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Assessment of *McTPS2* Gene Expression in German Chamomile (*Matricaria chamomilla* L.) under the Influence of Abiotic Elicitors

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ABSTRACT

German chamomile (*Matricaria chamomilla* L.) is one of the most significant medicinal plants globally, known for its extensive therapeutic applications. Terpenoids, the largest group of secondary metabolites in plants, are synthesized through pathways catalyzed by terpene synthase (TPS), a key enzyme. Elicitors, both biotic and abiotic, play a pivotal role in stimulating physiological responses and enhancing the expression of genes involved in secondary metabolite production. This study investigates the expression of the *McTPS2* gene in German chamomile under the influence of different concentrations of salicylic acid (0, 250, 500, 1000, and 1500 µM), methyl jasmonate, and jasmonic acid (0, 50, 100, and 150 µM) at various time intervals (0, 4, 8, 24, 48, and 72 hours post-treatment). This study was conducted in the central laboratory of the Agriculture Faculty of Yasouj University. The elicitors were applied via foliar spraying during the sixth, eighth, and tenth weeks after planting. Leaf samples were collected weekly during late vegetative growth, 48 hours after treatment. Following RNA extraction and cDNA synthesis, *McTPS2* gene expression was analyzed using semi-quantitative PCR. The results revealed significant changes in *McTPS2* expression in response to elicitor treatments. The highest expression levels were observed with 150 µM methyl jasmonate, 100 µM jasmonic acid, and 1000 µM salicylic acid. Notably, *McTPS2* expression peaked at 8 and 24 hours post-treatment with methyl jasmonate and 8 hours with jasmonic acid. However, expression levels subsequently declined to control levels at other time points (4, 48, and 72 hours). These findings demonstrate that all tested elicitors effectively enhanced *McTPS2* gene expression and could be utilized to boost secondary metabolite production in German chamomile.

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1. Introduction

Elicitors are materials originating from abiotic or biotic sources that stimulate stress responses in plants, leading to increased synthesis and accumulation of secondary metabolites or the biosynthesis of novel ones. The type of elicitor, its concentration, and the method of application are key factors that influence the effectiveness of elicitor-induced secondary metabolite production (Naik and Al-Khayri, 2016). On the basis of nature, elicitors can be divided into two types: abiotic and biotic. Abiotic elicitors comprise substances that are of nonbiological origin and are grouped in physical, chemical, and hormonal factors. Biotic elicitors are the substances of biological origin that include polysaccharides originated from plant cell walls (e.g., chitin, pectin, and cellulose) and microorganisms (Naik and Al-Khayri, 2016). Jasmonates and methyl jasmonate (methyl ester of jasmonate) are endogenous plant hormones that are synthesized through the octadecanoid biosynthetic pathway, and in this biosynthetic pathway, linolenic acid is converted to jasmonic acid. (Schaller, 2001).

German chamomile has diploid (2n=2x=18) and tetraploid (2n=4x=36) varieties. Diploid varieties have shorter growth and lower plant height than tetraploid varieties, and the tetraploid types have the highest secondary metabolites (Chauhan *et al*., 2021). The most important compounds in the essential oil of chamomile flowers are flavonoids and coumarins (El Mihyaoui *et al*., 2022). An important and valuable

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component of chamomile essential oil is chamazulene, which is formed from a precursor called matricin (prochamazulene) (Sah *et al*., 2022). Alphabiosabol is one of the most important medicinal components in German chamomile, which is a sesquiterpene (Zhu *et al*., 2015). Terpenes are classified based on the number of 5-carbon units. Ten-carbon terpenes that contain two isoprene units are called monoterpenes. Monoterpene derivatives include limonene, camphor, linalool, and geraniol (Masyita *et al*., 2022). In plants, the methyl-erythritol phosphate (MEP) pathway in the plastids and the mevalonate (MVA) pathway in the cytosol are the locations of the biosynthesis of terpenes, producing the precursors of terpenes, isopentyl diphosphate and dimethylallyl diphosphate (Fig. 1) (Wang *et al*., 2018). The MVA pathway is mediated by the conversion of acetyl-coenzyme A to 3-hydroxy-3-methylglutaryl-coenzyme A by the HMGR gene (Van Klink *et al*., 2003). The *McTPS2* is an important gene in terpene synthase (TPS) family, and its product may be a key enzyme in the synthesis of alpha-bisabolol in German chamomile (Zhu *et al*., 2015).

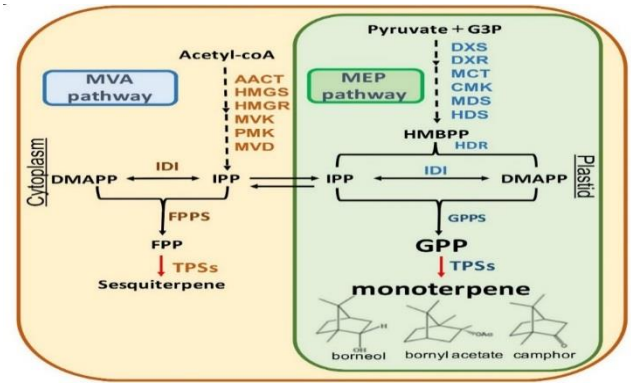


Figure 1. Monoterpene and sesquiterpene biosynthesis pathway (A) and the structures of the monoterpenes in A. villosum (B). AACT, acetoacetyl-CoA thiolase; HMGS, 3-hydroxy-3 methyl glutaryl coenzyme A synthase; HMGR, 3-hydroxy-3-methyl glutaryl coenzyme A reductase; MVK, mevalonate kinase; PMK, 5-phosphomevalonate kinase; MVD, mevalonate diphosphate decarboxylase; IDI, isopentenyl diphosphate isomerase; FPPS, farnesyl diphosphate synthase; TPS, terpene synthase; DXS, 1-deoxy-D-xylulose-5-phosphate synthase; DXR, 1-deoxy-D-xylulose-5-phosphate reductoisomerase; MCT, 2-C-methyl-Derythritol-4- (cytidyl-5-diphosphate) transferase; CMK, 4-(cytidine 5′-diphospho)-2-Cmethyl-D-erythritol kinase; MDS, 2-C-methyl-D-erythritol 2,4-cyclodiphosphate synthase; HDS, 1-hydroxy-2-methyl-2-(E)-butenyl-4-diphosphate synthase; HDR, 1-hydroxy-2-methyl-2-(E)-butenyl-4-diphosphate reductase; GPPS, geranyl diphosphate synthase (Wang *et al*., 2018).

Kianersi et al. (2023) showed that the different MeJA dosages considerably increased the rosmarinic acid, total phenolic contents (TPC), and total flavonoid phenolic contents (TFC) in both species of *Salvia* subg. *Perovskia* Kar L. compared with the control treatment. The number of transcripts for PAL (phenylalanine ammonia lyase), 4CL (4-coumarate-CoA ligase), and RAS (rosmarinic acid) synthase increased; therefore, the effects of MeJA are probably caused by activating of genes in the phenylpropanoid pathway.

Furthermore, 100 M MeJA concentration caused an increase in the relative expression of *TPS2* (beta-terpinene synthase) and *CYP71D178* genes in *Thymus migricus* 7.47 and 9.86-fold compared with the control, respectively. This research showed that different concentrations of MeJA influenced metabolic pathways and, by inducing expression changes, caused rising essential oil production (Kianersi *et al*., 2021). In another research, gene expression assessment under methyl jasmonate treatment showed that both *DXS* and *TcGLIP* genes were up-regulated in response to this elicitor. This research showed that using methyl jasmonate in seedling stage could be used as a proper elicitor to increase pyrethrin production (Dabiri *et al*., 2017). Su et al. (2015) showed that using methyl jasmonate for eliciting *M. recutita* significantly increased the transcriptional level of (E)-β-farnesene (*βFS*) gene and the content of (E)-β-farnesene. The transcriptional level of *βFS* gene was approximately 11.5-fold higher than the control treatment and the (E)-β-farnesene emission level ranged approximately from 0.082 to 0.695 μg g^{-1} after 24 h treatment. Another suitable abiotic elicitor is salicylic acid. In research, the expression of 1-deoxy-dxylulose-5-phosphate reductoisomerase (*DXR*) and gamma-terpinene synthase (*GTS*) genes under the effect of salicylic acid, methyl jasmonate and UV-B rays was assessed. This research showed that the expression of those genes exhibited significant alterations in treatment by the above elicitors (Ghobadi *et al*., 2017).

This study aimed to evaluate the changes in *McTPS2* gene expression in German chamomile in response to three types of abiotic elicitors—salicylic acid, methyl jasmonate, and jasmonic acid. By obtaining initial information on their effects, these elicitors could potentially be used to enhance the production of secondary metabolites in chamomile. While previous research has typically examined the effect of a single elicitor on gene expression, the simultaneous comparison of the three abiotic elicitors in this study represents a novel approach. Additionally, analyzing the impact of these elicitors on *McTPS2* gene expression at different time points after treatment and

identifying the most effective elicitor and optimal treatment time are unique aspects of this research. To date, the comparative effects of these three abiotic elicitors on gene expression have not been explored, making this investigation one of the study's key innovations.

2. Materials and methods

2.1. Design of specific primers

Based on the sequence of the *McTPS2* gene (accession number I6R4V5.1) that was presented by Zhu et al. (2015), specific primers were designed using Primer3 software and their annealing temperature and other properties were calculated using the online program Oligo Calc. To study the relative expression of the target gene, the reference gene (housekeeper) glyceraldehyde phosphate dehydrogenase (GAPDH) was used. The designed primers (R-GAPDH and F-GAPDH) are presented in Table 1.

Table 1. Characteristics of the used primers

Primer name	Primer sequence (5`→3`)	Fragment length (bp)
McMCTPS2-F	AAGGTTACACAGGCACGAGG	652
McMCTPS2-R	TGCATCACCCATAGCAGCAA	652
GAPDH-F	AGCACAGCGACATCACACTC	197
GAPDH-R	AACAACCTTCTTGGCACCAC	197

2.2. Treatment of plant samples with salicylic acid, methyl jasmonate and jasmonic acid

Plant samples were treated with salicylic acid, methyl jasmonate and jasmonic acid (Sigma Aldrich, Kohan chemistry, Tehran). German chamomile seeds obtained from "Pakan Bazr Company" in Isfahan were cultivated in the growth chamber (temperatures of day and night 25 and 18 Celsius, respectively; and a photoperiod of 16 hours of light and 8 hours of darkness) after surface disinfection with sodium hypochlorite. Salicylic acid (0, 250, 500, 1000 and 1500 µM), methyl jasmonate and jasmonic acid (0, 50, 100 and 150 µM) were sprayed on German chamomile leaves at 6, 8 and 10 weeks after planting. Samples were taken from the control and treated leaves of all three replicates before treatment and at times 0, 4, 8, 24, 48 and 72 hours after treatment.

2.3. RNA extraction from leaf tissue and cDNA synthesis

RNA extraction from control and treated leaf tissue was performed using Trizol solution. After confirming the presence of RNA using 1% agarose gel and staining with ethidium bromide, the concentration of RNA was determined with a spectrophotometer and the extracted RNAs were concentrated to make cDNA. cDNA synthesis was performed using a kit from Yekta Tajhiz Azma Company and in accordance with the manufacturer's instructions. To examine the semi-quantitative expression of the *McTPS2* gene, semi-quantitative RT-PCR was performed with three replicates and according to Tables 2-4.

Table 2. The composition of the materials used in PCR reaction

Materials	Used volume (µL)	Concentration in stock solution (pM)
H_2O	5	-
Forward primer	2.5	10
Reverse primer	2.5	10
Master mix	11	-
cDNA	4	-
Total volume	25	

Table 3. Thermal cycle of PCR reaction of *MCTPS2* gene

Cycle No.	Step	Temperature (ºC)	Time (s)
1	First denaturation	94	180
	Denaturation	95	60
32	Annealing	62	30
	Extension	72	60
1	Final extension	72	600

Table 4. Thermal cycle of PCR reaction of *GADPH* gene

Cycle No.	Step	Temperature (ºC)	Time (s)
1	First denaturation	94	600
	Denaturation	95	15
40	Annealing	60.5	60
	Extension	72	60
1	Final extension	72	600

2.4. Statistical analysis

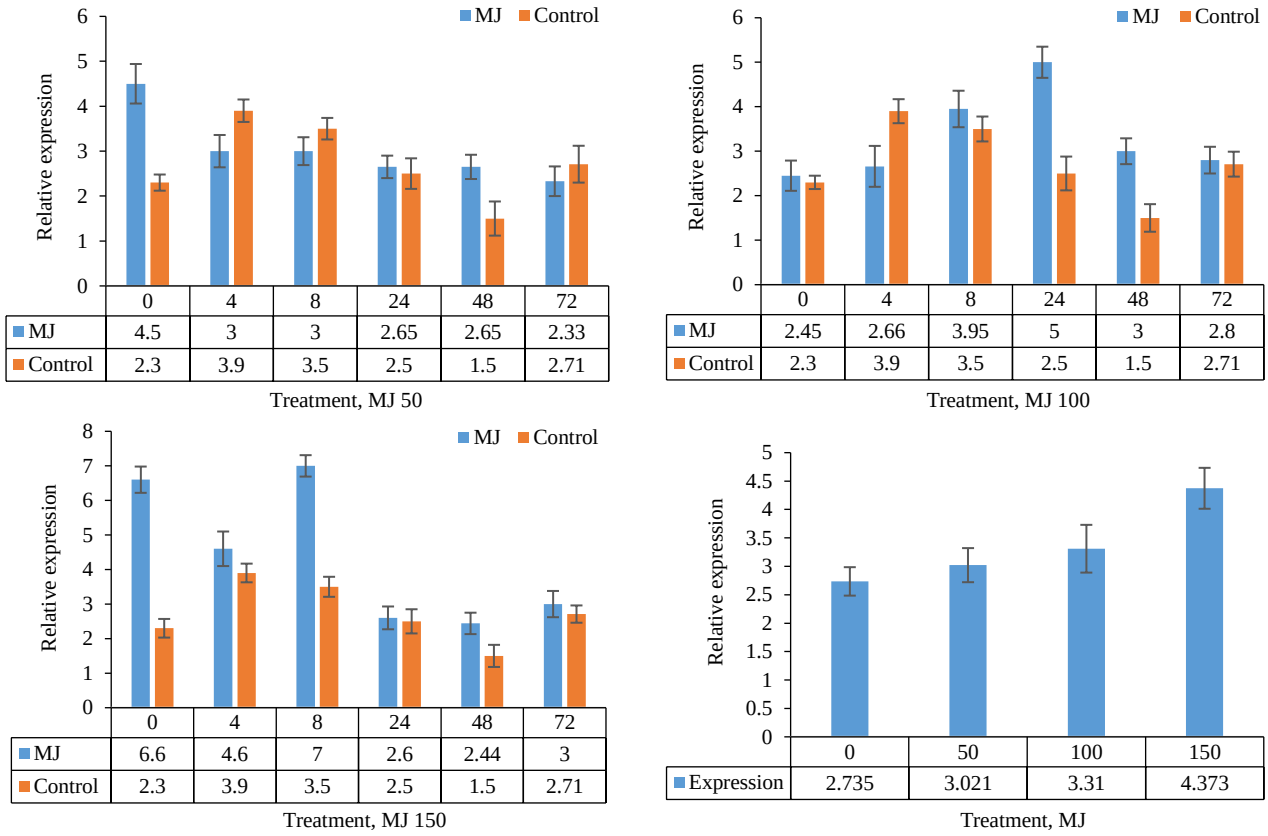
Using GelQuantNET software, gel images were converted to quantitative data. The experiments were analyzed based on a completely randomized design with three replicates. Comparison of data means was performed using the LSD test at a probability level of 5% using SAS software.

3. Results and discussion

RNA extraction was performed from leaf tissue of German chamomile medicinal plant, which used 1% agarose gel and reading of optical absorption by spectrophotometry showed that it had good quantity and quality, such that the ratio of wavelengths 260 to 280 nm in the samples was between 1.8 to 2.

3.1. Methyl jasmonate

The results of assessing *McTPS2* gene expression in German chamomile leaves treated with various concentrations of methyl jasmonate revealed that the gene's expression was significantly influenced by the elicitor's concentration. At a concentration of 50 µM methyl jasmonate, gene expression initially decreased during the early hours after treatment but showed an increase above control levels 48 hours post-treatment. At 100 µM methyl jasmonate, gene expression began to rise 4 hours after treatment, with higher expression levels observed at 8 and 48 hours compared to the control. The highest expression level was recorded 24 hours post-treatment. By 72 hours, the gene expression in treated plants returned to levels comparable to the control (Fig. 2). At a concentration of 150 µM methyl jasmonate, the highest gene expression was observed 8 hours after spraying, followed by a decline. These findings indicate that methyl jasmonate induces a gradual and then rapid effect on *McTPS2* gene expression. Among all tested concentrations, 150 µM had the most pronounced effect on enhancing *McTPS2* expression, with a significant difference compared to the control, while 50 µM exhibited the least impact (Fig. 2).



	0	4	8	24	48	72
MJ	4.5	3	3	2.65	2.65	2.33
Control	2.3	3.9	3.5	2.5	1.5	2.71

	0	4	8	24	48	72
MJ	2.45	2.66	3.95	5	3	2.8
Control	2.3	3.9	3.5	2.5	1.5	2.71

	0	4	8	24	48	72
MJ	6.6	4.6	7	2.6	2.44	3
Control	2.3	3.9	3.5	2.5	1.5	2.71

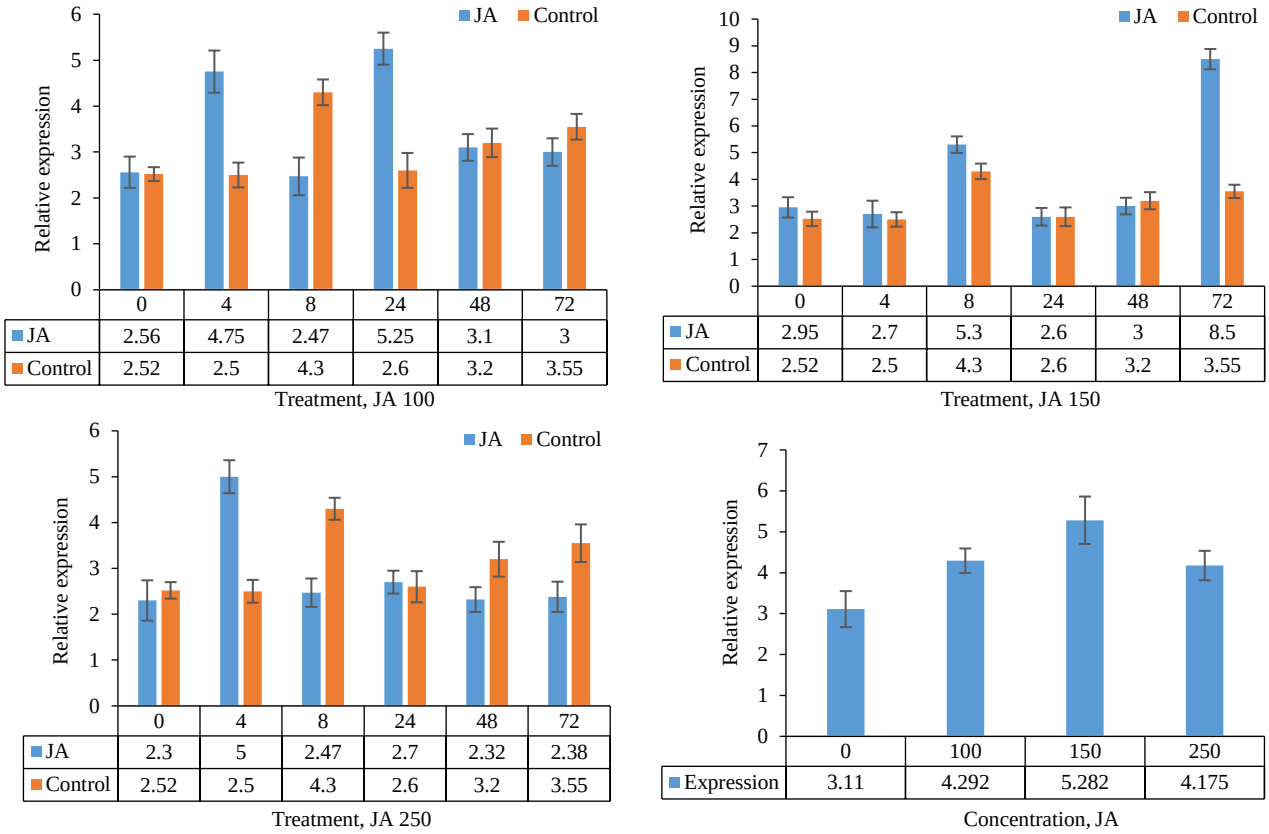
	0	50	100	150
Expression	2.735	3.021	3.31	4.373

Figure 2. Relative expression of *McTPS2* gene treated with 50, 100 and 150 µM concentrations of methyl jasmonate and comparison of the relative expression of *McTPS2* gene in different concentrations of methyl jasmonate

3.2. Jasmonic acid

The treatment of German chamomile leaves with various concentrations of jasmonic acid significantly affected the relative expression of the *McTPS2* gene. Gene expression increased in all treatments during the early hours post-application. At 100 µM, the highest expression was observed 24 hours after spraying, followed by a decline. With 150 µM, expression increased at 8 hours, decreased at 24 hours, then peaked at 72 hours before declining again. At 250 µM, expression increased at 4 hours after spraying. Among the tested concentrations, 100 µM jasmonic acid had the most pronounced effect on *McTPS2* gene expression, showing a statistically significant difference compared to the control.

The results indicate that low concentrations of jasmonic acid (≤100 µM) effectively enhance *McTPS2* gene expression in German chamomile. However, at higher concentrations (150 µM), jasmonic acid appears to lose its eliciting properties and may act as an inhibitor, impeding the gene expression enhancement process (Fig. 3).



	0	4	8	24	48	72
JA	2.56	4.75	2.47	5.25	3.1	3
Control	2.52	2.5	4.3	2.6	3.2	3.55

	0	4	8	24	48	72
JA	2.95	2.7	5.3	2.6	3	8.5
Control	2.52	2.5	4.3	2.6	3.2	3.55

	0	4	8	24	48	72
JA	2.3	5	2.47	2.7	2.32	2.38
Control	2.52	2.5	4.3	2.6	3.2	3.55

	0	100	150	250
Expression	3.11	4.292	5.282	4.175

Figure 3. Relative expression of *McTPS2* gene treated with 100, 150 and 250 µM concentrations of Jasmonic acid and comparison of the relative expression of *McTPS2* gene in different concentrations of Jasmonic acid

3.3. Salicylic acid

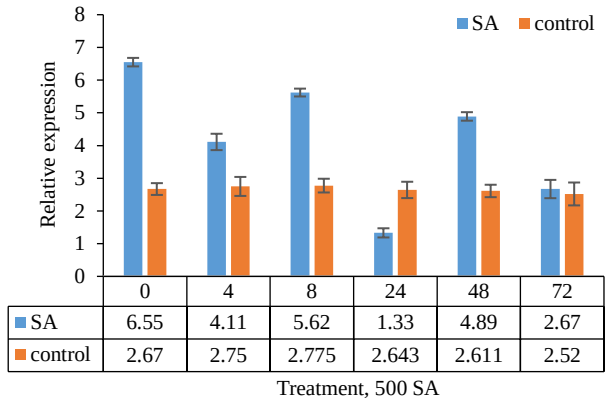
The results of this study showed that the expression of *McTPS2* gene was affected by treatment with salicylic acid. The highest level of this gene expression was observed at a concentration of 250 µM at 48 hours, at a concentration of 500 µM at time zero, and at concentrations of 1000 and 1500 µM at 24 hours after spraying. The level of expression of this gene at concentrations of 250 and 1000 µM increased in the early hours after treatment. The concentration of 1000 µM salicylic acid had the greatest effect on increasing expression 24 hours after treatment, and the lowest effect was observed at a concentration of 500 µM at the same time. According to the obtained results, with increasing concentration of salicylic acid, the gene expression improves and the concentration of 1000 µM has a greater effect on this gene expression. The results showed that the increase in gene expression from 250 to 1000 µM concentration of salicylic acid has an increasing trend and reaches its peak at a concentration of 1000 µM and then at a concentration of 1500 µM, the expression level of this gene decreases. These results indicate that salicylic acid has a stimulating effect on the plant up to a concentration of 1000 µM and has increased the expression level of the gene, but at a concentration of 1500 µM the role of stimulation changes to inhibition and causes a decreasing trend in expression (Fig. 4). These findings suggest a concentration-dependent response of the *McTPS2* gene to jasmonic acid treatment in German chamomile, with optimal effects observed at moderate concentrations.

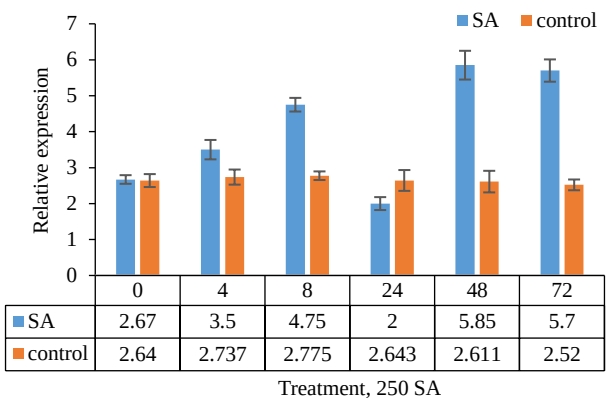
Various elicitors such as chitosan, beta-glucan, yeast extract and chemical elicitors such as methyl jasmonate and salicylic acid have been reported to induce the secondary restresses creation in plants (Davis and Croteau, 2000). Salicylic acid and methyl jasmonate are two examples of harmless natural elicitors that act as compounds that stimulate the production of secondary metabolites by inducing pseudo-stress (Wang *et al*., 2009; Divya *et al*., 2014). In this study, an assessment of the effects of chemical elicitors on the expression of the studied gene showed that the highest increase in *McTPS2* gene expression was at concentrations of 1000 µM salicylic acid, 100 µM jasmonic acid, and 150 µM methyl jasmonate. Elicitors, as stimulators and inducers, increase gene expression and the production of proteins involved in the production of secondary metabolites. In a study on

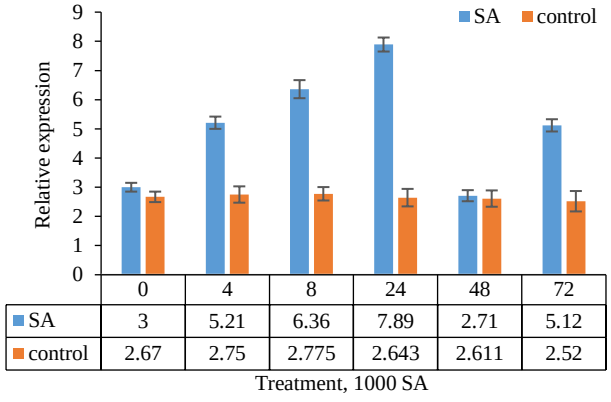
Datura stramonium L., methyl jasmonate as a chemical elicitor was effective in increasing the gene encoding the tropinone reductase I enzyme, and the increase in gene expression was confirmed in samples treated with methyl jasmonate (Rasi *et al*., 2024).

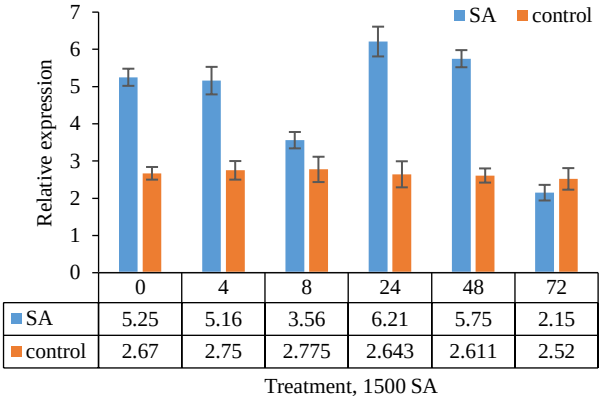
In basil, abiotic elicitors such as methyl jasmonate, methyl salicylate, and chitosan increased the gene expression of O-methyltransferase enzymes such as *CVOMT* (Deschamps *et al*., 2008; Rashidi *et al*., 2020). The effect of different concentrations of salicylic acid (0, 0.01, and 0.1 mM) as a messenger molecule on the expression of *H6H* and *PMT* genes in hairy roots and seedlings of Shabizak was also investigated. The expression of *H6H* gene and *PMT2* isoform increased in hairy roots of Shabizak at concentration of 0.01 mM salicylic acid. The expression of *PMT2* isoform also increased in plant roots at a concentration of 0.01 mM (Moradi *et al*., 2011).

The effect of salicylic acid and methyl jasmonate elicitors on the enzyme phenylalanine ammonia-lyase (PAL) in artichoke callus was also studied, and the results showed that the PAL enzyme production was affected by the treatments applied (Samadi *et al*., 2015). In the other study, it was found that a concentration of 50 mg L^{-1} salicylic acid in fenugreek cell culture increased the production of trigonelline by two times compared to the control (Esmaeilzadeh Bahabadi and Rezaei, 2013). The results of the present study are often consistent with the results of above researchers.









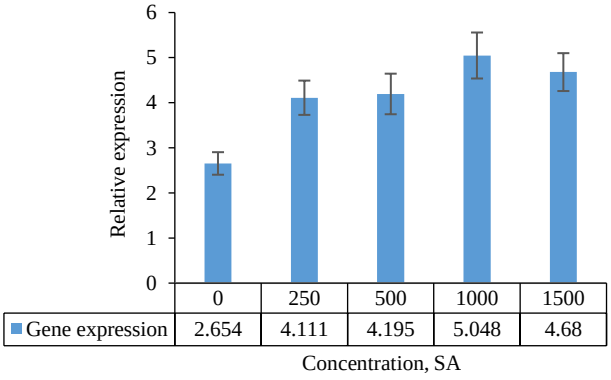


Figure 4. Relative expression of *McTPS2* gene treated with 0, 250, 500, 1000 and 1500 µM concentrations of salicylic acid and comparison the relative expression of *McTPS2* gene in different concentrations of salicylic acid

The expression level of three MEP pathway genes in the medicinal plant Ajwain increased after 24 hours of methyl jasmonate treatment. The increased expression of the mentioned genes could be a factor in the high production of α-terpinene content in the essential oil of the flowers. Methyl jasmonate increases the production of monoterpenes by stimulating the biosynthesis pathway of secondary compounds and also by affecting the expression level of genes (Sadat Noori *et al*., 2019). Elyasi et al. (2015) assessed the expression levels of genes involved in the biosynthetic pathway of monoterpenes and triterpenes in the medicinal plant *Nigella sativa* under the influence of salicylic acid elicitor. The results showed that the expression of monoterpene synthase, geranyl diphosphate synthase, beta-amyrin synthase, and squalene epoxidase genes in leaves treated with salicylic acid differed from control. In the present study, the increased expression of the *McTPS2* gene after treatment with Jasmonic acid, Methyl Jasmonate and salicylic acid was observed and it is expected that this will lead to an increase in the level of secondary metabolites in chamomile.

4. Conclusion

In conclusion, this study demonstrates that *McTPS2* gene expression in German chamomile is significantly influenced by abiotic elicitors, with methyl jasmonate, jasmonic acid, and salicylic acid all showing potential for enhancing expression levels. Optimal concentrations and application times vary for each elicitor, with 150 µM methyl jasmonate, 100 µM jasmonic acid, and 1000 µM salicylic acid proving most effective. These findings provide valuable insights for optimizing elicitor use to boost secondary metabolite production in German chamomile. Unfortunately, due to time and funding restrictions, we could not use GC or TLC for assessing terpene production content in this research, but we propose that future researchers do this complementary test.

Conflict of interests

All authors declare no conflict of interest.

Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

Consent for publications

All authors read the final manuscript and approved it for publication.

Availability of data and material

The authors declare that they embedded all data in the manuscript.

Authors' contributions

Asad Masoumiasl: designing the idea, analyzing and writing the article. Zohreh Chahabkari: doing, analyzing and writing the article.

Informed consent

The authors declare not to use any patients in this research.

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