



Article

Elicitation of Medicinal Plants In Vivo—Is It a Realistic Tool? The Effect of Methyl Jasmonate and Salicylic Acid on Lamiaceae Species

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Abstract: Salicylic acid (SA) and methyl jasmonate (MeJa) are prominent phytohormones that are involved in stress reactions. Both compounds may influence the biosynthesis of secondary compounds; however, scientific experiments in vivo are rare and contradictory. This paper reports on a study on the elicitation of volatiles and total phenolics (TPC) by MeJa and SA. The subjects were four *Lamiaceae* species studied in open field conditions in Budapest (Hungary). According to the results, both elicitors provoked specific responses in each plant species depending on the dosage applied and the parameter studied; 2 mM of SA stimulated essential oil (EO) accumulation in marjoram and peppermint, while in hyssop 0.1 mM was optimal. MeJa proved to be effective only in marjoram and in basil. In marjoram, *cis*-sabinene hydrate was decreased and in hyssop, isopinocampone was increased by both dosages of SA. In peppermint, pulegone content was reduced by 2 mM SA, but no significant change of the major components of basil EO was detected. SA was successful in increasing TPC and antioxidant activity (AC) in three of the experimental species, but not in hyssop. In marjoram, only 0.1 mM induced TPC and eventually AC, while in peppermint and basil both dosages of SA were effective. Optimisation of the treatments is suggested in further in vivo experiments.

Keywords: elicitor; medicinal and aromatic plants; essential oil; phenolic content; antioxidant capacity



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1. Introduction

The Lamiaceae family consists of a large number of medicinal and aromatic plants (MAP); annual or perennial; with a worldwide distribution [1]. They are widely used in traditional medicine, in the perfumery, pharmaceutical, and cosmetics industries; and as flavoring agents in gastronomy, all due to their bioactive secondary compounds [2]. Some of the most widely used and popular species of this family are marjoram, peppermint, hyssop, and basil.

Sweet marjoram (*Origanum majorana* L.); also known as *Majorana hortensis* Moench; is a popular Mediterranean species traditionally used to treat gastrointestinal disturbances, cough, bronchial diseases, and headaches [3,4]. The herb contains volatile compounds, characteristically sabinene and terpinene derivatives. Like other species of the genus, marjoram is also rich in phenolics and caffeic acid derivatives, but ascorbic acid and carotenoids have been detected as well [5,6].

Peppermint (*Mentha piperita* L.) is a flavor-rich species of dark green leaves, a hybrid of spearmint (*Mentha spicata*) and water mint (*Mentha aquatica*). It is used as a flavoring agent and is a key ingredient in herbal infusions [7]. Fresh or dried leaves of peppermint are rich in essential oils (EO) with the main component being l-menthol; furthermore, they contain phenolic compounds, such as rosmarinic acid, hesperidin, and luteolin-7-O-rutinoside [8,9].

Hyssop (*Hyssopus officinalis* L.), originating from eastern Asia, has been heavily used both as a culinary and as a medicinal herb, similar to the related species mentioned above,

the main active ingredient is EO, with pinocamphone, β -pinene and pinocarvone as the main compounds. Besides, the drug is rich in caffeic acid derivatives [10,11].

Sweet basil (*Ocimum basilicum* L.) is one of the most popular species used in food as a fresh or dried herb. The attractive aroma is due to the volatile components, among which linalool, camphor, and methyl-chavicol are present in the highest ratios, depending on the chemotype. The health-promoting effects are attributed to the high phenolic content, including rosmarinic acid and caffeic acid, with its derivatives [12,13].

In the recent past, several strategies have been studied which increase the production of secondary metabolites (SMs) of MAPs, including elicitation. The application of chemical elicitors on plants triggers defense reactions, which might lead to an elevated concentration of different SMs [14]. Among different elicitors, salicylic acid (SA) and methyl jasmonate (MeJa) are well known phytohormones involved in biotic and abiotic stress reactions [15,16]. When applied exogenously, both compounds could induce the synthesis of SMs and subsequently enhance the biological activities both in cell plant cultures and in vivo plants [17,18]. However, scientific data on in vivo applications are much rarer and more contradictive, which indicates the need for further research.

This paper describes the effect of MeJa and SA in different concentrations, studied on four *Lamiaceae* species: marjoram, peppermint, hyssop, and basil. Emphasis was placed on the accumulation and composition of their EO, phenolic content and antioxidant properties.

2. Materials and Methods

2.1. Experimental Site, Plant Material and Treatments

The experiments were conducted at the Experimental Station of the University of Agricultural and Life Sciences (MATE), in Budapest, Hungary (47.398820, 19.149270). The experimental plant material, with its origin, is summarized in Table 1.

Table 1. Plant material and its origin.

Species	Taxon	Origin
<i>Hyssopus officinalis</i>	population	seed collection in cultivated stand, Meran, Italy
<i>Origanum majorana</i>	variety 'Magyar'	superelite seeds stock of MATE
<i>Mentha piperita</i>	variety 'Mexian'	stolons from mother plantation of MATE
<i>Ocimum basilicum</i>	variety 'Genovese'	gene bank accession of MATE

Marjoram and basil were propagated by seed sowing at the beginning of April 2020 in a greenhouse, and the well-developed seedlings were planted into the open field in early June. In the case of the perennial species, we used two-year-old stands. The hyssop was propagated from seedlings and the peppermint was done vegetatively, via stolons at the end of March in the previous year. The experiments were arranged in a completely randomized block design with a plot size of 10 m² in three replications for each treatment. The soil characteristics and temperature data during the experimental period are summarized in Table 2 and Figure 1 respectively.

Table 2. The soil composition of the experimental plot.

Measured Parameter	pH H ₂ O	Humus Content %	Lime Content %	K _A	NO ₂ + NO ₃ -N mg/kg	P ₂ O ₅ mg/kg	K ₂ O mg/kg	Zn mg/kg	Mg mg/kg	Mn mg/kg
Experimental station soil	7.82	2.84	0.34	25	6.93	412.89	245.54	4.09	131.78	25.64

We started the treatments two weeks before the optimal harvesting stage (full flowering) of each species. The plants were sprayed with MeJa and SA supplied by Sigma-Aldrich (Schnellendorf, Germany) and Kévés Béla Kft. (Soltvadkert, Hungary) respectively in two dosages: 0.1 and 2.0 mM, dissolved in water. The control plots were sprayed only with

water. All solutions were sprayed onto the aboveground shoots, uniformly distributed with a hand sprayer (approximately 50 mL per plant). The treatments were applied twice with an interval of one week (Table 3). One week after the second treatment, sampling of each species was carried out according to our previous research experiences. The aerial parts of the plants were harvested by cutting the plants at approximately 10 cm above the soil surface. The samples were air-dried in shade under ambient temperature.

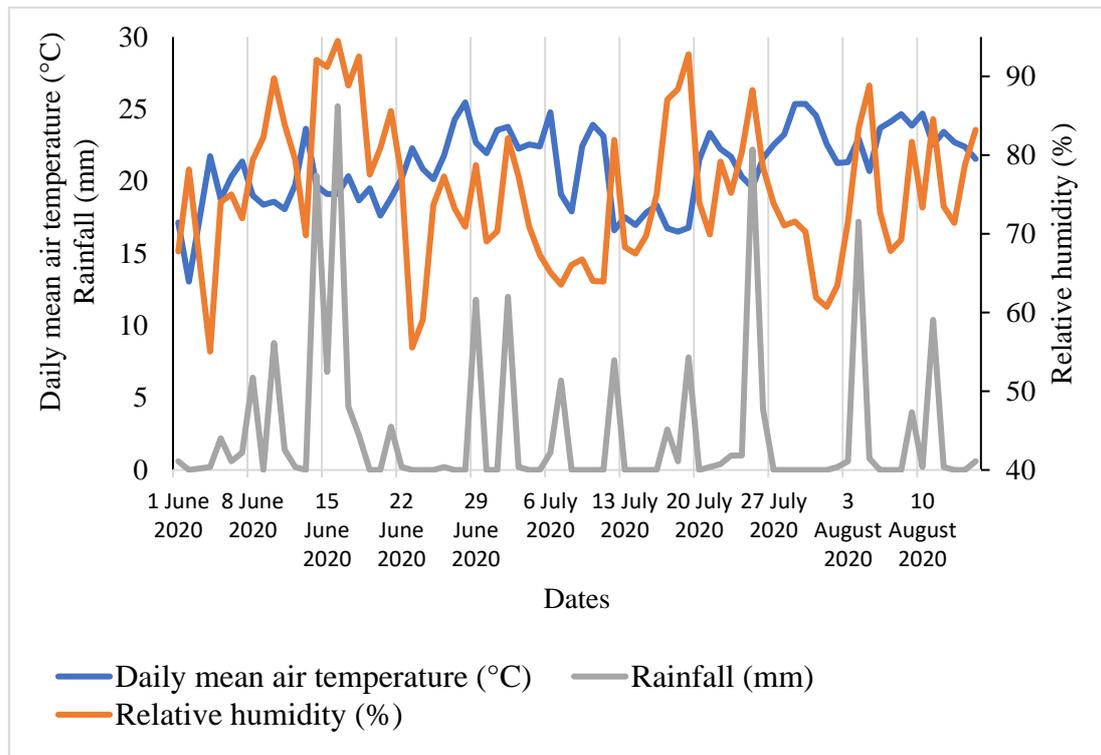


Figure 1. Daily mean air temperature (°C), rainfall (mm), and relative humidity (%) of the experimental field in summer 2020.

Table 3. Treatment and harvesting times of the experimental species.

Plant	1st Treatment	2nd Treatment	Harvesting
Hyssop	12 June 2020	19 June 2020	26 June 2020
Peppermint	19 June 2020	26 June 2020	2 July 2020
Marjoram	26 June 2020	2 July 2020	10 July 2020
Basil	29 July 2020	5 August 2020	13 August 2020

2.2. Chemical Analysis

2.2.1. EO Content

After drying the plants for 2 weeks, we placed them in the laboratory. Leaves were separated from stem parts, and they were used in three replicates for EO distillation; 20 g dried material from each sample was hydro-distilled in a Clevenger type apparatus using 500 mL of water for 1.5 h for peppermint and 2 h for the other species, according to the method recommended by the VII Hungarian Pharmacopoeia. The oils were collected, and traces of water were removed with anhydrous sodium sulfate. Then, the extracts were separated with a syringe filter and stored in an airtight vial in a refrigerator at 4 °C before analysis.

2.2.2. EO Composition

The identification of the active components of the EO was performed by GC–MS. We used two devices: an Agilent Technologies 6890N instrument equipped with HP–5MS capillary column (5% phenyl, 95% dimethyl polysiloxane, length: 30 m, film thickness: 0.25 mm i.d. \times 0.25 μ m); and an Agilent Technologies MS 5975 inert mass selective detector, both supplied by Agilent technologies international Sàrl (Rolle, Switzerland). The carrier gas was helium (1 mL min^{−1}). The temperature during the analysis was scheduled at 60 °C initially, then raised by a rate of 3 °C/min up to 240 °C; the final temperature remained for 5 min. The injector and detector temperatures were 250 °C. Split ratio: 30:1; 10 μ L of EO was diluted with n-hexane to 1 mL and from this, the injected quantity was 0.2 μ L. Ionization energy was 70 eV. The MS was recorded in full scan mode, which revealed the total ion current (TIC) chromatograms (mass range m/z 50–500 μ ma). The identification of the EO components was based on the comparison of their linear retention indices, which were calculated using the generalized equation of Van Den Dool and Kratz [19] with literature data, and by matching recorded mass spectra with those in mass spectral library references (NIST MS Search 2.0 library, Wiley 275) and a mass spectra library [20].

2.2.3. Total Phenolic Content (TPC)

For the determination of the TPC, 1 g powdered dried plant material was obtained by grinding the dry leaves and sifting them with a 500 μ m diameter sieve. We then added 100 mL boiling distilled water (used as a solvent), which was extracted after 24 h. Finally, the extracts were filtered and stored frozen awaiting further measurements. The quantification of total phenolic content was determined by the modified method of Singleton and Rossi [21]. The sample solution of 0.5 mL was placed in a test tube, and then 2.5 mL Folin–Ciocalteu’s reagent (10 v/v%) was added. After 1 min of incubation, 2 mL of sodium carbonate (700 mM) was added. The absorbance was measured at 760 nm in a Thermo Evolution 201 spectrophotometer after a 5 min incubation period in hot water (50 °C). Gallic acid (300 mM) was used as the chemical standard for calibration. The total phenolic content of the sample was expressed as mg of gallic acid equivalents per g of dry weight of extract (GAE mg·g^{−1} d.w.). A blank was prepared which contain distilled water instead of extract. The measurements were carried out in three replications.

2.2.4. Antioxidant Capacity (AC)

The antioxidant capacity was determined by the application of the ferric reducing antioxidant power (FRAP) assay developed by Benzie and Strain [22], with a few modifications. FRAP reagent was prepared fresh, in order to contain three things: sodium acetate buffer (pH 3.6), TPTZ (2,4,6-tripiridil-s-triazin) in HCl, and FeCl₃·6H₂O solution (20 mmol/L), in the proportion 10:1:1 (v/v/v); 10 μ L of the previously extracted test sample was added to 1.5 mL of acting FRAP reagent and 40 μ L distilled water. The absorbance of the solution was then measured at 593 nm after 5 min using the above-mentioned spectrophotometer. A blank was made to contain distilled water instead of the sample and ascorbic acid was used as a positive control. FRAP values of samples were calculated from the standard curve equation and expressed as mg ascorbic acid equivalent (AAE)·g^{−1} of dry extract.

2.2.5. Statistical Analysis

Data were evaluated using means, standard deviations, and one-way analysis of variance using IBM SPSS Statistics 25. Normality of the residuals was proved by the Shapiro–Wilk test, the homogeneity of variances was tested by Levene’s method, and finally, the control and treated samples were separated by Tukey’s post hoc tests if homogeneity assumption was satisfied, and the separations were modified by Games–Howell’s post hoc tests of homogeneity of variances was violated. The *p*-value less than 0.05 was considered statistically significant.

3. Results and Discussion

3.1. Essential Oil Content

Our results showed different results for the EO depending on the elicitor, its dosage, and the plant species. Figure 2 represents the EO content expressed by mL/100 g of dry material.

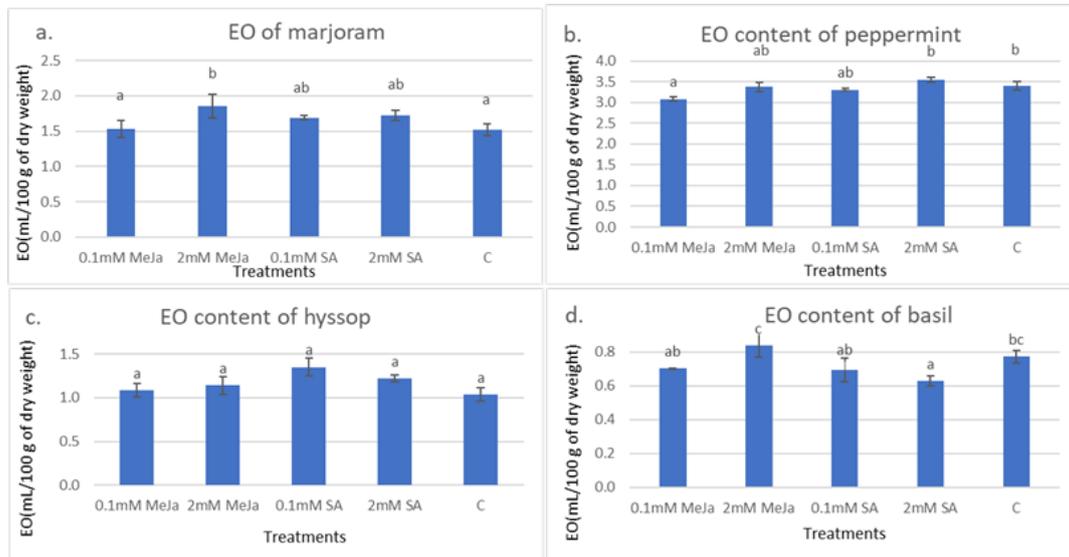


Figure 2. The effect of MeJa and SA on the EO content of the subject plants; (a) marjoram, (b) peppermint, (c) hyssop, and (d) basil; Data are expressed as means \pm SD; means with different letters are significantly different ($p < 0.05$).

In marjoram, higher dosages both of MeJa and SA were significantly more effective than lower dosages, but none of them differed statistically from the control, except for the 2 mM of MeJa. The latter and 2 mM of SA increased the EO content by 23% and 15% respectively.

In peppermint, similarly, the higher dosage of SA resulted in a slight increase of the EO content, while the lower (0.1 mM) dosage was not effective. However, treatments with MeJa seem to stop the accumulation of volatiles, interestingly. Especially the 0.1 mM treatment caused a significant decrease.

Hyssop also showed greater sensitivity to SA than to MeJa. The highest EO content (0.35 mL/100 g d.w.) was measured in the samples sprayed with 0.1 mM of SA. The higher dosage of it also elevated EO content but was not significant. Spraying with MeJa in either concentration had no significant elicitor effect on the volatiles of this species.

Basil showed a distinct reaction to the treatments compared to the previously mentioned species, as the EO content dropped in consequence of each treatment, except for the 2 mM of MeJa. Especially the higher dosage of SA resulted in a significant decrease of the volatile accumulation, by approximately 20%.

Our findings partly agree with a few studies where the application of different dosages of SA or MeJa/JA did not have a significant difference on the accumulation of EO in other *Lamiaceae* species, such as summer savory (*Satureja hortensis*) and thyme (*Thymus daenensis* Celak) [23,24].

Yadegari et al. [25] showed that a low dosage of SA (0.1 mM) failed to enhance the EO production of sage (*Salvia officinalis*) in contrast to higher dosages. At the same time, elicitation with 0.1 mM of MeJa was effective for increasing the EO percentage in anise hyssop (*Agastache foeniculum*) [26].

3.2. Essential Oil Composition

The results of GC-MS analysis of marjoram in Table 4 revealed the presence of 15 compounds reaching 97.4–98.6% of the total area percentages were identified in the EO. In each sample, *cis*-sabinene hydrate and terpinen-4-ol were detected as major components, however, their ratios changed according to the treatments.

Table 4. The chemical composition of the EO of marjoram.

Component	RI ¹	Elicitors				C ²	Sign. ³
		0.1 mM MeJa	2 mM MeJa	0.1 mM SA	2 mM SA		
Sabinene	976	3.42 ^a	3.19 ^a	4.52 ^a	3.77 ^a	3.52 ^a	ns
β-Myrcene	995	0.76 ^a	0.70 ^a	1.03 ^a	0.86 ^a	0.80 ^a	ns
α-Terpinene	1018	2.24 ^a	2.29 ^a	2.87 ^a	2.75 ^a	2.12 ^a	ns
β-Phellandrene	1029	2.18 ^a	2.22 ^a	2.48 ^a	2.19 ^a	2.08 ^a	ns
γ-Terpinene	1056	4.96 ^a	4.83 ^a	5.47 ^a	5.48 ^a	4.30 ^a	ns
trans-Sabinene hydrate	1070	7.10 ^a	6.99 ^a	6.65 ^a	7.18 ^a	6.57 ^a	ns
α-Terpinolene	1085	1.12 ^a	1.63 ^a	1.29 ^a	1.25 ^a	0.98 ^a	ns
cis-Sabinene hydrate	1096	43.54 ^{ab}	42.74 ^{ab}	37.77 ^a	40.99 ^a	48.24 ^b	*
cis-p-Menth-2-en-1-ol	1126	0.96 ^a	1.09 ^a	1.07 ^a	1.11 ^a	0.85 ^a	ns
Terpinen-4-ol	1175	14.02 ^{ab}	13.28 ^{ab}	12.67 ^{ab}	14.99 ^b	11.62 ^a	*
α-Terpineol	1189	4.14 ^a	4.56 ^a	4.52 ^a	4.57 ^a	4.70 ^a	ns
trans-Sabinene hydrate acetate	1247	2.48 ^a	2.76 ^a	3.96 ^a	3.95 ^a	2.47 ^a	ns
Linalyl acetate	1250	3.00 ^a	3.36 ^{ab}	3.44 ^{ab}	3.51 ^{ab}	4.27 ^b	**
β-Caryophyllene	1420	3.88 ^b	3.69 ^{ab}	4.14 ^b	3.11 ^a	3.22 ^a	*
Bicyclogermacrene	1497	3.63 ^b	3.63 ^b	4.20 ^b	2.26 ^a	2.89 ^a	*
Monoterpenes		89.91 ^{ab}	89.61 ^{ab}	87.75 ^a	92.60 ^b	92.52 ^b	*
Sesquiterpenes		7.51 ^{ab}	7.32 ^{ab}	8.33 ^b	5.38 ^a	6.11 ^{ab}	*
Total		97.42	96.92	96.08	97.98	98.63	

Notes: ¹ Retention indices; ² control sample; ³ the level of significance: ns = not significant, * = significance level at 5%, ** = significance level at 1%; Values designated by the different letters are significantly different.

The concentration of the sabinene hydrate isomers decreased as a consequence of all treatments, among which significant differences of 22% and 16% were detected in the ratio of *cis*-sabinene hydrate due to the spraying with 0.1 mM and 2 mM of SA, respectively. At the same time, the ratio of terpinen-4-ol was increased by all treatments and significant (30%) elevation was registered at the higher dosage of SA. Furthermore, the two sesquiterpenes identified in the samples both increased due to the spraying of both dosages of MeJa and 0.1 mM of SA. The highest concentration of beta-caryophyllene was obtained by 0.1 mM SA, while the same dosage increased bicyclogermacrene by approximately 45%. As a result, the ratio of total sesquiterpenes in the oil was elevated, too.

The findings about the elicitation of marjoram with SA in Egypt were partly in accordance with ours: the treatment of 0.1 mM of SA increased the ratio of both *cis*-sabinene hydrate and terpinen-4-ol in the EO [27]. Interestingly, elicitation by the application of compost (Nitrogen-fixers + *Bacillus circulans*) had the same results as those of our study: ratio of the sabinene hydrate decreased, but that of terpinen-4-ol was elevated [28].

The statistical analysis of the EO composition of peppermint in Table 5 revealed that in the ratio of the main compounds menthol and menthone, there are no significant differences in the treated samples compared with the control (Table 5). Only the ratio of pulegone was reduced after spraying 2 mM of SA by approximately 43%, which seems to be advantageous considering the EU regulation on limits for pulegone and menthofuran [29]. Yet, in another experiment, 0.1 mM of SA was able to increase the menthol and the menthyl acetate concentration significantly, when applied exogenously to peppermint [30]. On the other hand, it appears that a physical elicitor, such as UV-B may have more effect on the peppermint EO quality, where UV radiation greatly increased menthofuran, menthyl acetate, and menthone but significantly decreased the menthol level. This can be a serious drawback due to the quality requirements and importance of the menthol compound in the

industry [31]. In our experiment, the treatments likewise did not cause significant changes in the total mono and sesquiterpene ratio.

Table 5. The chemical composition of the EO of peppermint.

Component	RI ¹	Elicitors				C ²	Sign. ³
		0.1 mM MeJa	2 mM MeJa	0.1 mM SA	2 mM SA		
Limonene	1029	5.33 ^a	5.23 ^a	6.015 ^a	6.145 ^a	5.51 ^a	ns
1,8-Cineol	1034	4.27 ^a	3.94 ^a	4.70 ^a	4.98 ^a	4.28 ^a	ns
γ -Terpinene	1056	0.90 ^a	1.03 ^a	0.94 ^a	0.88 ^a	1.00 ^a	ns
Menthone	1158	32.92 ^a	35.15 ^a	34.12 ^a	31.81 ^a	35.05 ^a	ns
Menthofuran	1168	7.56 ^a	7.91 ^a	7.52 ^a	7.41 ^a	7.7 ^a	ns
Menthol	1171	30.67 ^a	27.73 ^a	29.46 ^a	31.02 ^a	27.79 ^a	ns
Pulegone	1236	1.80 ^{ab}	2.06 ^a	1.44 ^{ab}	1.12 ^b	1.96 ^a	*
Piperitone	1249	1.50 ^a	1.66 ^a	1.60 ^a	1.58 ^a	1.57 ^a	ns
Menthyl acetate	1291	4.56 ^a	4.12 ^a	3.91 ^a	3.98 ^a	4.57 ^a	ns
Germacrene D	1482	1.49 ^a	1.77 ^a	1.48 ^a	1.68 ^a	1.78 ^a	ns
Monoterpenes		89.53 ^a	88.85 ^a	89.71 ^a	88.94 ^a	89.45 ^a	ns
Sesquiterpenes		1.49 ^a	1.77 ^a	1.48 ^a	1.68 ^a	1.78 ^a	ns
Total		91.02	90.62	91.19	90.62	91.23	

Notes: ¹ Retention indices; ² control sample; ³ the level of significance: ns = not significant, * = significance level at 5%; Values designated by the different letters are significantly different.

The EO analysis of hyssop in Table 6 reveals that the ratio of β -phellandrene decreased significantly, by 46% with 0.1 mM SA, however, the other treatments had no significant effects. Pentylbenzen and the main component isopinocampone changed significantly due to the SA treatments. Their concentrations were elevated by 65% and 60% respectively when 0.1 mM was applied, and by 39 and 28% with 2 mM of SA. Interestingly, MeJA in 2 mM concentration also elevated the ratios of the two compounds mentioned, by the same rate. The highest percentage of isopinocampone was detected by 0.1 mM SA, around 46% which may be advantageous considering the biological activities and wide use of this compound in perfumery and cosmetics [32,33]. SA was proven in other studies as well to be an important elicitor in increasing the main EO components in *Achillea millefolium* L. [34], *Citrus aurantium* L. [35] and *Melissa officinalis* [36]. Among sesquiterpenes, β -bisabolol was reduced after spraying 2 mM of MeJa and 0.1 mM of SA by 66% and 65%, respectively. Overall, our results demonstrated a significant decrease in total sesquiterpenes with both dosages of MeJa and 0.1 mM of SA, which contradicts a previous report that SA was able to stimulate the production of sesquiterpenes of hyssop [37].

Table 7 shows the result of the CG-MS analysis of the basil EO. It can be established that there was no significant difference for the major component linalool after the application of either of the elicitors. Among monoterpenes, only 1.8-cineole and iso-bornyl acetate changed significantly.

The first compound fell by 48% due to the 0.1 mM SA treatment, while the second one rose with 2.0 mM MeJa but dropped with 2.0 mM SA. Sesquiterpenes were characteristically more strongly affected. Both α -guaiene and bicyclgermacrene levels were enhanced with the lower dosages of both elicitors; 0.1 mM MeJa and 0.1 mM SA increased α -guaiene by 42% and 44%, respectively; and bicyclgermacrene was 70% and 72%, respectively. Besides, 0.1 mM SA was able to increase β -elemene and bicyclgermacrene by 61% and 72%, respectively. In parallel, the same lower dosage of MeJa reduced the ratio of *trans*- α -bergamotene compound by 38%, while 0.1 mM SA increased it approximately by 24%. Based on the above, the present result could not support the large increase (113%) in the ratio of linalool following application of 0.1 mM of SA, a result which was registered in a previous experiment under hydroponic conditions [38].

Some other reports also indicate different results with basil, depending on the elicitor and the cultivar. A concentration of 0.5 mM MeJa was proven to increase linalool level in the Genovese cultivar under salinity stress, while it decreased the same component in the

Rubi cultivar [39]. Elicitation with copper sulfate in vitro significantly increased eugenol while inducing some compounds that were absent in the untreated samples [40]. In our study, no qualitative differences were detected in the spectrum. The total ratio was shifted significantly in the direction of monoterpenes due to the higher dosage of MeJa; and was shifted in the opposite direction by increasing the sesquiterpenes after the lower dosage of SA.

Table 6. The chemical composition of the EO of hyssop.

Component	RI ¹	Elicitors				C ²	Sign. ³
		0.1 mM MeJa	2 mM MeJa	0.1 mM SA	2 mM SA		
Sabinene	976	1.04 ^a	1.06 ^a	1.05 ^a	0.89 ^a	0.74 ^a	ns
β-Pinene	981	5.20 ^a	5.74 ^a	5.93 ^a	4.47 ^a	3.44 ^a	ns
β-Myrcene	995	2.56 ^a	2.03 ^a	1.49 ^a	1.65 ^a	2.14 ^a	ns
β-Phellandrene	1029	14.46 ^c	10.61 ^{abc}	5.89 ^a	8.12 ^{ab}	12.85 ^{bc}	*
Linalool	1097	1.12 ^a	1.05 ^a	1.00 ^a	0.99 ^a	1.10 ^a	ns
Benzene <pentyl->	1152	2.93 ^b	3.18 ^{bc}	3.78 ^c	3.19 ^{bc}	2.29 ^a	*
Pinocarvone	1166	0.18 ^a	0.32 ^b	0.37 ^b	0.63 ^c	0.14 ^a	*
Isopinocampone	1170	36.33 ^b	37.30 ^b	46.36 ^c	37.16 ^b	29.07 ^a	*
β-Bourbonene	1383	0.44 ^a	0.35 ^a	0.50 ^a	0.37 ^a	0.32 ^a	ns
α-Gurjunene	1410	0.48 ^a	0.37 ^a	0.52 ^a	0.62 ^a	0.53 ^a	ns
β-Caryophyllene	1420	1.84 ^a	1.55 ^a	1.90 ^a	2.05 ^a	1.99 ^a	ns
Alloaromadendrene	1462	1.89 ^a	1.51 ^a	1.97 ^a	2.29 ^a	2.10 ^a	ns
Germacren-D	1482	4.01 ^a	3.12 ^a	4.38 ^a	4.72 ^a	4.61 ^a	ns
Bicyclogermacrene	1497	4.62 ^a	4.02 ^a	4.91 ^a	5.81 ^a	5.46 ^a	ns
Elemol	1553	5.75 ^a	5.42 ^a	5.10 ^a	5.68 ^a	6.03 ^a	ns
Spathulenol	1584	0.51 ^a	0.55 ^a	0.41 ^a	0.54 ^a	0.79 ^a	ns
Caryophyllene-oxide	1590	0.62 ^a	0.83 ^a	0.47 ^a	0.69 ^a	1.06 ^a	ns
cis-Isolongifolene	1611	0.70 ^a	0.94 ^a	0.58 ^a	1.01 ^a	1.28 ^a	ns
γ-eudesmol	1630	1.69 ^a	1.77 ^a	1.43 ^a	1.64 ^a	2.73 ^a	ns
Tau-murolol	1647	0.89 ^a	1.32 ^a	0.70 ^a	1.25 ^a	2.18 ^a	ns
β-eudesmol	1653	1.33 ^a	1.52 ^{ab}	0.99 ^a	1.31 ^a	2.21 ^b	*
α-eudesmol	1656	1.60 ^a	2.37 ^a	1.11 ^a	1.57 ^a	2.40 ^a	ns
β-bisabolol	1671	4.53 ^{ab}	4.22 ^a	4.11 ^b	5.05 ^{ab}	6.18 ^b	*
Monoterpenes		60.88 ^b	58.09 ^{ab}	62.07 ^b	53.90 ^{ab}	49.48 ^a	*
Sesquiterpenes		30.86 ^b	29.82 ^b	29.03 ^b	34.56 ^{ab}	39.83 ^a	*
Total		94.67	91.09	94.88	91.65	91.60	

Notes: ¹ Retention indices; ² control sample; ³ the level of significance: ns = not significant, * = significance level at 5%; means designated by the different letters are significantly different.

Table 7. The chemical composition of the EO of basil.

Component	RI ¹	Elicitors				C ²	Sign. ³
		0.1 mM MeJa	2 mM MeJa	0.1 mM SA	2 mM SA		
1,8-Cineole	1034	6.64 ^{ab}	7.83 ^{ab}	4.78 ^a	7.79 ^{ab}	9.33 ^b	*
Linalool	1097	50.07 ^a	53.58 ^a	46.24 ^a	51.28 ^a	46.74 ^a	ns
Camphor	1144	0.56 ^a	0.57 ^a	0.45 ^a	0.24 ^a	0.60 ^a	ns
α-Terpineol	1189	0.98 ^a	1.04 ^a	1.10 ^a	1.14 ^a	1.15 ^a	ns
Iso-bornyl acetate	1281	1.55 ^b	1.98 ^c	1.71 ^{bc}	1.14 ^a	1.69 ^{bc}	*
Eugenol	1361	2.94 ^a	2.54 ^a	3.04 ^a	3.19 ^a	2.11 ^a	ns
β-Elementene	1391	1.00 ^{ab}	0.78 ^a	1.20 ^b	0.86 ^{ab}	0.75 ^a	*
trans-α-Bergamotene	1437	3.52 ^a	4.71 ^b	7.05 ^c	5.40 ^b	5.70 ^b	*
α-Guaiene	1439	0.91 ^b	0.69 ^{ab}	0.92 ^b	0.74 ^{ab}	0.64 ^a	*
α-Humulene	1454	0.75 ^b	0.56 ^a	0.71 ^{ab}	0.62 ^{ab}	0.58 ^a	*
(+)-epi-Bicyclosesquiphellandrene	1464	0.64 ^{ab}	0.49 ^a	0.73 ^b	0.59 ^{ab}	0.64 ^{ab}	*
Germacrene D	1482	2.82 ^{ab}	2.30 ^a	3.55 ^b	2.69 ^{ab}	2.39 ^a	*

Table 7. Cont.

Component	RI ¹	Elicitors				C ²	Sign. ³
		0.1 mM MeJa	2 mM MeJa	0.1 mM SA	2 mM SA		
Bicyclogermacrene	1497	1.08 ^b	0.57 ^a	1.10 ^b	0.80 ^{ab}	0.64 ^a	**
α -Bulnesene	1506	2.87 ^a	2.24 ^a	2.95 ^a	2.48 ^a	2.15 ^a	ns
cis- γ -Cadinene	1515	3.02 ^b	2.18 ^a	3.34 ^b	2.99 ^b	2.93 ^{ab}	*
δ -Cadinene	1524	0.65 ^{ab}	0.51 ^a	0.88 ^b	0.69 ^{ab}	0.74 ^{ab}	**
Spathulenol	1584	1.25 ^b	0.82 ^a	1.01 ^{ab}	0.95 ^a	0.91 ^a	*
1,10-di-epi-Cubenole	1621	1.30 ^a	1.11 ^a	1.36 ^a	1.18 ^a	1.36 ^a	ns
Tau-cadinol	1644	9.42 ^a	8.01 ^a	9.66 ^a	9.34 ^a	9.34 ^a	ns
Monoterpenes		62.75 ^{ab}	67.54 ^b	57.32 ^a	64.78 ^{ab}	61.62 ^{ab}	*
Sesquiterpenes		29.23 ^{ab}	24.98 ^a	34.46 ^b	29.32 ^{ab}	28.77 ^{ab}	*
Total:		91.97	92.67	91.78	94.10	90.38	

Notes: ¹ Retention indices; ² control sample; ³ the level of significance: ns = not significant, * = significance level at 5%, ** = significance level at 1%; Values designated by the different letters are significantly different.

3.3. Total Phenolic Content

The effect of treatments on the total phenolic content (TPC) of the four species is demonstrated in the bar graph below (Figure 3). TPC is expressed by mg GAE/g d.w. of the. After the treatments, significant differences were observed. The TPC of marjoram ranged between 200 and 360 mg GAE/g d.w., the lowest one with foliar application of 2 mM of MeJa and the highest one with 0.1 mM of SA. This latter treatment increased the TPC by approximately 36% compared to the control. Various studies have mentioned the elicitation effect of MeJa and JA in enhancing bioactive compounds including phenolic compounds and flavonoids in different plant species, such as butter lettuce (*Lactuca sativa* L.), melon (*Cucumis melo*), and Saint John's wort (*Hypericum perforatum*), whether applied in vivo or in vitro [41–43]. However, Zlotek observed the failure of MeJa to change the TPC especially in marjoram [44]. In our study, the 0.1 mM and 2 mM of MeJa decreased the content by approximately 27% and 31%, respectively.

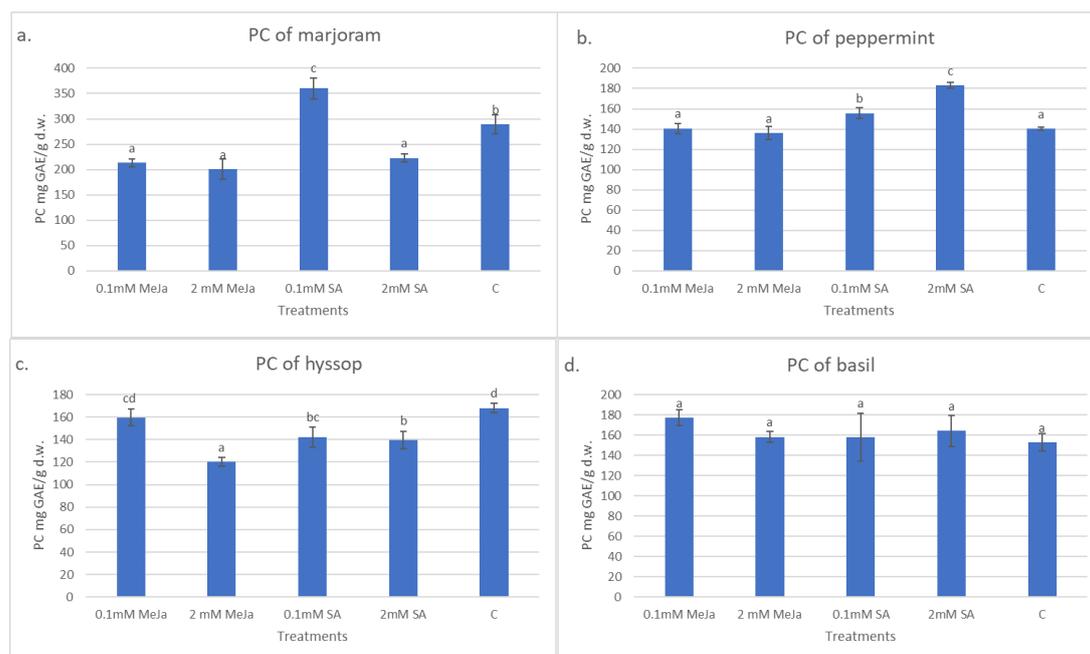


Figure 3. The effect of MeJa and SA on TPC of the subject species; (a) marjoram, (b) peppermint, (c) hyssop, and (d) basil; Data are expressed as means \pm SD; means with different letters are significantly different ($p < 0.05$).

In the case of peppermint, both SA dosages elevated the TPC, while treatment with MeJa did not result in any significant changes. The effect of SA on the phenolic accumulation in peppermint was also previously observed, where increasing the TPC by 65% and 31% was reached after treatment with the dosages of 0.5 and 2 mM, respectively [45].

As for hyssop and basil, the applied elicitors had contradictory results. All the treatments decreased the TPC in hyssop significantly, and the sample treated with 2 mM of MeJa was lower than the control by 28%. However, in basil, the treatments increased the TPC and the concentration 0.1 mM of MeJa was the most effective. The latter findings are partly in agreement with Kim et al. [46] where the 0.1 mM of MeJa could not increase the TPC in basil, but a higher dosage (0.5 mM of MeJa) was effective.

3.4. Antioxidant Capacity

The effect of treatments on the AC of the four species (expressed by mg AAE/g d.w.) is demonstrated in Figure 4. The results closely correlate with the TPC data in all species and for all treatments. For both marjoram and hyssop, the treatments decreased the AC except for the lower dosage of SA treatment in marjoram, which showed a 50% stronger activity than the control. In hyssop, each treatment decreased the AC except for the lower dosage of MeJa. This is in contradiction to several reports about the effect of MeJa in elevating the AC; not only in healthy plants but also in plants subjected to water deficit stress, where this phytohormone presumably enhances the protection mechanisms [42,47,48].

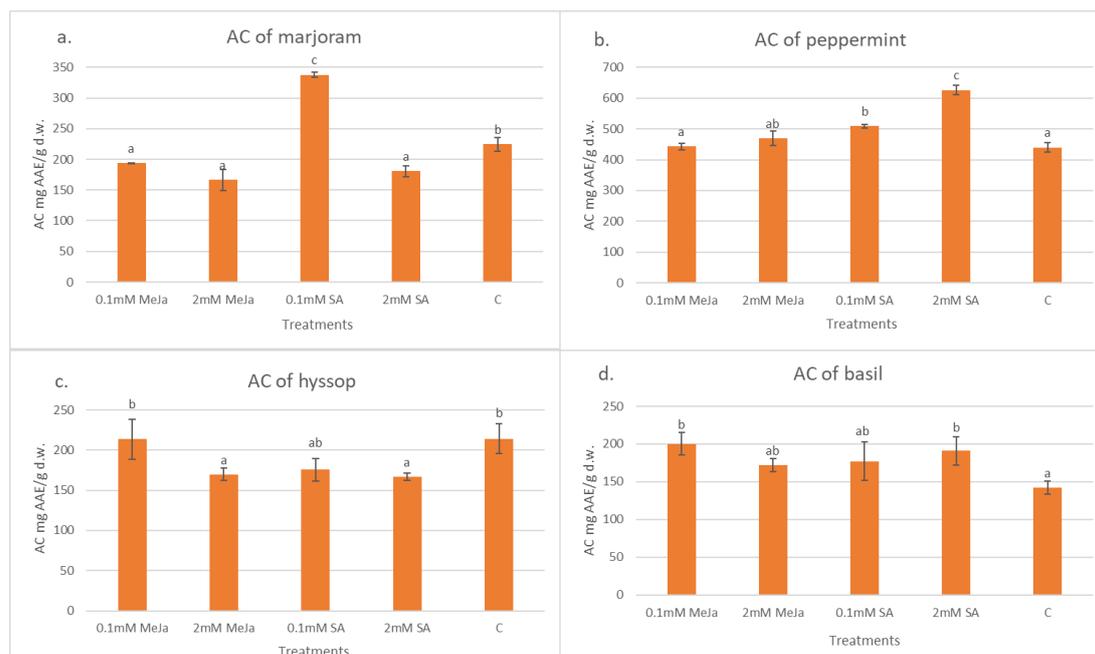


Figure 4. The effect of MeJa and SA on the antioxidant activity of the subject species; (a) marjoram, (b) peppermint, (c) hyssop, and (d) basil; Data are expressed as means \pm SD; means with different letters are significantly different ($p < 0.05$).

Similarly, to these publications, in the case of peppermint, both dosages of SA were able to increase the AC in our experiment also, where the 2 mM dosage resulted in the highest activity. This result is similar to that of Figueroa Pérez et al. [45] where different dosages of SA ranging between 0.5 and 2 mM increased the AC. As for MeJa treatments, no significant differences were registered.

SA is a plant hormone that plays a pivotal role in regulating physiological and biosynthetic processes. If applied exogenously, SA triggers a hypersensitive response by causing a temporary increase of reactive oxygen species (ROS) followed by phenolic compounds, biosynthesis and elevated antioxidant activity [49,50]. It was found that MeJa is effective

only in basil for stimulating the accumulation of phenolic compounds and increasing AC. A considerable amount of literature supports the contribution of polyphenols in lowering the risk of health disorders, such as cancer, cardiovascular diseases, chronic inflammations, degenerative diseases, and diabetes. This is because of their strong antioxidant activity and ability to scavenge free radicals, thus reducing oxidative damage [51,52].

For basil, all treatments increased the AC but only 0.1 mM of MeJa and 2 mM of SA were significant, where they raised AC by 40% and 35%, respectively. The results of Wang et al. [53] and Blanch et al. [54] support these findings, as they found that both SA and MeJa increased the AC in blackberries (*Rubus* sp.) and table grapes (*Vitis vinifera*).

4. Conclusions

The elicitors MeJa, and SA used in this research showed specific responses in each plant species, depending on the dosage applied and the parameter studied.

SA stimulated the EO accumulation in three model species. However, MeJa proved to be effective only in marjoram where the higher concentration significantly elevated the volatile production. In the case of basil, both elicitors induced contrasting reactions—the volatile accumulation was stopped and the EO content decreased.

SA also demonstrated a higher efficacy in altering the quantitative spectrum of the Eos of marjoram, peppermint and hyssop. While no significant change of the major components of basil EO was detected in consequence of SA and MeJa treatments. It may be of practical importance too, that some treatments—primarily those using SA—were able also to shift the ratios of total mono and sesquiterpenes significantly in all the species except peppermint.

Moreover, our results confirmed several earlier publications about the strong connection between the TPC and antioxidant activity. SA was successful in increasing these two parameters in all of the experimental species except hyssop.

The experiments demonstrated that elicitation is a potentially effective tool for influencing both the accumulation level and the quantitative spectrum of the volatiles. Besides, TPC and AC can be changed by means of well-established treatments. At the same time, it was found that the subject *Lamiaceae* species show different sensitivity to the applied concentrations of MeJa and SA. Concerning the EO content and composition, under the experimental conditions, marjoram showed the strongest reactions while basil was the least sensitive. In the context of phenolics and AC, however, basil showed higher sensitivity and more reactions and hyssop was less influenced. We were able to establish that elicitation *in vivo* is a gentle tool in influencing the accumulation of SMs in medicinal plants; however, the result is dependent not only on the elicitor compound and its concentrations but also on the target species and the type of accumulated molecules. Based on the presented first results, optimization of the treatments is suggested in further *in vivo* experiments.

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