistance (TISR). This is associated with the enhanced activity of defence enzymes, e.g. guaiacol peroxidase (GPX), syringaldazine peroxidase (SPX), PAL and polyphenol oxidase (PPO), and an increase in the phenolic (PC) concentration. Other results indicated that TISR might depend on the accumulation of MeSA, salicylic acid glucosylated conjugates (SAGC), and β-cyclocitral (Nawrocka et al., 2018). When faba beans seeds were soaked in MeSA or SA

solutions to determine their repellent effect on *Aphis craccivora*, the treatment elongated the nymphal stage, reduced survival and increased wing formation, so SA and MeSA induced resistance in beans (El-Solimany, 2020). In seedless table grape (*Vitis vinifera* L.) MeSA treatment during the preharvest stage alleviated the postharvest disease caused by *B. cinerea*. MeSA increased phenolic compound levels, and the activity of the antioxidant enzymes ascorbate peroxidase (APX), catalase (CAT) and POD, leading to better quality grapes and higher concentrations of ascorbic, succinic and fumaric acids (Fig. 3) (García-Pastor et al., 2020a).

7.2. Abiotic stress

MeSA was also proposed as a signal molecule in plant responses to abiotic stresses as it improved plant tolerance against chilling injury as a seed soaking treatment in cucumber plants (Seydpour and Sayyari, 2016). In *Prunus armeniaca* L. cv. Kate sprayed with MeSA after full blossom, the soluble sugar content and related enzyme activities increased, which appeared to be connected with induced chilling tolerance (Fan et al., 2021). Treating the leaves of watermelon (*Citrullus lanatus* L.) cv. Charleston grey seedlings with MeSA solution also induced chilling tolerance. The treatment increased the leaf chlorophyll content and relative water content, and decreased the level of malondialdehyde, alleviating chilling injury (Ghanbari et al., 2018). The vapour treatment increased antioxidant enzyme activity, induced heat shock proteins and reduced the lipid peroxidation level, leading to less pronounced membrane degradation in horticultural crop plants (Ding et al., 2001; Asghari and Aghdam, 2010). Soaking seeds of rice varieties in MeSA solutions enhanced growth rate, phytic, total phenolic and flavonoid contents and increased α-amylase activity after salinity stress leading to enhanced physiological and biochemical properties of the plants (Fig. 4) (Thu et al., 2020). In *Viola odorata* L. a combination of MeSA treatment with NaCl moderated the reduction in weight and leaf and root lengths caused by high salinity (Safaa et al., 2021).

8. Other physiological and developmental processes

MeSA has been reported to affect seed germination, cell growth, respiration, net assimilation rate, stomatal closure, VOC profiles, phenolic and flavonoid contents, antioxidant enzyme activities, nodulation in legumes, fruit yield, senescence-associated gene expression or biotic stress responses (Tang et al., 2015; Kalaivani et al., 2016; Liu et al., 2018; Thu et al., 2020). However, the observed mode of action can be depended on the type of the application.

8.1. Using different application techniques

8.1.1. Seed priming
Treatment of rice seeds with MeSA significantly increased the peroxidase enzyme activity, which in turn led to the altering of plant physiology that was beneficial for crop protection against bacterial blight disease (Kalaivani et al., 2021). MeSA seed priming was also effective as a plant resistance inducer against cowpea aphid in faba bean (El-Solimany, 2020). Seed soaking with MeSA also enhanced the physiological and biochemical properties of rice under salt stress condition, which was related to elevated seed growth, α-amylase activity, phytic acid, and flavonoid contents (Thu et al., 2020).

8.1.2. Spraying technique
The flavonoid content increased after 2 days in the leaves of tea plants (*Camellia sinensis* L.) sprayed with MeSA solution, which was due to the increased activity of PAL pathway *via* the upregulated gene expression of the flavonoid synthesis enzymes CsPAL, CsC4H (cinnamate 4-hydroxylase: C4H), Cs4CL (p-coumarate CoA ligase: 4CL), CsCHS (chalcone synthase: CHS), CsCHI (chalcone isomerase: CHI), CsF3H (flavanone 3-hydroxylase: F3H), CsDFR (dihydroflavonol 4-reductase:
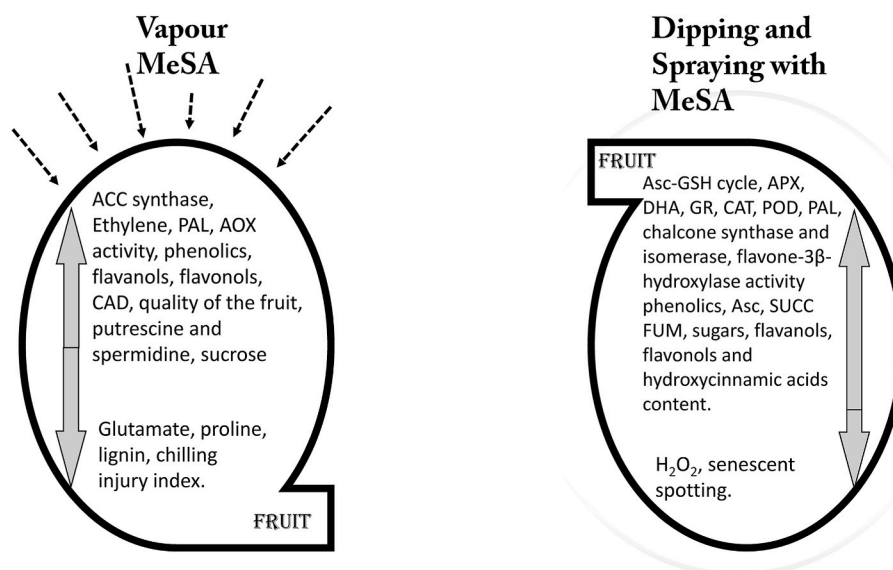
Fig. 3. Summary of the physiological changes taking place in fruit treated with MeSA as vapour or dipping/spraying. (ACC: 1-amino 1-carboxyl cyclopropane, PAL: phenylalanine ammonia-lysase, AOX: antioxidant enzymes, CAD: cinnamyl-alcohol dehydrogenase, Asc-GSH cycle: Ascorbate-glutathion cycle, DHA: dehydroascorbate, GR: glutathion reductase, CAT: catalase, POD: peroxidase, Asc: Ascorbate, SUCC: succinic acid, FUM: fumaric acid.)
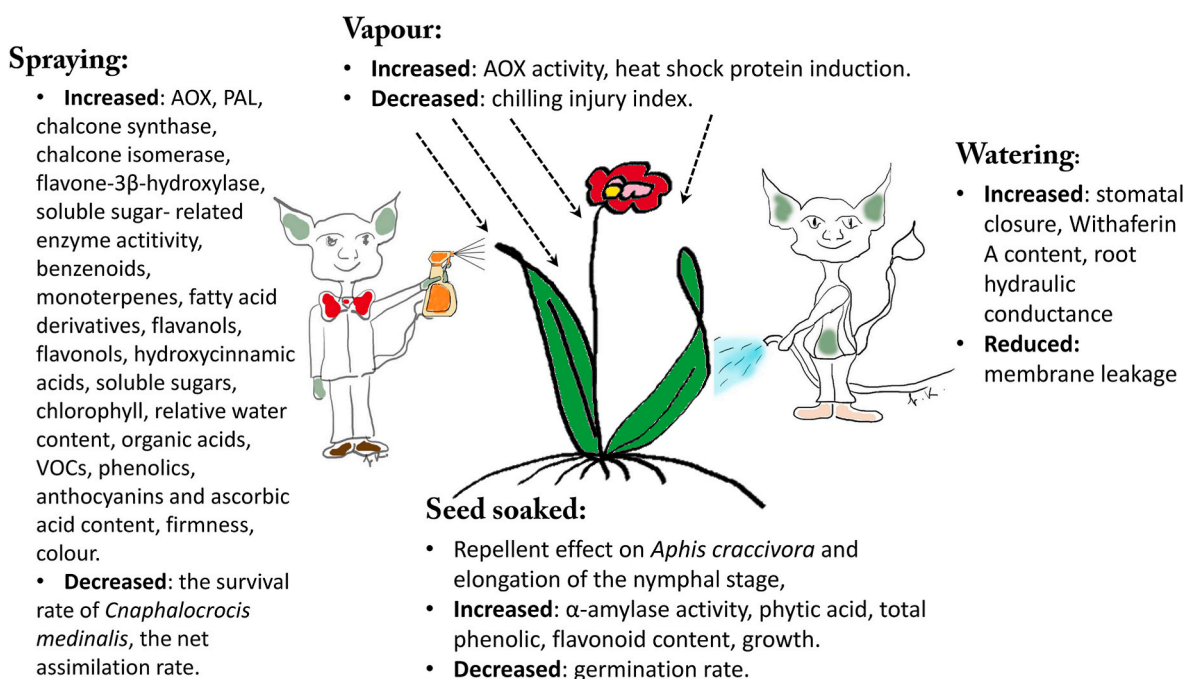
Fig. 4. Summary of the physiological changes taking place in plants treated with MeSA using various modes of application, namely vapour, spraying, seed soaking and watering. (PAL: phenylalanine ammonia-lysase, TAL: Tyrosine ammonia-lysase, AOX: antioxidant enzymes, VOCs: volatile organic compounds.)

DFR), CsANS (anthocyanidin synthase: ANS) and CsUFGT (udp-glucose flavonoid 3-o-glucosyl transferase: UFGT) (Li et al., 2019). In another experiment, tea plants were sprayed with solutions of JA, SA, or theirs volatile ester derivatives, MeJA, and MeSA, and the induced VOCs were measured. SA and MeSA induced MeSA production, while the jasmonates did not. Based on principal component and hierarchical cluster analyses, salicylates and jasmonates induced compounds belonging to different cluster classes (Long et al., 2020). When silver birch (*Betula pendula Roth*) was sprayed with various concentrations of MeSA, no significant relationship was found between stomatal conductance and the concentrations, but the net assimilation rate was significantly reduced by the treatments in a concentration-dependent manner. MeSA increased the amount of benzenoids, monoterpenes and fatty acid-derived compounds (Liu et al., 2018). However, when apple trees (Malus domestica; 'Topaz') were sprayed with MeSA during fruit maturation, the activity of PAL, chalcone synthase and isomerase, and flavone-3β-hydroxylase was increased, leading to elevated levels of flavanols, flavonols and hydroxycinnamic acids, but decreased the fruit quality (Gacnik et al., 2021). When chickpea (*Cicer arietinum* var. GNG1581) was watered with MeSA alone or in combination with L-phenylalanine, the precursor of MeSA in the phenylpropanoid pathway, MeSA treatment induced PAL and tyrosine ammonia-lyase enzyme activities, and increased phenol, flavonoids and condensed tannin contents in the leaves, and the combination was even more

effective. In addition, it has been shown that the phenylpropanoid pathway not only induced the accumulation of phenols and flavonoids, but also increased antioxidant capacity (Thappa and Guleria, 2021). Sweet cherry fruit had better quality (size, colour and firmness) when the trees were treated with MeSA solution 3 times (1. at pit hardening, 2. initial colour changes and 3. onset of ripening) (Giménez et al., 2015).

8.1.3. Hydrophonic treatment

When SA derivatives (SA, MeSA, acetylsalicylate, propyl salicylate, amyl salicylate, benzyl salicylate, and salicin) were added to the medium of *Arabidopsis thaliana* (Columbia ecotype and mutants) MeSA was found to caused the maximum stomatal closure, being more effective than SA, salicin, or acetylsalicylate, suggesting that the stomatal closure induced by MeSA could restrict pathogen entry into the leaves (Agurla et al., 2020). Interestingly, 24-h hydroponic MeSA treatment on *Withania somnifera* increased the withaferin A content (which is an anti-inflammantory, anti-tumor and immunosuppressive compound) and reduced membrane leakage compared to the control plants (Gorelick et al., 2015). Tomato wild-type and *def-1* (deficient in JA synthesis mutant) plants were watering with MeSA solution and the arbuscular mycorrhizal fungi (AMF) symbioses and the AMF regulation of root hydraulic conductance were examined under both well-watered and drought conditions. It was found, that the AMF regulation of root hydraulic conductance was increased in *def-1* plants (Sánchez-Romera et al., 2018).

8.1.4. Vapour exposure

The effects of MeSA treatment on leaves may also depend on the age of the leaf. In an experiment on wheat, the 1st or 2nd-3rd leaves were treated with the same concentration of MeSA. In the case of the oldest (1st) leaves, the free SA content increased, while the bound form and the activity of catalase exhibited no change. In contrast treatment of younger leaves enhanced the bound form and the activity of catalase (Janda et al., 2021). Exposure of poplar leaves (*Populus Simonii × Populus Pyramibalis c.v* and *Populus deltoids*) to MeSA decreased the amount of gallic acid, catechinic acid, pyrocatechol and ferulic acid (An et al., 2006). When Bidens pilosa (Asteraceae) was exposed to MeSA vapour, the metabolomics profile showed a decrease in the chalcone, okanin di-acetylglucoside, flavonoid, chicoric and caftaric acid contents, while PAL activity was induced. In this experiment, exposure to MeJA affected the same secondary metabolites, suggesting that a cross-talk mechanism exists between the SA and JA pathways (Ramabulana et al., 2020).

8.1.5. Impact of MeSA during storage

MeSA treatment may also be used during the storage of fruits or vegetables. When pomegranate trees were sprayed preharvest, the treatment increased the fruit quality, including firmness, colour, sugar and organic acid contents. The phenolic, anthocyanin and ascorbic acid contents increased in the arils of the pomegranate fruit (García-Pastor et al., 2020a). MeSA vapour treatments during ripening increased the expression of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase genes (*Le-ACS2* and *Le-ACS4*) and decreased *Le-ACS6* transcription, regulating the ethylene biosynthesis (Ding and Wang, 2003). Contrary to this finding, when kiwi fruit (*Actinidia deliciosa* 'Hayward') was vapour treated with MeSA, ethylene production significantly decreased (Aghdam et al., 2009).

When pepper fruits were stored at low temperature, vapour treatment with MeSA increased the conversion of glutamate into proline and increased the sucrose content (Seo et al., 2020). Exogenously applied MeSA participated in the regulation of yellowing in 'Zaosu' pears by degradation of chlorophyll during storage (Zhang et al., 2019). Dipping 'Sucrier' banana in MeSA solution during ripening stage 3, decreased H_2O_2 accumulation and senescent spotting (Chotikakham et al., 2019). Similar treatment increased the storability of sweet cherry (Giménez et al., 2015) and tomato (Min et al., 2018). When 'Sucrier' bananas were sprayed with MeSA solution during storage, there was an increase in the

activity of ascorbate-glutathione cycle which eliminates ROS and decreases oxidative membrane damage (malondialdehyde and protein carbonyl contents), and changes were observed in the content of non-enzymatic antioxidants (reduced glutathione and ascorbate) and the activity of antioxidant enzymes APX, dehydroascorbate peroxidase (DHAR) and glutathione reductase (GR) (Chotikakham et al., 2020). During storage, the appearance of grey mold caused by *Botrytis cinerea* declined after treatment with MeSA and L-arginine due to an increase in superoxide dismutase (SOD), CAT, PAL and polyphenol oxidase activities and in the expression level of pathogenesis-related protein 1 gene. In addition the total contents of phenolics, polyamines and nitric oxide was elevated after the treatment (Zhang et al., 2017). When the effect of low temperature was tested in cold-susceptible and resistant rice genotypes, increased MeSA contents were found in both genotypes, while SA only increased in the resistant genotype under cold conditions (Wani et al., 2021). In kiwi fruit (*Actinidia deliciosa* cv Xuxiang) MeSA treatment inhibited lignin accumulation after cold storage by inducing PAL pathway, which was manifested in the increased expression of *AcPAL* genes and the activity of cinnamyl-alcohol dehydrogenase (CAD) (Li et al., 2017). The chilling injury index, skin browning, and surface pitting and drying up decreased in pomegranate. Treatment with MeSA was able to maintain membrane structure, low values of electrolyte leakage and good fruit quality (firmness, total acidity) (Sayyari et al., 2011). MeSA vapour treatment increased the endogenous polyamine content, especially that of putrescine and spermidine, which were able to reduce chilling injury (Valero et al., 2015).

9. Comparison of the effects of SA and MeSA

MeSA as a VOC can induce indirect defence by attracting the natural enemies of herbivores. In addition MeSA also induces the emission of VOCs, again promoting indirect defence, as found during spider mite infection on lima bean, tomato and pear (Aljbory and Chen, 2018; De Boer et al., 2004; Dicke, 1994; Ozawa et al., 2000). Treating poplar cuttings (*P. × euramericana* 'Nanlin 895') with MeSA induced several VOCs, including (*Z*)-3-hexen-1-ol and (*Z*)-3-hexenyl acetate emissions (Tang et al., 2015). Earlier results showed that (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate were highly attractive to male insects of *Melolontha hippocastani* (Ruther et al., 2002) and *Manduca sexta* (Fraser et al., 2003), respectively. MeSA spraying before infection reduced the feeding activity of *Cnaphalocrocis medinalis* in rice plants (Indhumathi et al., 2019). The same effect was observed in the case of glasshouse whitefly (*Trialeurodes vaporariorum* Westwood) on tomato (Conboy et al., 2020).

In *Arabidopsis* plants grown on medium and treated with MeSA or SA, MeSA induced greater stomatal closure than SA, but in the *nia1* and *nia2* mutants (which are unable to produce NO) stomatal closure could not induced by either MeSA or SA, but by NADPH oxidase, which can be activated by MeSA or abscisic acid (ABA) in a same way (Agurla et al., 2020).

When table grape cultivars were sprayed with SA or MeSA, then inoculated with *Botrytis cinerea*, MeSA reduced the pathogenic effects to a greater extent than SA. Although both the compounds changed the contents of sugars and the activity of CAT, APX and POD, the ester form had more significant effects, namely increased the level of glucose, fructose and glucosides, while decreased the total antioxidant activity more efficiently than SA (García-Pastor et al., 2020b). Faba bean seeds were soaked in MeSA or SA solution to monitor the priming effect on *Aphis craccivora*. The SA treatment protracted the nymphal stage for a longer period then MeSA, but a low concentration of MeSA (50 ppm) increased the wing formation of the aphids compared to SA and decreased the percentage of apterious adults. However, a high concentration (200 ppm) of SA, caused greater changes in the alatae and apterae forms compared to MeSA priming (El-Solimany, 2020).

When the fruit of plum trees sprayed with MeSA or SA during the on-tree plum phase, then stored at 10 °C for 50 days, SA treatment resulted in a higher total phenolic content after storage than MeSA, though the

rise of antioxidant enzyme activity to the same level (Martínez-Esplá et al., 2017). When the fruit of pomegranate trees sprayed with SA or MeSA before harvest were stored at the same temperature for 90 days, SA increased the total phenolics and anthocyanins to a higher extent than MeSA, while MeSA increased the succinic acid and glucose contents more than SA (García-Pastor et al., 2020a).

10. Concluding remarks and future prospects

The role of SA under stress conditions is already relatively well-characterised, while the role of MeSA is much less understood. Although MeSA and SA are often mentioned simply as the volatile and non-volatile forms of the same compound, it is worth highlighting their differences, in order to reveal the independent role and action mechanism of MeSA. SA is methylated to MeSA by SAMT, while MeSA is transformed to SA by SABP2. It is true that since SA and MeSA are mutual precursors, it is often difficult to differentiate between their individual effects. In several cases SA and MeSA act in the same way; for example, the signalling cascade of each of the compound has an important role under biotic stress. SA and MeSA are also mobile signal compounds in plants to induce SAR, although MeSA is more hydrophobic and volatile than SA. Therefore, it can spread easier and act faster than SA, but the signalling differences and similarities are still unclear. Plants also emit MeSA as an indicator of biotic stress or induce indirect defence *via* attract the enemies of herbivores. The MeSA is also attractive signal for various bugs and induce defence mechanism the intact plants. In addition, exogenous MeSA was more effective in stomatal closure than SA. Results suggest that although there are still many open questions related to the mode of action of MeSA, it could also be a promising compound in practical agriculture to improve the tolerance of plants to various stress factors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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