International Journal of Advanced Biochemistry Research

ISSN Print: 2617-4693
ISSN Online: 2617-4707
NAAS Rating: 5.29
IJABR 2025; 9(7): 763-775
www.biochemjournal.com
Received: 13-04-2025
Accepted: 16-05-2025

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Jasmonic acid as a metabolic switch for eugenol biosynthesis and floral volatile enhancement in *Ocimum basilicum*

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DOI: https://www.doi.org/10.33545/26174693.2025.v9.i7j.4836

Abstract
The present investigation elucidates the modulatory influence of exogenous jasmonic acid (JA) on the essential oil content and compositional dynamics of *Ocimum basilicum* L. (sweet basil) across critical ontogenetic stages—35, 50, and 65 days after sowing (DAS). Foliar treatments included JA at concentrations of 0.3 mM (JA 1), 0.6 mM (JA 2), and 0.9 mM (JA 3), alongside a control (2% ethanol in double-distilled water). At the highest tested concentration (0.9 mM; JA 3), markedly augmented the essential oil yield in both foliar and floral tissues, with maximum enhancement recorded in leaf tissues at 50 DAS and floral tissues at 65 DAS. Gas chromatography-mass spectrometry (GC-MS) profiling revealed a distinct dose- and stage-responsive upregulation in key phenylpropanoid constituents, notably eugenol and methyl eugenol. JA 3-treated leaves exhibited a striking enrichment of eugenol (22.57%) and methyl eugenol (7.21%) at 50 DAS, underscoring the pivotal role of JA in potentiating phenylpropanoid pathway flux. Simultaneously, monoterpenes such as thujene exhibited a marked decline under JA elicitation, suggesting a metabolic reallocation favouring specialized phenolic biosynthesis. The floral essential oil profile mirrored this trend, albeit with differential compound dominance and dose sensitivity, affirming a tissue-specific regulatory mechanism. Collectively, these findings substantiate the role of jasmonic acid as a potent biochemical elicitor, capable of enhancing both the quantitative and qualitative attributes of essential oil biosynthesis in sweet basil through transcriptional and metabolic reprogramming aligned with developmental cues.

Keywords: Sweet basil, jasmonic acid, essential oil, GC-MS, growth stages

1. Introduction
The genus *Ocimum*, a prominent representative of the tribe Ocimeae within the subfamily Nepetoideae (order Lamiales, family Lamiaceae), encompasses over 150 species widely distributed across tropical and subtropical regions (Nguyen *et al*., 2021) [21]. Among these, *Ocimum basilicum* L. (sweet basil) is a globally cultivated aromatic and medicinal herb recognized for its rich repository of bioactive compounds and multifaceted utility in culinary, pharmaceutical, and industrial domains (Ilic *et al*., 2019) [7]. Characterized as a tetraploid (2n=48), sweet basil thrives in diverse agro-climatic conditions and is extensively cultivated in countries such as France, Italy, Egypt, and India—with Uttar Pradesh emerging as a major production hub due to its favourable edaphic and climatic conditions (Gingade *et al*., 2014) [6].

Sweet basil's economic and therapeutic significance is largely attributed to its essential oils, concentrated in glandular trichomes on aerial tissues, predominantly leaves and flowers. These volatile oils are enriched with terpenoids and phenylpropanoids—most notably eugenol, methyl eugenol, estragole, and linalool—endowing the plant with antimicrobial, antioxidant, and anti-inflammatory activities (Labra *et al*., 2004; Simon, 1985) [10, 19]. Notably, the composition and yield of essential oils are subject to substantial modulation by genetic, developmental, and environmental cues, thereby necessitating strategies to enhance both quantitative and qualitative phytochemical traits in basil.

Among elicitation strategies, jasmonic acid (JA) and its derivatives—key oxylipin-based phytohormones derived from α-linolenic acid—have emerged as potent modulators of secondary metabolism in medicinal plants (Sohn *et al*., 2022; Miclea *et al*., 2020) [20, 13].

JA not only orchestrates plant defense signaling and developmental processes but also activates genes involved in specialized metabolite biosynthesis, including phenylpropanoids and terpenoids (Kim *et al*., 2006; Kianersi *et al*., 2022) [9, 8]. Previous studies have demonstrated that exogenous JA application enhances essential oil content, antioxidant capacity, and accumulation of phenolics and flavonoids in *O. basilicum*, primarily by upregulating the phenylpropanoid pathway (Zlotek *et al*., 2016; Malekpoor *et al*., 2016) [22, 12].

Despite the increasing scientific attention toward jasmonate-elicited enhancement of phytochemicals, limited data exist regarding the dynamic responses of sweet basil to varying concentrations of JA across different growth stages, particularly in relation to essential oil biosynthesis. Understanding the developmental window and optimal JA concentration for maximal secondary metabolite induction remains critical for improving basil's essential oil yield under field conditions.

Therefore, the present study was undertaken with the objectives; to evaluate the effect of varying concentrations of jasmonic acid (0.3 mM, 0.6 mM, and 0.9 mM) essential oil accumulation in sweet basil leaves and flowers at distinct growth stages (35, 50, and 65 DAS) and to assess the compositional variation of essential oils via GC-MS profiling, This approach aims to delineate the elicitor-induced modulation of secondary metabolism in sweet basil and optimize agronomic practices for quality-oriented cultivation.

2. Material and Methodology

2.1Experimental Site and Plant Material

The field experiment was conducted during the *kharif* season of 2023-24 at two locations within the Anand Agricultural University (AAU), Gujarat, India: the Medicinal and Aromatic Plants Research Station and the Department of Biochemistry, B. A. College of Agriculture. The experimental cultivar used was *Ocimum basilicum* L. 'Gujarat Anand Basil-1' (GAB-1), a regionally adapted genotype known for high essential oil content.

2.2 Experimental Design and Treatments

The study was laid out in a Randomized Block Design (RBD) with five replications and four treatments:

- **T_0 (Control):** 2% ethanol (no jasmonic acid)
- **T_1 (JA1):** 0.3 mM jasmonic acid
- **T_2 (JA2):** 0.6 mM jasmonic acid
- **T_3 (JA3):** 0.9 mM jasmonic acid

Each plot measured 3.0 × 2.25 m² with a spacing of 60 × 45 cm² between plants. Observations were recorded at three distinct growth stages: 35 DAS (vegetative stage), 50 DAS (pre-flowering stage), and 65 DAS (full flowering stage).

Fig 1: Image of sweet basil plant

Fig 2: Foliar application of jasmonnic acid on sweet basil plant (20 DAT)

2.3 Preparation and Application of Jasmonic Acid Solutions

Jasmonic acid (JA) solutions were prepared by first dissolving the required quantity of JA in 2% ethanol, due to its limited water solubility. The final concentrations were diluted with double-distilled water to obtain 0.3, 0.6, and 0.9 mM working solutions for JA1, JA2, and JA3, respectively. Ethanol at 2% concentration ensured effective foliar penetration without phytotoxic effects, as supported by earlier reports (Zlotek *et al*., 2016; Malekpoor *et al*., 2015) [22, 11]. At 20 days after transplanting, plants were sprayed with the JA treatments until runoff using a hand-held sprayer, whereas control plants received only 2% ethanol solution.

2.4 Essential Oil Extraction from Leaves and Flowers

Fresh leaf or flower samples (250 g) were harvested at each of the three growth stages (35, 50, and 65 DAS), chopped into ~5 mm segments, and subjected to hydro-distillation using a Clevenger-type apparatus for 6 hours, following the procedure outlined by Tangpao *et al*. (2018) [21]. This technique enabled efficient release of essential oils by rupturing oil glands through fine chopping. After distillation, the essential oil layer was separated from the

aqueous phase using petroleum ether and stored in amber-colored vials at 4 °C to prevent photo-oxidation and volatilization losses. Oil yield was calculated using the formula:

Leaf oil = Total weight (with oil) of vial - Empty vial weight

$$\text{Leaf oil (\%)} = \frac{\text{Weight of oil} \times 100}{\text{weight of leaf sample}}$$

Fig 3: Hydro Distillation Unit and Leaf Essential oil of Sweet Basil

2.5 GC-MS Analysis of Essential Oil Composition

Essential oil samples were analysed using a GC-MS system (Thermo Scientific Focus-Polaris Q) equipped with a DB-5MS capillary column (30 m × 0.25 mm, 0.25 µm film thickness) and an electron ionization (EI) detector at 70 eV. The injection volume was 1 µL (diluted in petroleum ether), and the split ratio was 1:20. The oven temperature program was as follows: initial temperature 60 °C (held for 5 min), increased at a rate of 5 °C/min to 250 °C, and maintained at 250 °C for 3 min. The injector, ion source, and transfer line temperatures were maintained at 240 °C, 220 °C, and 240 °C, respectively. Helium was used as the carrier gas at a flow rate of 1.0 mL min^{-1}.

Volatile compounds were identified by comparing mass spectral data and retention indices with entries in the NIST Library (Version 2.0, 2005) and published literature (Adams, 2005) [1]. Semi-quantitative analysis was carried out by calculating the relative peak area percentage of each component using the area normalization method, where no external standards were employed.

2.6 Data Analysis

The relative abundance of essential oil components was expressed as area percentages derived from the total ion chromatogram. Compound identification was confirmed based on mass spectral matching, retention index comparison, and literature validation (Adams, 2005) [1]. All data were statistically analysed using appropriate tools to assess treatment effects across growth stages.

3. Result and Discussion

3.1 Effect of Jasmonic Acid on Leaf Essential Oil Content

Jasmonic acid (JA) treatments markedly influenced the essential oil content of sweet basil leaves at all three developmental stages (35, 50, and 65 days after sowing - DAS). A clear stage- and dose-dependent enhancement in oil yield was observed (Table 1). Among the treatments, 0.9 mM JA (JA 3) consistently resulted in the highest leaf essential oil content, registering 0.37% at 35 DAS, 0.61% at 50 DAS, and 0.46% at 65 DAS, all of which were significantly superior to both the control and lower JA doses. Moderate improvements were also recorded under JA 2 (0.6 mM) and JA 1 (0.3 mM), although these remained statistically at par with each other at certain stages. Importantly, the pre-flowering stage (50 DAS) proved to be the most responsive period for essential oil biosynthesis, with the overall mean oil yield peaking at 0.49%, compared to 0.33% at 35 DAS and 0.37% at 65 DAS. The observed increase under JA_3 at 50 DAS (0.61%) suggests a synergistic interaction between the plant's ontogenetic peak of secondary metabolism and the bio-elicitation potential of jasmonic acid.

Table 1: Effect of jasmonic acid on leaf essential oil content at different growth stages of sweet basil

Treatments	Leaf Essential Oil (%) Different Growth Stages		
	35 DAS	50 DAS	65 DAS
Control	0.29	0.38	0.31
JA 1	0.31	0.44	0.32
JA 2	0.34	0.51	0.38
JA 3	0.37	0.61	0.46
Mean	0.33	0.49	0.37
S. Em	0.01	0.02	0.01
CD at 5%	0.04	0.05	0.04
CV %	8.06	7.88	7.70

The stage-specific trend in oil accumulation aligns with the developmental biology of basil, wherein trichome density and metabolic flux towards terpenoid biosynthesis are maximized during active vegetative expansion and early flowering. Earlier studies by Kim *et al.* (2006) [9] demonstrated that methyl jasmonate significantly upregulated terpene synthase genes in basil, enhancing monoterpene production such as linalool and eugenol. Similarly, Malekpoor *et al.* (2015) [11] reported elevated methyl chavicol content following exogenous JA application without signs of phyto-toxicity.

JA-mediated enhancement in essential oil content can also be attributed to its role in increasing the density and maturity of glandular trichomes, which serve as major reservoirs for volatile compounds (Zlotek *et al.*, 2016) [22]. At 35 DAS, although JA application resulted in improved oil yield over control, the biosynthetic capacity appeared constrained due to immature trichomes. Conversely, at 65

DAS, a mild decline in oil content compared to 50 DAS may be attributed to resource reallocation toward reproductive growth, leaf senescence, or downregulation of metabolic pathways under combined developmental and environmental stress cues (Palesh & Abdollahi Mandoulakani, 2020) [15]. These findings affirm that foliar application of JA, particularly at 0.9 mM concentration, acts as a potent elicitor of terpenoid metabolism and is most effective when applied before the onset of flowering (around 50 DAS).

3.2 Effect of Jasmonic Acid on Flower Essential Oil Content

Flower essential oil accumulation in sweet basil was initiated only after 40 DAS, in accordance with the plant's natural phenology. No oil yield was recorded at 35 DAS due to the absence of floral structures. However, at 50 and 65 DAS, jasmonic acid treatments induced a substantial increase in flower oil content compared to the control (Table 2). At 50 DAS, JA_3 (0.9 mM) exhibited the highest flower oil content (0.41%), followed by JA_2 (0.36%) and JA1 (0.25%), all significantly superior to the control (0.19%). A similar pattern was observed at 65 DAS, with JA_3 again achieving the highest oil content (0.40%), outperforming JA2 (0.37%), JA1 (0.33%), and the control (0.30%).

Table 2: Effect of jasmonic acid on flower essential oil content at different growth stages of sweet basil

Treatments	Flower Essential Oil (%)		
	Different Growth Stages		
	35 DAS	50 DAS	65 DAS
Control	-	0.19	0.30
JA 1	-	0.25	0.33
JA 2	-	0.36	0.37
JA 3	-	0.41	0.40
Mean	-	0.30	0.35
S. Em	-	0.01	0.01
CD at 5%	-	0.03	0.04
CV %	-	6.94	7.43

Contrary to the leaf oil trend, flower essential oil continued to increase slightly from 50 DAS to 65 DAS, likely reflecting the peak metabolic activity and full maturity of floral tissues. According to Gang *et al*. (2001) [4] and Pichersky & Gershenzon (2002) [16], flowers synthesize elevated levels of volatiles to attract pollinators, with JA further amplifying this process by activating defense- and reproduction-related pathways. The high flower oil yield under JA3 at both stages substantiates its role in upregulating floral terpenoid biosynthesis. Interestingly, while leaf essential oil peaked at 50 DAS and declined thereafter, the flower oil continued to rise, eventually surpassing leaf oil content at 65 DAS. This suggests that flower tissues may become the primary sink for terpenoids during the reproductive phase, as metabolic prioritization shifts away from senescing leaves (Ghassemi-Golezani *et al*., 2011) [5]. The superior oil content in JA-treated flowers also aligns with observations by Zlotek *et al*. (2016) [22], who reported that JA enhances floral glandular trichome density and stimulates genes related to volatile production.

3.3 Leaf Essential oil profiling using GC-MS analysis

3.3.1 GC-MS Profiling of Leaf Essential Oil Composition at Different Growth Stages

At 35 DAS, GC-MS analysis revealed a dose-dependent enhancement in key volatile compounds. In JA-treated samples, eugenol increased from 5.24% in the control to 11.96% in the JA 3, while methyl eugenol exhibited a similar rise from 2.07% to 4.67%. Estragole, the predominant compound, showed a modest increase with JA 1 and JA 2 (76.24%) but declined to 61.89% in JA_3, suggesting a metabolic shift toward eugenol biosynthesis at higher JA concentrations. Concurrently, thujene levels decreased with increasing JA dose, and minor constituents, such as isoledene and cadinadene, displayed variable responses—cadinadene being undetectable in the control and JA_1 but reaching 8.66% in JA 3.

Table 3: Leaf essential oil composition variation in control and jasmonic acid treated sweet basil plants at 35 DAS

Leaf essential oil composition variation at 35 DAS				
Compounds	Control	JA 1	JA 2	JA 3
	Area %	Area %	Area %	Area %
Eugenol	5.24	7.68	8.77	**11.96**
Estragole	66.74	76.24	75.7	61.89
Methyl Eugenol	2.07	2.46	3.52	**4.67**
Thujene	9.65	9.37	4.77	3.5
Isoledene	3.65	0.93	2.32	3.99
Cadinadene	-	-	4.91	8.66

At 50 DAS, the response to JA treatment was markedly pronounced. Eugenol content surged from 6.57% in the control to a peak of 22.57% in JA 3, while methyl eugenol increased from 2.85% to 7.21% under the highest JA dose. Estragole maintained a substantial presence (55.35% to 63.36%) across all treatments, implying that its biosynthetic pathway was less influenced by JA. The concomitant decline in thujene from 9.44% to 4.78% in JA_3 further underscored the metabolic redirection toward phenylpropanoid synthesis. Minor alterations in isoledene and cadinadene levels were observed, reflecting a nuanced, treatment-dependent modulation of the overall volatile profile.

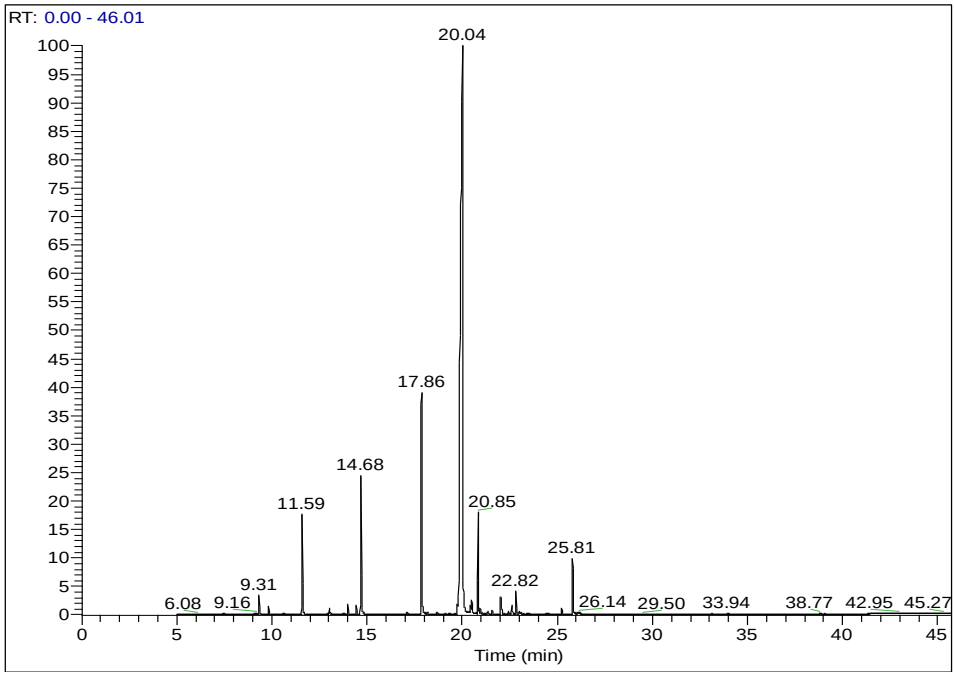
Table 4: Leaf essential oil composition variation in control and jasmonic acid treated sweet basil plants at 50 DAS

Leaf essential oil composition variation at 50 DAS				
Compounds	Control	JA 1	JA 2	JA 3
	Area %	Area %	Area %	Area %
Eugenol	6.57	10.2	13.19	**22.57**
Estragole	60.91	63.36	55.35	60.82
Methyl Eugenol	2.85	3.99	5.8	**7.21**
Thujene	9.44	6.61	5.55	4.78
Isoledene	3.36	3.67	3.61	3.78
Cadinadene	5.06	6.71	7.31	3.05

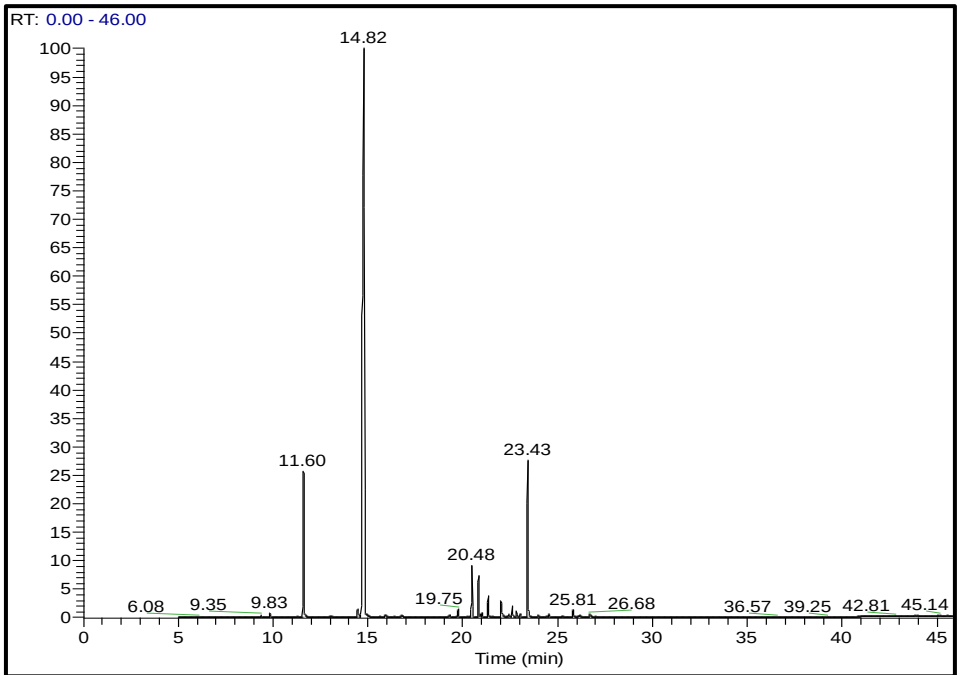
At 65 DAS, JA-induced enhancements persisted, albeit at a moderated magnitude compared to the 50 DAS peak. Eugenol content increased from 3.99% in the control to 14.91% in JA 3, and methyl eugenol similarly rose from 2.21% to 5.13%. However, the response was less robust than at mid-growth, likely reflecting senescing metabolic activity and resource reallocation in more mature tissues. Notably, estragole peaked under JA_2 (62.98%) but decreased with JA 1 and JA 3, whereas thujene exhibited a significant elevation in JA_3-treated samples (21.67%), hinting at complex, stage-specific regulatory interactions between the phenylpropanoid and monoterpene pathways.

Table 5: Leaf essential oil composition variation in control and jasmonic acid treated sweet basil plants at 65 DAS

Leaf essential oil composition variation at 65 DAS				
Compounds	**Control**	**JA 1**	**JA 2**	**JA 3**
	Area %	**Area %**	**Area %**	**Area %**
Eugenol	3.99	8.51	11.55	**14.91**
Estragole	49.22	32.13	62.98	32.71
Methyl Eugenol	2.21	2.95	3.71	**5.13**
Thujene	15.07	15.65	2.91	21.67
Isoledene	4.79	9.29	4.52	4.78
Cadinadene	5.95	9.16	4.83	8.76



Control



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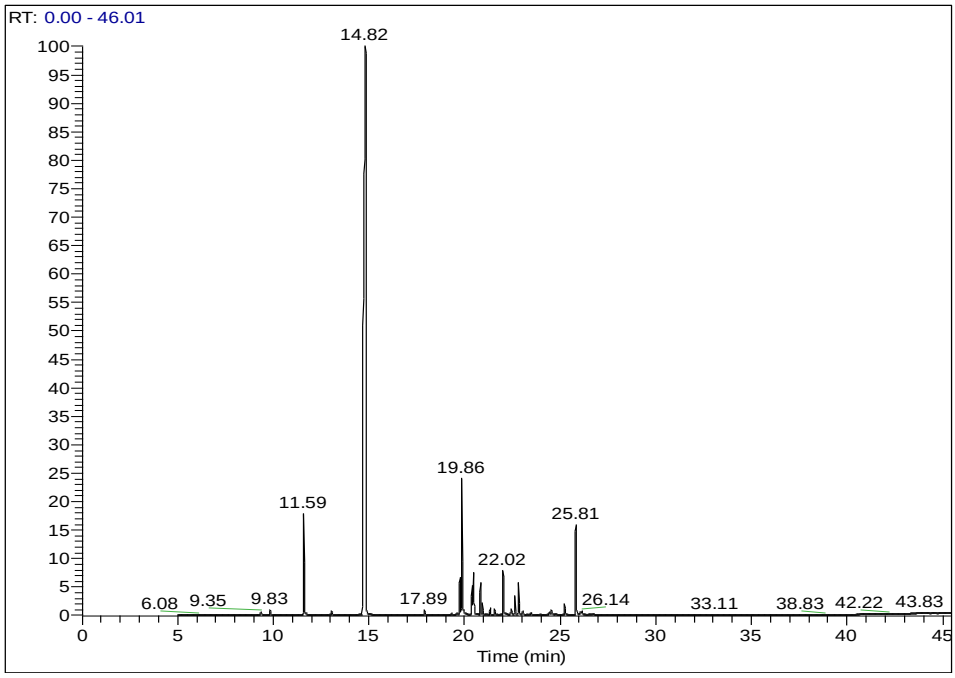

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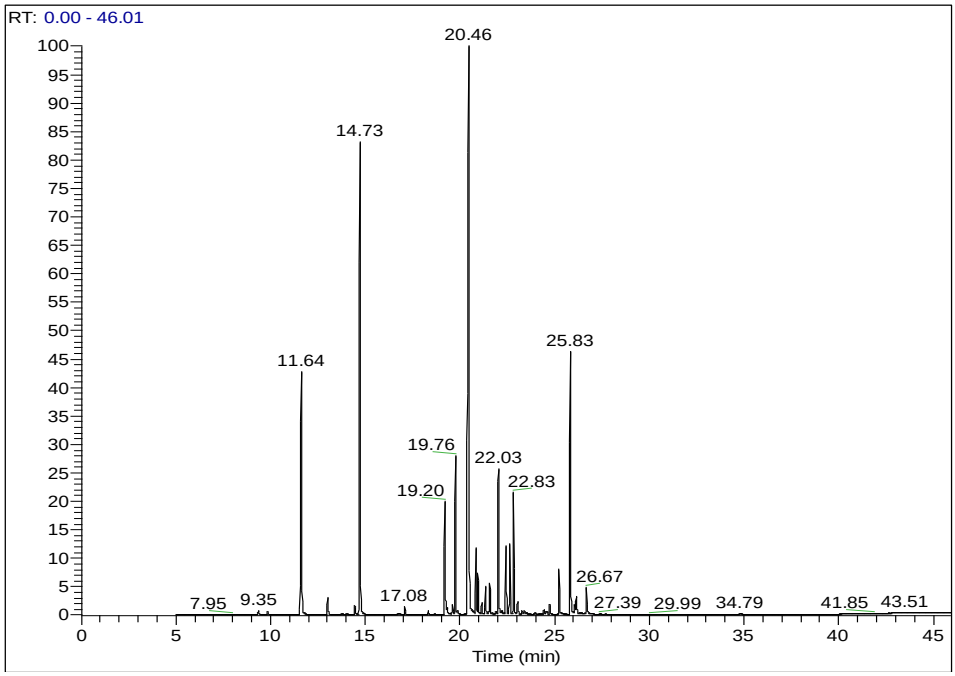
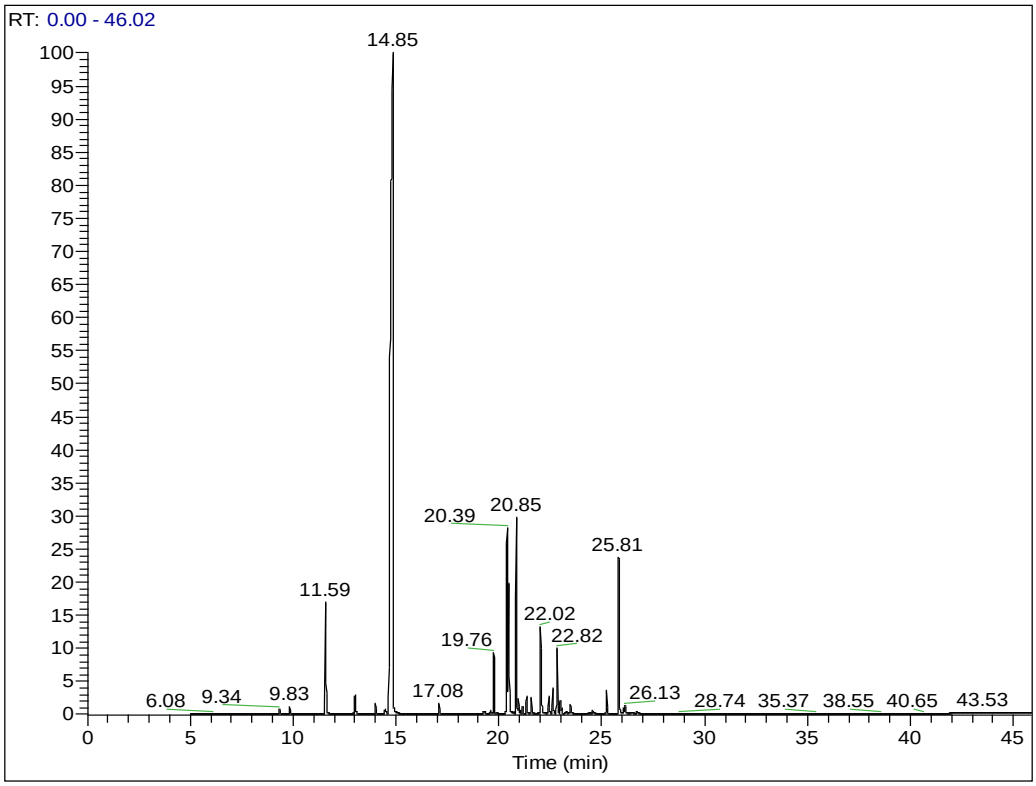


JA 3

Fig 4: GC-MS chromatogram of leaf essential oil composition at 35 DAS at different JA treatments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20.39
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11.59
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22.82
19.76
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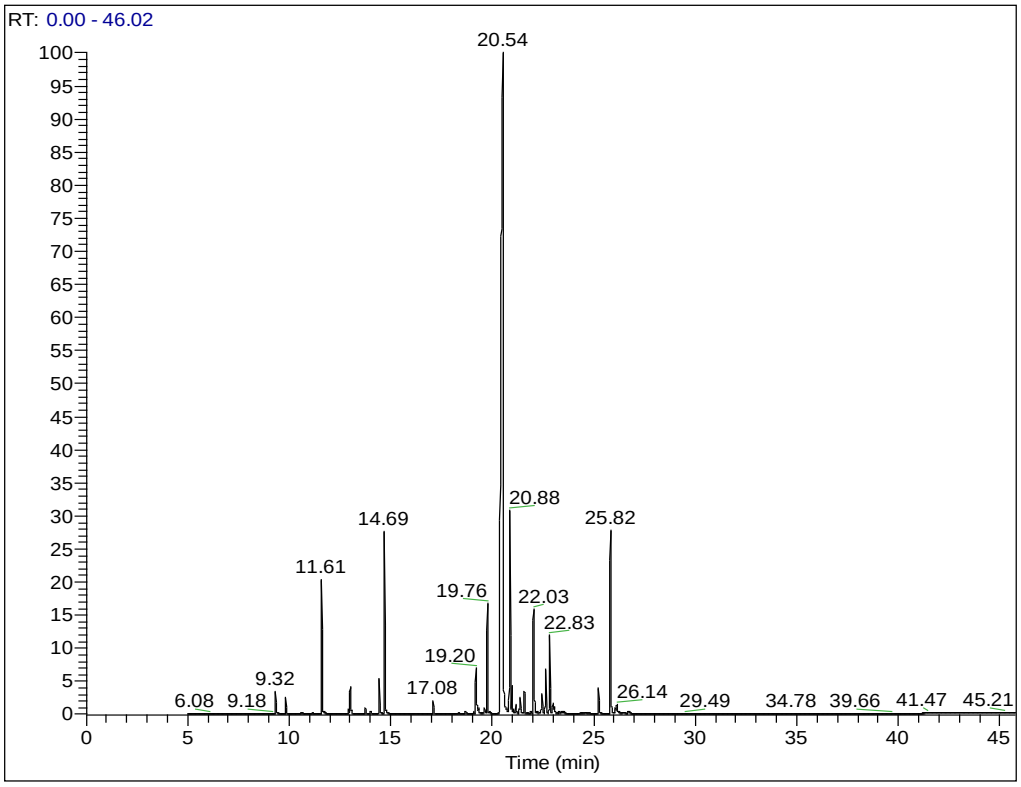
Time (min)

Control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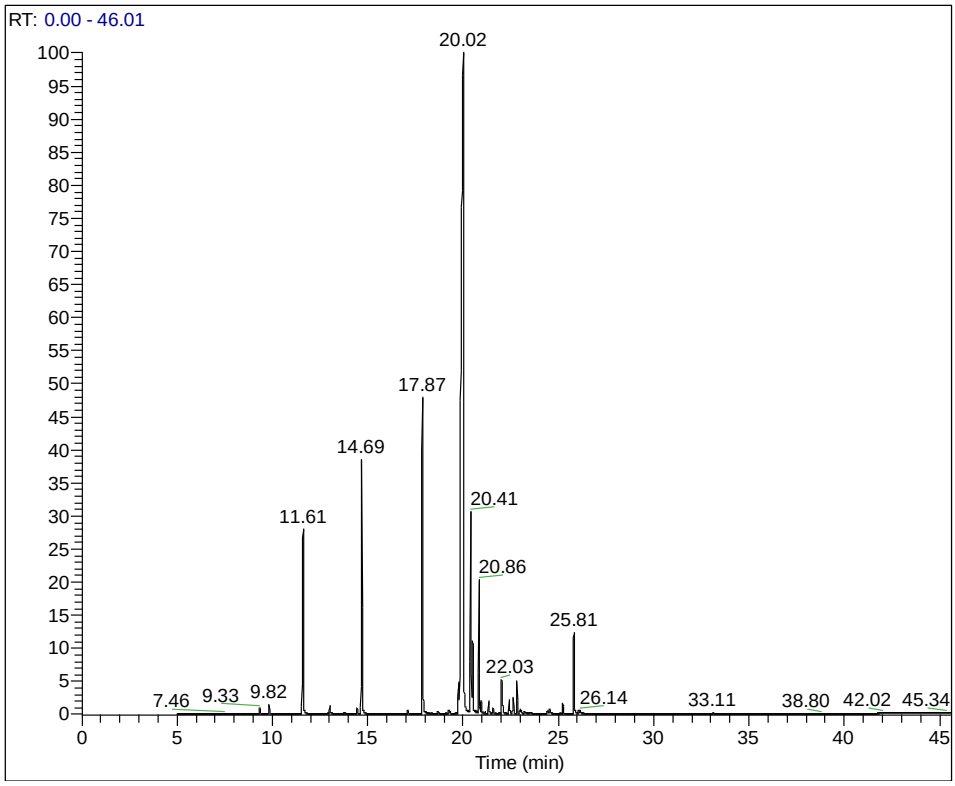

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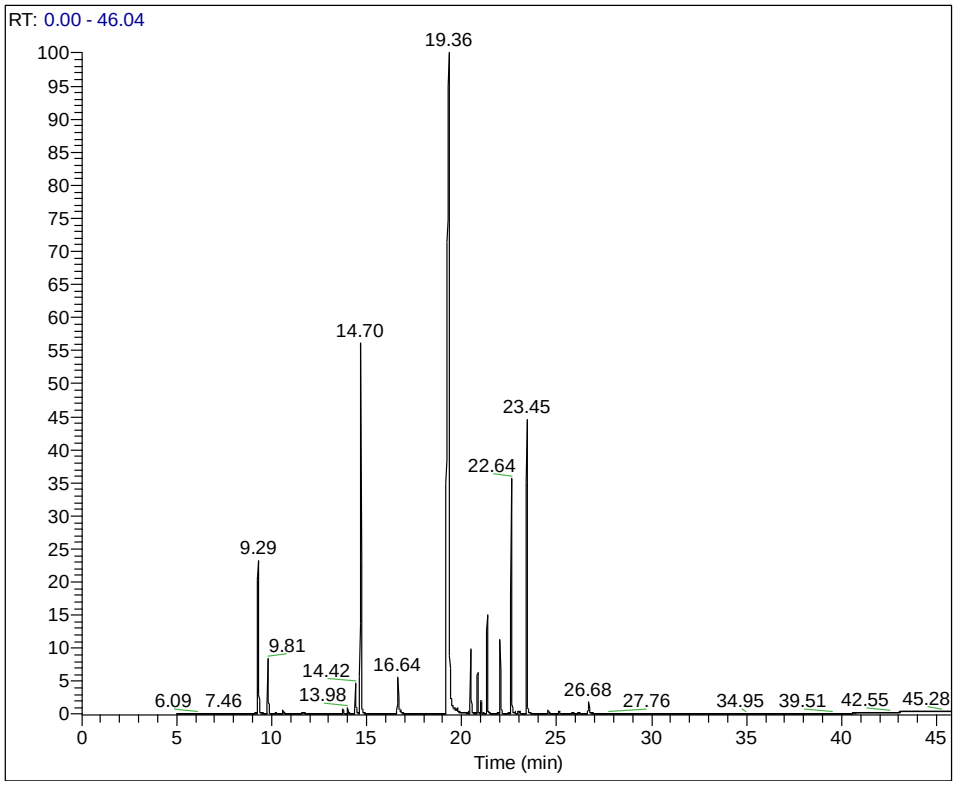
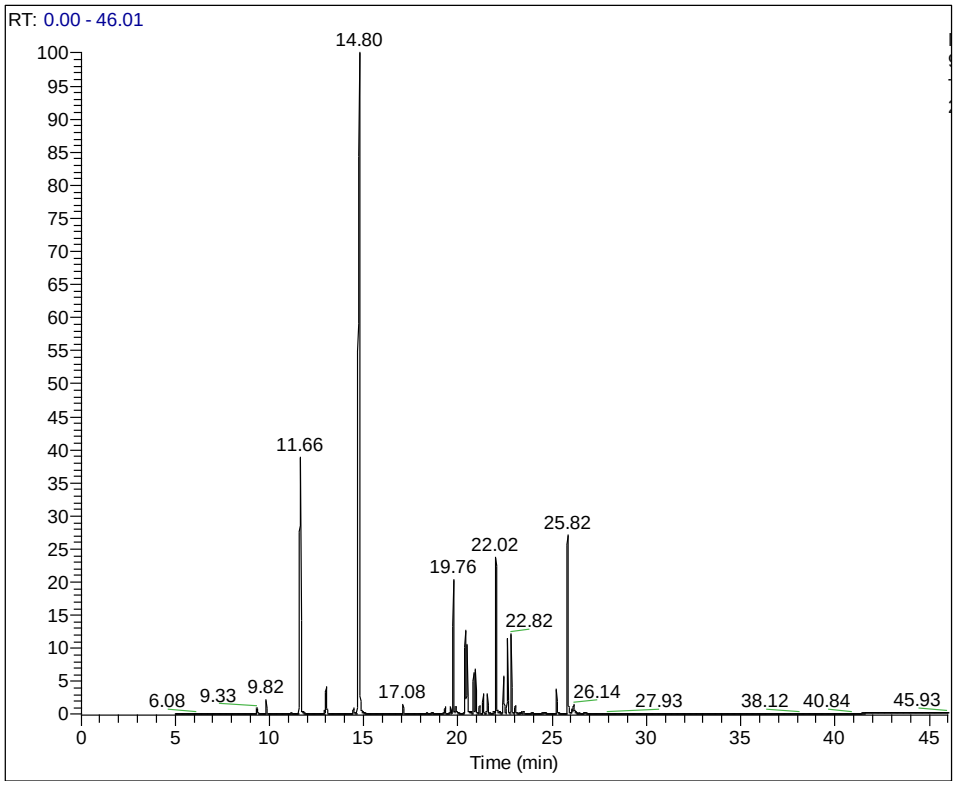


JA 3

Fig 5: GC-MS chromatogram of leaf essential oil composition at 50 DAS at different JA treatments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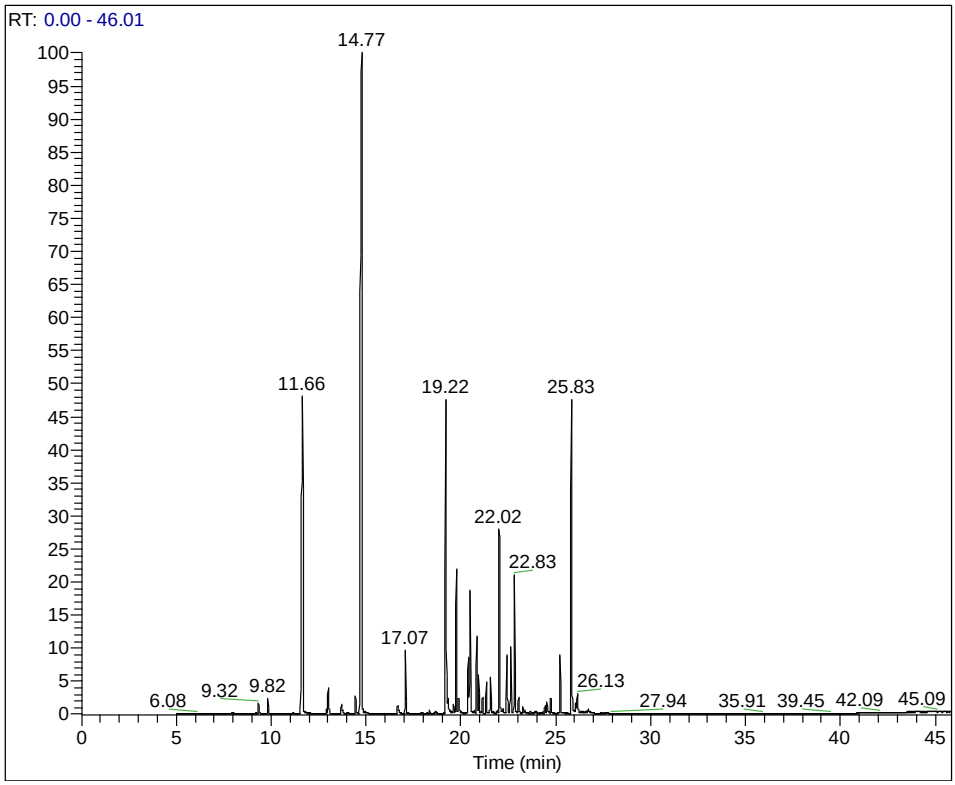
38.12
40.84
45.93
Time (min)

Control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Time (min)

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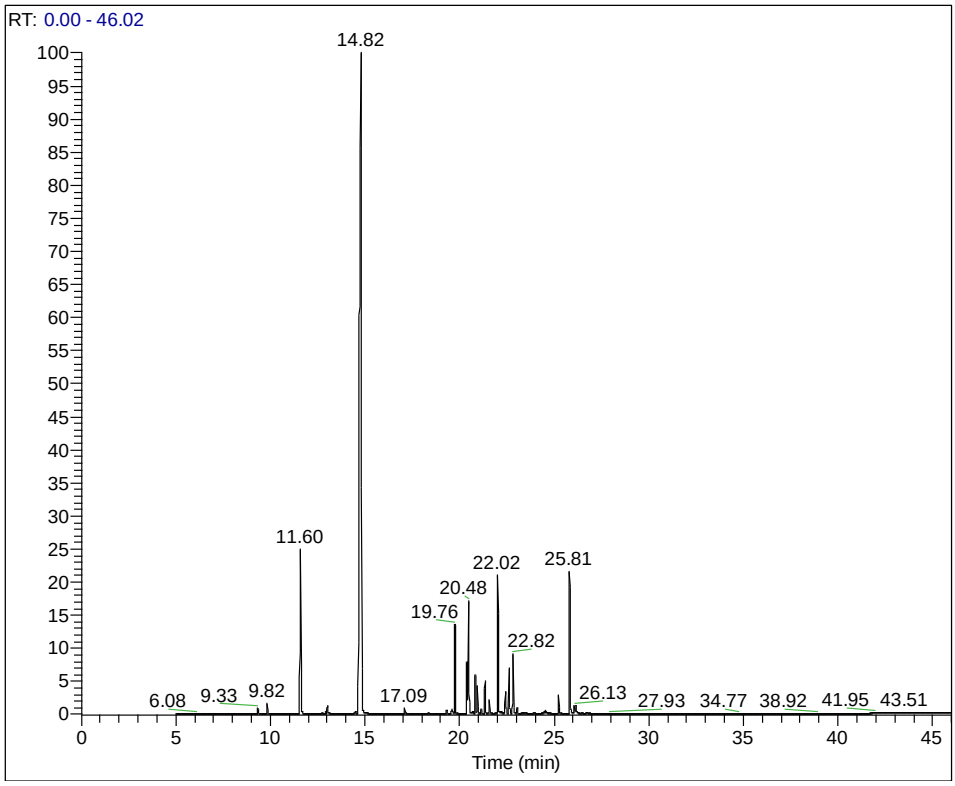
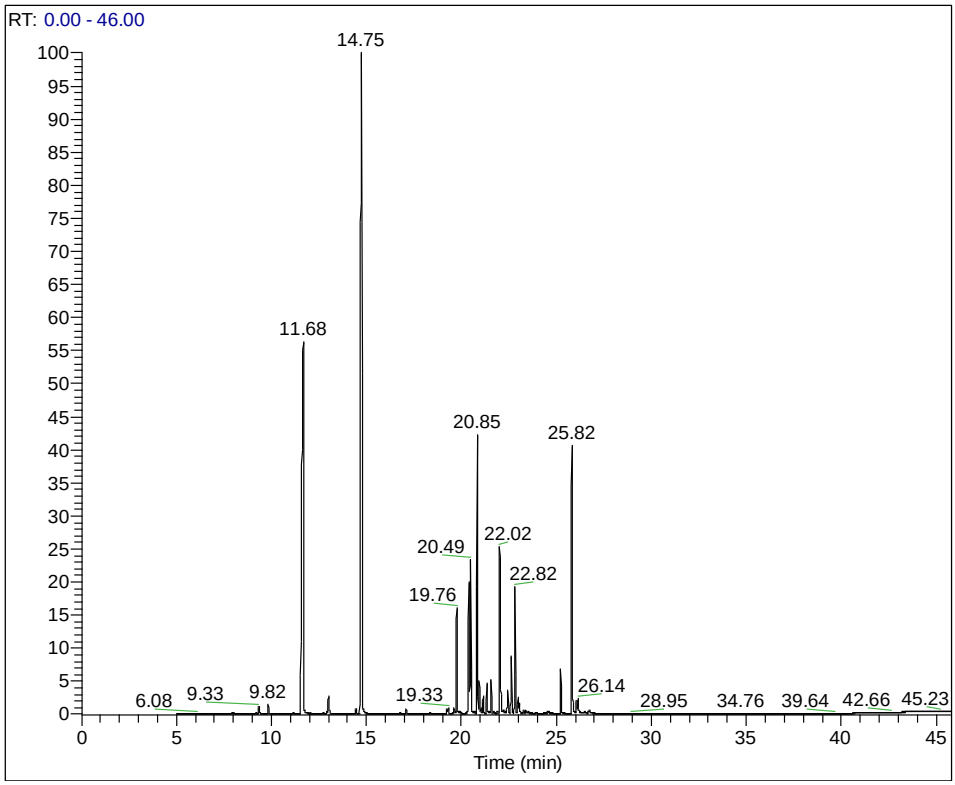


JA 2



JA 3

Fig 6: GC-MS chromatogram of leaf essential oil composition at 65 DAS at different JA treatments

These shifts are mechanistically consistent with JA's role in activating the phenylpropanoid pathway. JA signaling leads to degradation of JAZ repressors via the *COI1-JAZ* complex, thereby liberating transcription factors that upregulate genes such as *PAL*, *C4H*, *CCR*, *CAD*, and specifically *EGS* and *EOMT* reported by Reddy *et al*. (2021) [17] and Rezaie *et al*. (2020) [18]. The elevated eugenol at 50 DAS likely reflects maximal expression and enzymatic activity of EGS proteins in glandular trichomes, as sweet basil produces eugenol predominantly in peltate glands (Reddy *et al*., 2021) [17]. Methylation of eugenol to methyl eugenol by EOMT, which requires S-adenosyl methionine as a methyl donor, also increased under JA, consistent with prior biochemical reports Gang *et al*. (2002) [3]. The

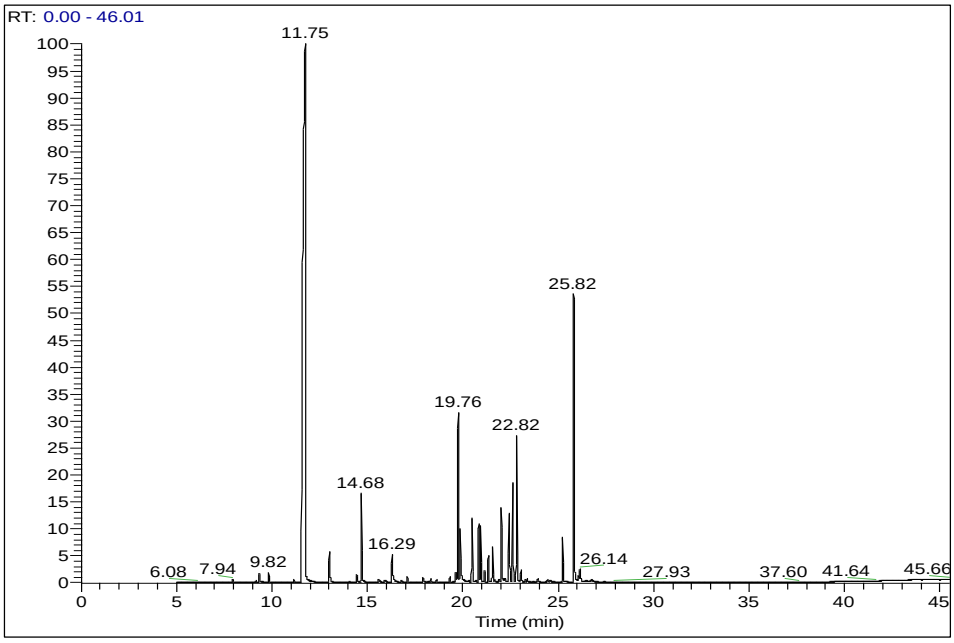
developmental rise-fall pattern observed—maximum at 50 DAS and lower at 65 DAS—can be attributed to ontogenetic regulation of enzyme expression and glandular trichome activity. Gene expression and enzyme activity for EOMT decline as leaves mature, reducing methylation capacity later in development as reported by Deschamps and Simon (2006) [2]. Thus, JA applied at mid-vegetative stage enhances flux through both eugenol biosynthesis and methylation, while older tissues exhibit attenuated responsiveness.

3.4 Flower Essential oil profiling using GC-MS analysis

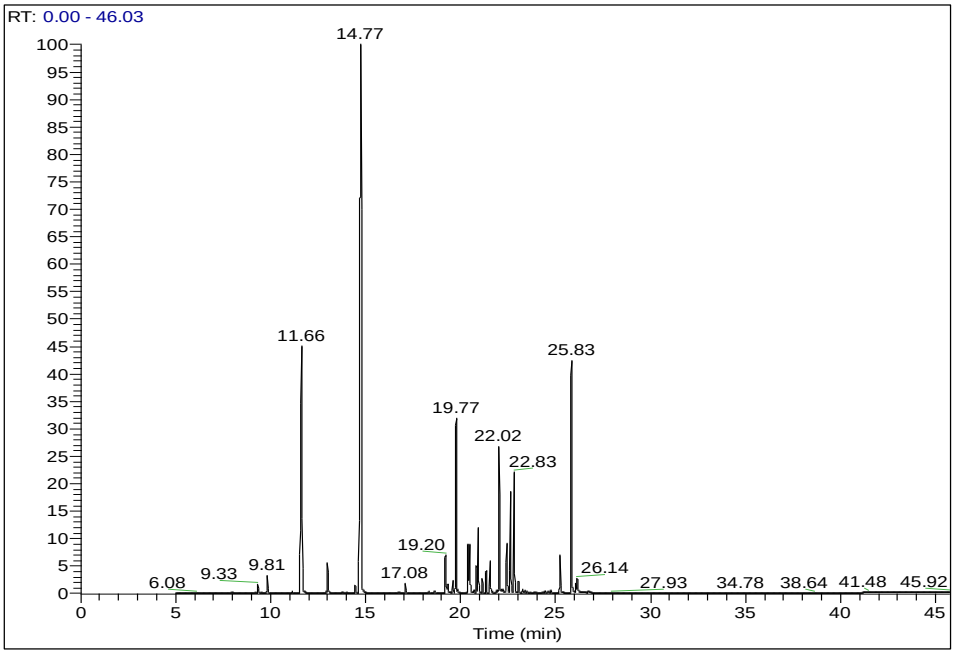
At 65 DAS, JA treatments influenced flower essential oil composition in sweet basil. As data summarized in, eugenol content increased in all treatments compared to the control (2.76%), with the highest in JA 1 (6.1%), followed by JA 3 (5.57%) and JA 2 (5.18%). Similarly, methyl eugenol rose from 1.97% in control to 3.21% (JA 1), 3.97% (JA 2) and 5.48% (JA 3), showing a dose-responsive increase. In contrast, thujene decreased sharply from 53% (control) to 16.11% (JA 1), 32.78% (JA 2) and 6.91% (JA 3). Estragole and isoledene also varied, while cadinadene was reduced under all JA treatments. These changes highlight JA's role in enhancing eugenol and methyl eugenol biosynthesis.

Table 6: Flower essential oil composition variation in control and jasmonic acid treated sweet basil plants at 65 DAS

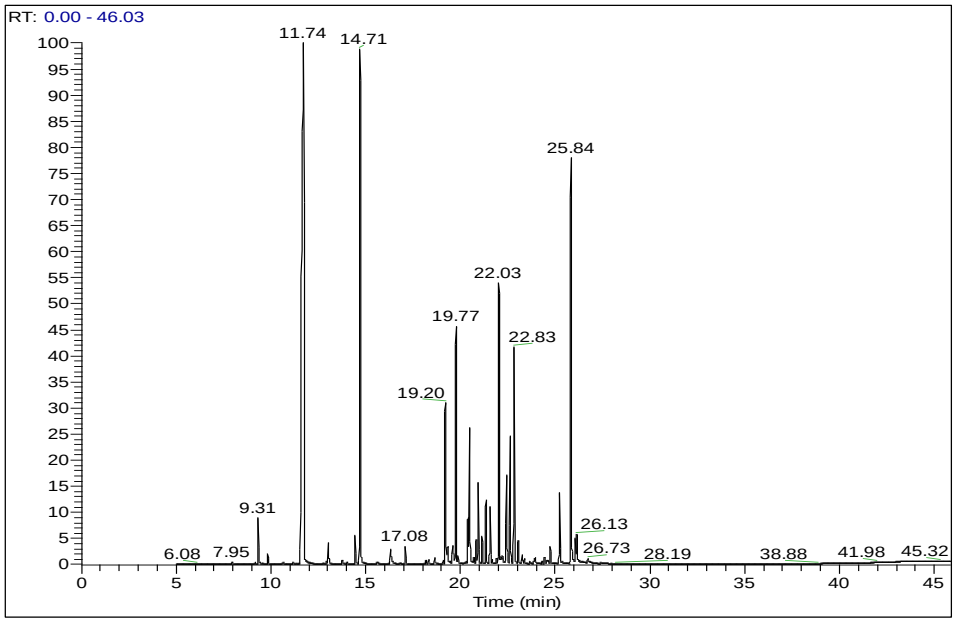
Leaf essential oil composition variation at 65 DAS				
Compounds	**Control**	**JA 1**	**JA 2**	**JA 3**
	Area %	**Area %**	**Area %**	**Area %**
Eugenol	2.76	6.1	5.18	5.57
Estragole	2.72	36.8	12.54	20.2
Methyl Eugenol	1.97	3.21	3.97	5.48
Thujene	53	16.11	32.78	6.91
Isoledene	2.19	4.81	6.39	2.47
Cadinadene	9.66	8.76	4.35	2.42



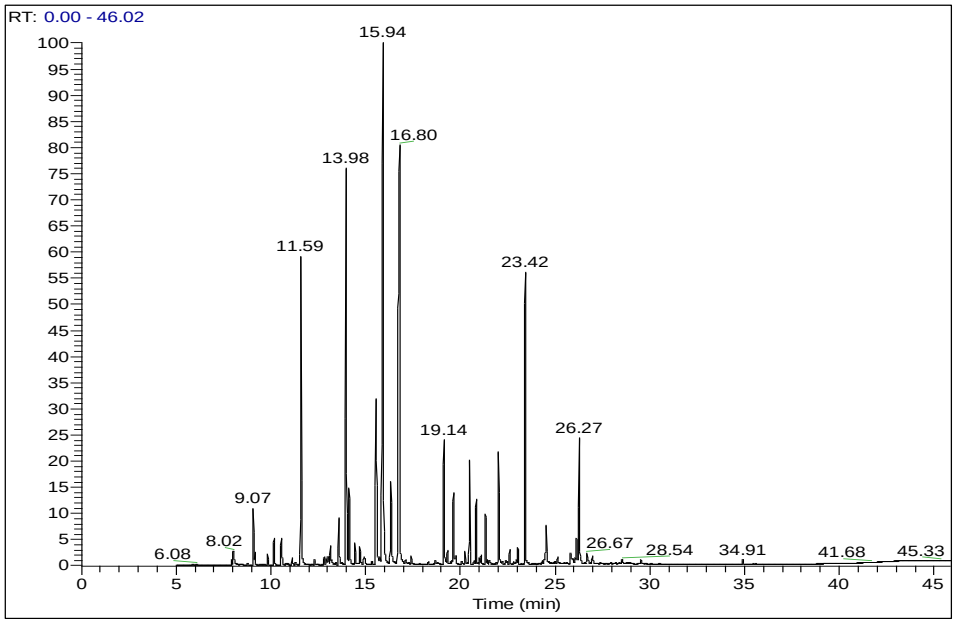
Control



JA 1



JA 2



JA 3

Fig 7: GC-MS chromatogram of flower essential oil showing peaks at 65 DAS at different JA treatments

At 65 DAS, jasmonic acid significantly altered the flower essential oil profile of sweet basil, especially enhancing eugenol and methyl eugenol content. Eugenol peaked under JA 1, and then declined at higher concentrations, consistent with Kim *et al*. (2006) [9], who reported maximum eugenol at 0.5 mM MeJA in basil. Zlotek *et al*. (2016) [22] also showed that low JA doses increased methyl eugenol, while higher doses shifted the profile toward other volatiles, confirming dose-dependent effects. Malekpoor *et al*. (2016) [12] observed JA-induced enhancement in phenolic content, supporting the activation of phenylpropanoid biosynthesis. Talebi *et al*. (2018) [23] further confirmed that JA treatment modifies basil oil composition, particularly increasing methyl eugenol. The distinct peak of eugenol in JA 1-treated flowers versus JA 3-treated leaves suggests tissue-specific regulation, possibly via enzymes like PAL and eugenol synthase. A simultaneous reduction in monoterpenes like thujene indicates a shift in metabolic flux toward phenolics. These findings clearly confirm that JA influences essential oil composition in a dose- and tissue-dependent manner, with moderate doses being more effective for floral eugenol enrichment.

4. Conclusion

This investigation highlights jasmonic acid as a potent elicitor for enhancing essential oil yield and modulating its phytochemical profile in *Ocimum basilicum* L. Application of 0.9 mM JA (JA 3) significantly augmented leaf and flower oil content, with a pronounced elevation in eugenol and methyl eugenol, particularly at the pre-flowering stage (50 DAS). GC-MS profiling revealed a JA-driven metabolic shift from monoterpenes toward phenylpropanoid derivatives, indicating a targeted activation of biosynthetic pathways such as PAL-EGS-EOMT. The dynamic response of essential oil composition across developmental stages and tissues underscores the spatio-temporal regulation of

secondary metabolism under JA influence. Leaf oil peaked at mid-vegetative growth, while flower oil continued to rise until full bloom, reflecting tissue-specific metabolic prioritization. These findings not only validate JA's role in reprogramming volatile biosynthesis but also present a strategic agronomic approach for maximizing the commercial and therapeutic value of sweet basil through precise elicitor application. In essence, timely foliar application of JA offers a sustainable, non-genetic intervention to elevate essential oil quality in basil—bridging plant defense signaling with phytochemical enhancement in a developmentally optimized manner.

5. References

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