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Probing the scent code: comparative metabolite profiling of essential oils in two Lavandula species across phenological stages

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ABSTRACT

The genus *Lavandula* (Lamiaceae) comprises aromatic plants widely cultivated for their essential oils, which are valued for their applications in perfumery, cosmetics, and herbal medicine. This study presents a comparative metabolomic analysis of essential oils from *Lavandula angustifolia* Mill. and *Lavandula* × *intermedia* Emeric ex Loisel. at two phenological stages—vegetative and flowering—to decode their scent profiles and underlying chemical divergence. Gas chromatography–mass spectrometry (GC-MS) revealed significant qualitative and quantitative differences in oil yield and composition between species and developmental stages. *L. angustifolia* exhibited a floral aroma chemotype dominated by linalool (40.7–50.2%) and linalyl acetate, particularly during flowering, whereas *L.* × *intermedia* displayed a sharper, medicinal profile characterized by 1,8-cineole (up to 52.6%) and borneol, especially in the vegetative phase. Multivariate analyses (hierarchical clustering and PCA) confirmed clear chemotypic segregation based on species and developmental stages, identifying distinct metabolic signatures: a linalool-rich chemotype in *L. angustifolia* and a 1,8-cineole/borneol-rich chemotype in *L.* × *intermedia*. Oxygenated monoterpenes were the dominant compound class in all samples, with the highest abundance in flowering *L. angustifolia* (91.7%). Developmental transitions notably influenced metabolite profiles, indicating transcriptional regulation of terpene biosynthesis. These findings provide insights into species-specific secondary metabolism and support targeted cultivation strategies for perfumery, cosmetics, and medicinal applications based on genotype × environment × development interactions.

Keywords: *Aromatic plant, Lamiaceae, Lavender, Linalool, Phenology, Vegetative stage*

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Introduction

The growing interest in essential oils across diverse industries—including food and beverage, aromatherapy, personal care, cosmetics, and pharmaceuticals—is largely attributed to their favorable safety profile, as they are classified as Generally Recognized as Safe (GRAS) by the United States Food and Drug Administration (FDA) (1). These natural volatile compounds are employed either individually or as functional additives in various formulations. Their therapeutic potential stems from a complex composition rich in hundreds of bioactive phytochemicals, particularly terpenoids (including monoterpenoids and sesquiterpenoids) and phenylpropanoids, which are responsible for a wide array of biological and pharmacological effects (2, 3). Essential oils are typically extracted from different parts of aromatic plants—such as leaves, stems, flowers, bark, and roots—using a range of extraction techniques. Extensive studies have confirmed their potent antioxidant, antimicrobial, anti-inflammatory, antiallergic, anticonvulsant, and antidepressant activities (1).

The genus *Lavandula* L. (Lamiaceae) comprises approximately 39 to 41 recognized species along with numerous subspecies and hybrids, mainly distributed across the Mediterranean Basin, Atlantic islands, North Africa, and parts of Southwest Asia (4, 5). Several species—especially *Lavandula angustifolia* Mill. and *Lavandula* × *intermedia* Emeric ex Loisel.—are widely cultivated worldwide, including in Iran, due to their aromatic properties, medicinal uses, and ornamental value (4, 6).

L. angustifolia, commonly known as English lavender, and *L.* × *intermedia*, a sterile hybrid of *L. angustifolia* and *L. latifolia*, are perennial shrubs with narrow gray-green leaves and flowers ranging from pale blue to deep violet (7). In Iranian traditional medicine, *Lavandula* species—locally called "Ostokhoddus"—have been used to treat gastrointestinal issues, nervous system disorders, and rheumatism (6). Pharmacologically, they are known for antidepressant, antispasmodic, anti-inflammatory, and antiemetic effects, which align with their modern applications in perfumery and cosmetics (6-8).

The chemical composition of *Lavandula* essential oils varies significantly depending on species, plant organ, geographical origin, and environmental factors like soil and climate (4, 9). In *L. angustifolia*, the essential oil is primarily composed of linalool and linalyl acetate, which were quantified at 20.9% and 26.5%, respectively, in Lithuanian cultivars (10). However, these values fluctuate based on genotype and cultivation conditions (5).

In contrast, *L.* × *intermedia* tends to produce higher levels of camphor and 1,8-cineole, compounds contributing to its more pungent aroma. For instance, in French samples of *L. stoechas* ssp. *stoechas*, fenchone ranged from 14.9% to 75.5%, camphor from 2.6% to 56.2%, and 1,8-cineole from 3.0% to 14.5% (11). In Greek populations, fenchone (48.8%) and 1,8-cineole (16.7%) were predominant (12), while Italian oils contained more than 10% fenchone and camphor (13). These differences in chemotypes are linked to both genetic variation and environmental conditions. García-Vallejo et al. (1990) reported linalool/borneol as the chemotype of *L. angustifolia* ssp. *pyrenaica* growing wild in Spain (14).

While the essential oil profiles of *L. angustifolia* and *L.* × *intermedia* have been previously characterized (1, 15), little attention has been given to how these profiles change throughout plant development. The present study is the first to perform a comprehensive comparison of essential oils at two distinct phenological stages (vegetative and flowering), highlighting developmental influences on metabolite composition and chemotype expression.

Material and methods

Plant materials

This study was conducted between 2022 and 2025 at the experimental field of the Agricultural Department of the Medicinal Plants and Drugs Research Institute, Shahid Beheshti University, located in Evin, northern Tehran (35°48′285″ N, 51°23′494″ E; elevation 1785 m). The region is classified as a semi-arid temperate zone. During the growing season, average minimum and maximum temperatures were −10.5°C and 38.5°C, respectively. The annual precipitation averaged 244.6 mm. The soil characteristics at a depth of 0–30 cm were as follows: sandy clay loam texture (54% sand, 11% silt, 35% clay), pH 8.0, electrical conductivity (EC) of 0.9 dS/m, organic carbon content of 0.13%, total nitrogen 0.016%, available phosphorus 5.8 ppm, and available potassium 120 ppm.

Transplants of *L. angustifolia* Mill. and *L.* × *intermedia* Emeric ex Loisel were obtained from the Seed Bank of the Medicinal Plants and Natural Products Research Institute (ACECR) and were cultivated in October 2022 with spacing of 50 cm between rows and 30 cm between plants. Aerial parts were harvested early in the morning from three-year-old plants (Fig 1A and 1B), using a randomized collection of 10 individuals per developmental stage. For the vegetative stage, only non-flowering shoots bearing leaves were collected. During the flowering stage, shoots with fully opened flowers were harvested. Plant material was immediately transported to the laboratory and air-dried at room temperature. Voucher specimens were deposited in the herbarium of the Medicinal Plants and Drugs Research Institute, Shahid Beheshti University, under accession numbers MP-882 (*L. angustifolia*) and MP-883 (*L.* × *intermedia*).

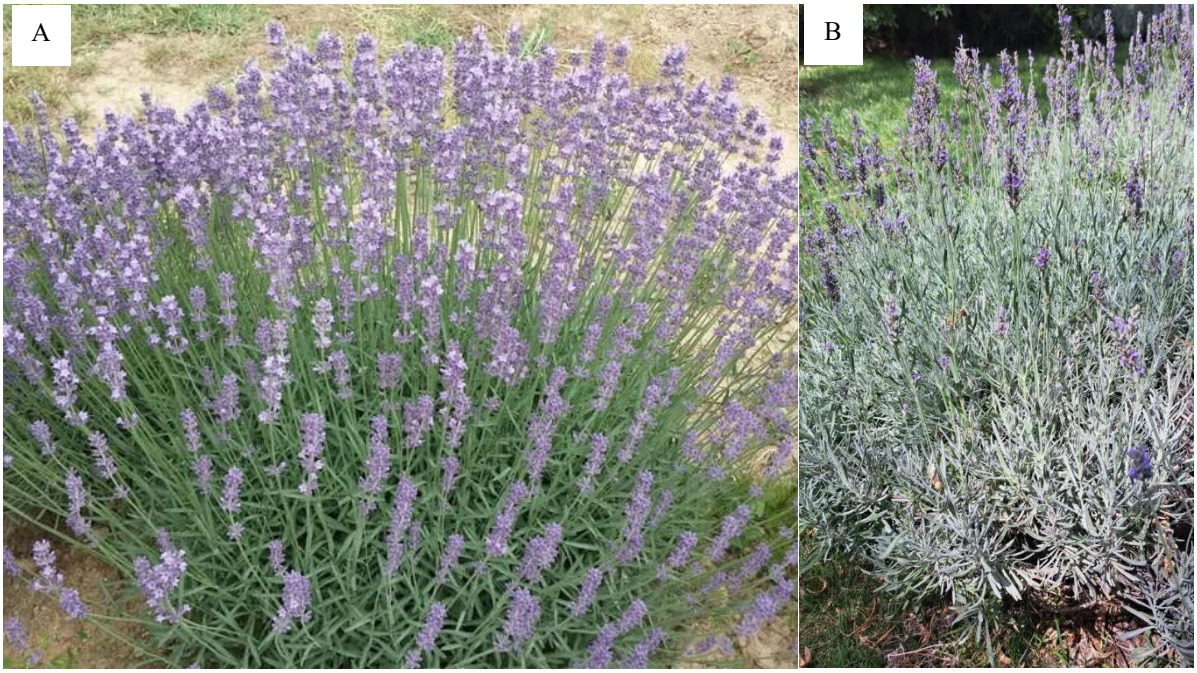

Fig. 1. Three-year-old *Lavandula angustifolia* Mill. (A) and *Lavandula* × *intermedia* Emeric ex Loisel. (B) at full flowering stage used in the present study.

Essential oil isolation

Essential oils were extracted from 100 g of air-dried aerial parts of each species via hydro-distillation using a Clevenger-type apparatus for 3 h (16). To ensure accuracy, this procedure was repeated three times for each plant sample to determine the essential oil content. The oils were dried over sodium sulfate to

remove any residual moisture and stored in a dark glass bottle at 4 °C for further analysis.

The analyses of the essential oil components were performed using two Gas Chromatography–Flame Ionization Detector (GC–FID) and Gas Chromatography–Mass Spectrometry (GC–MS) techniques according to the protocols established in previous studies. The GC analysis was carried out on a fused silica capillary DB-5 column (30 m × 0.25 mm inner diameter; film thickness 0.25 µm). The injector and detector were maintained at temperatures of 250 °C and 300 °C, respectively. Nitrogen served as the carrier gas, flowing at a rate of 1.1 ml/min. The temperature of the oven was programmed to increase from 60 °C to 250 °C at a rate of 4 °C per min, followed by a 10 min isothermal hold. The split ratio was set at 1:50. For the GC-MS analysis, a Thermoquest-Finnigan gas chromatograph was used, featuring a DB-5 fused silica capillary column (60 m × 0.25 mm inner diameter; film thickness 0.25 µm, connected to a TRACE mass spectrometer (Manchester, UK). Helium was used as the carrier gas, and the ionization voltage was set to 70 eV. The ion source and interface temperatures were maintained at 200 °C and 250 °C, respectively. The mass spectrometry analysis covered a range from 35 to 456 amu, with the oven temperature program mirroring that used in the GC analysis. All injections were performed in triplicates. The retention indices of the oil constituents were calculated under programmed temperature conditions using n-alkanes (C_6 to C_{24}). The constituents of the EOs were identified based on mass spectra. These spectra were compared with authentic standards from an internal reference mass spectra library (17).

Result and discussion

A comprehensive comparative analysis of essential oils extracted from *L. angustifolia* and *L.* × *intermedia* at two phenological stages—vegetative and flowering—revealed pronounced interspecific and developmental variations in both yield and chemical composition. The essential oil yield of *L. angustifolia* increased significantly from 0.5% in the vegetative stage to 3.4% in the flowering stage, while *L.* × *intermedia* showed a more modest increase from 0.7% to 1.8%, suggesting species-specific regulatory differences in secondary metabolite biosynthesis across developmental stages.

GC–MS profiling identified 41 and 40 constituents in *L. angustifolia* at vegetative and flowering stages, respectively, compared to 43 and 39 in *L.* × *intermedia* (Table 1). A total of 25 compounds were conserved across all samples, representing a core metabolomic fingerprint common to both species. However, the relative abundance and presence of several metabolites varied notably, underscoring both genetic divergence and developmental modulation of terpene biosynthesis.

Table 1. Essential oil composition of two *Lanandula* species cultivated in semi-arid temperate zone of Iran

Compound	CRI	*L. angustifolia*		*L. × intermedia*	
		Vegetative	Full flowering	Vegetative	Full flowering
α-Thujene	925	-	-	0.3	0.3
α-Pinene	935	-	-	2.5	0.6
Camphene	949	-	-	0.6	0.2
1-Octene-3-ol	962	0.1	0.1	-	0.4
3-Octanone	965	0.1	0.3	-	-
Sabinene	969	-	-	0.9	0.3
β-Pinene	976	-	-	2.0	14.4
Myrcene	982	1.0	1.2	1.8	1.6
Ethyl hexanoate	994	0.2	0.1	-	-
α-Pellandrene	1000	-	-	0.4	-
α-Terpinene	1007	-	-	0.1	-
δ-3-Carene	1009	0.1	-	2.9	0.3
p-Cymene	1015	-	-	0.8	0.1
1,8-Cineole	1026	2.8	2.7	52.6	46.1
cis-Ocimene	1037	1.2	1.4	0.1	2.0
γ-Terpinene	1052	0.2	0.1	0.2	0.9
Sabinene hydrate	1058	-	-	0.3	-
cis-Linalool oxide	1061	0.1	-	-	-
trans-Linalool oxide	1076	0.1	-	-	-
α-Terpinolene	1082	-	-	0.5	-
Linalool	1085	40.7	50.2	0.2	11.1
1-Octen-3-yl acetate	1098	0.6	-	-	-
Camphor	1130	0.4	0.2	5.6	2.8
trans-Verbenol	1135	-	-	0.2	-
Pinocarvone	1146	-	-	0.3	-
Lavandulol	1153	0.6	0.4	-	0.6
Borneol	1157	1.4	1.0	18.1	2.0
Cryptone	1162	-	-	2.4	-
Terpin-4-ol	1169	11.4	6.0	-	0.5
Hexyl butanoate	1174	0.4	0.3	-	-
α-Terpineol	1180	5.5	6.0	1.5	0.9
Myrtenol	1187	-	-	0.1	-
trans-Piperitol	1196	-	-	0.1	-
trans-Carveol	1204	-	-	0.1	-
Nerol	1214	0.7	0.7	-	-
2-*E*-Decanal	1240	-	-	-	2.5
Linalyl acetate	1243	14.2	13.7	-	
Lavandulyl acetate	1273	7.3	6.7	0.4	
Bornyl acetate	1275	0.2	-	-	1.2
α-Terpinenyl acetate	1337	-	-	-	0.6
Neryl acetate	1344	1.2	1.4	-	
Geranyl acetate	1362	2.3	2.7	0.3	0.5
β-Bourbenone	1391	-	-	-	1.3
β-Caryophyllene	1427	2.6	2.1	0.4	0.3
trans-β-Farnesene	1449	1.7	0.9	-	2.3
Germacrene-D	1485	0.4	0.2	-	0.4
δ-Cadinene	1507	-	0.1	-	-
α-Cadinol	1516	0.1	-	0.4	
Spathulenol	1575	-	-	-	0.2
Caryophyllene oxide	1584	0.4	0.1	0.6	-
Tau-Cadinol	1639	0.3	0.4	1.8	-
β-bisabolol	1676	-	-	0.1	0.1
Farnesol	1691	-	-	0.1	-
Monoterpene hydrocarbons		2.5	2.7	13.1	20.7
Oxygenated monoterpenes		89.5	91.7	82.2	66.3
Sesquiterpene hydrocarbons		4.7	3.3	0.4	4.3
Oxygenated sesquiterpene		0.8	0.5	3	0.3
Other compounds		1.0	0.8	-	2.9
Total identified		**98.5**	**99.0**	**98.7**	**94.5**

L. angustifolia oils were characterized by high levels of linalool (40.7–50.2%) and linalyl acetate (14.2–13.7%)—compounds associated with floral and pleasant aroma profiles. These results corroborate previous reports that identify *L. angustifolia* as a premier source of high-quality aromatic oils (7, 8). In contrast, *L.* × *intermedia* displayed a chemically distinct profile, with dominant levels of 1,8-cineole (52.6% in vegetative, 46.1% in flowering), borneol (18.1% and 2.0%), and camphor (5.6% and 2.8%), contributing to a sharper, more camphoraceous and medicinal scent (3). A notable developmental shift was observed in *L.* × *intermedia*, where β-pinene levels increased from trace amounts to 14.4% in the flowering stage, suggesting a reconfiguration of biosynthetic pathways possibly linked to floral signaling or defense mechanisms. In comparison with our results, Massoud et al. (2024) reported that *L.* × *intermedia* contained a higher proportion of linalool (44.15%) than *L. angustifolia* (32%). In contrast, the content of 1,8-cineole was greater in *L. angustifolia* (8.6%) compared to *L.* × *intermedia* (4.0%), highlighting interspecific differences in essential oil composition under different cultivated conditions.

In all samples, oxygenated monoterpenes were the most abundant class of compounds, particularly in *L. angustifolia* during flowering (91.7%). However, *L.* × *intermedia* demonstrated a decline in this class during flowering (66.3%), accompanied by a relative increase in monoterpene (20.7%) and sesquiterpene hydrocarbons (4.3%). These developmental and interspecific trends likely reflect the coordinated expression of terpene synthase genes and the influence of endogenous hormonal cues, such as jasmonates and gibberellins, during floral induction (18, 19).

Numerous studies have emphasized that the yield of essential oils from aromatic and medicinal plants is significantly influenced by the plant's developmental stage (20, 21). Arabacı et al. (2015) underscored the importance of harvesting these plants at specific phenological phases rather than arbitrarily, noting that the optimal timing for maximum essential oil accumulation must be carefully determined. Accordingly, harvesting schedules should be strategically aligned with the stage of development that ensures peak essential oil biosynthesis (22). Research on species such as *Hyptis suaveolens* (23), *Thymus vulgaris* L. (24), and *Mentha aquatica* L. (25) has demonstrated that essential oil yield tends to increase as the plant progresses through its growth stages. This trend is further corroborated by observations of minimal essential oil production during early vegetative stages, which may be attributed to limited activity of key enzymes involved in secondary metabolite biosynthesis at this phase (26).

To explore chemotypic variation, hierarchical clustering (Fig. 2) based on compound abundance separated the samples into four major groups. Clear species-specific clustering was observed, with *L. angustifolia* and *L.* × *intermedia* forming distinct branches, further subdivided by phenological stage. This pattern was especially pronounced in *L.* × *intermedia*, where vegetative and flowering stages diverged significantly. Compound-level clustering revealed four chemical groups: Cluster I was dominated by 1,8-cineole; Cluster II by linalool; Cluster III contained moderately abundant compounds such as linalyl acetate, terpinen-4-ol, and α-terpineol; and Cluster IV comprised low-abundance constituents that still contributed to differentiation.

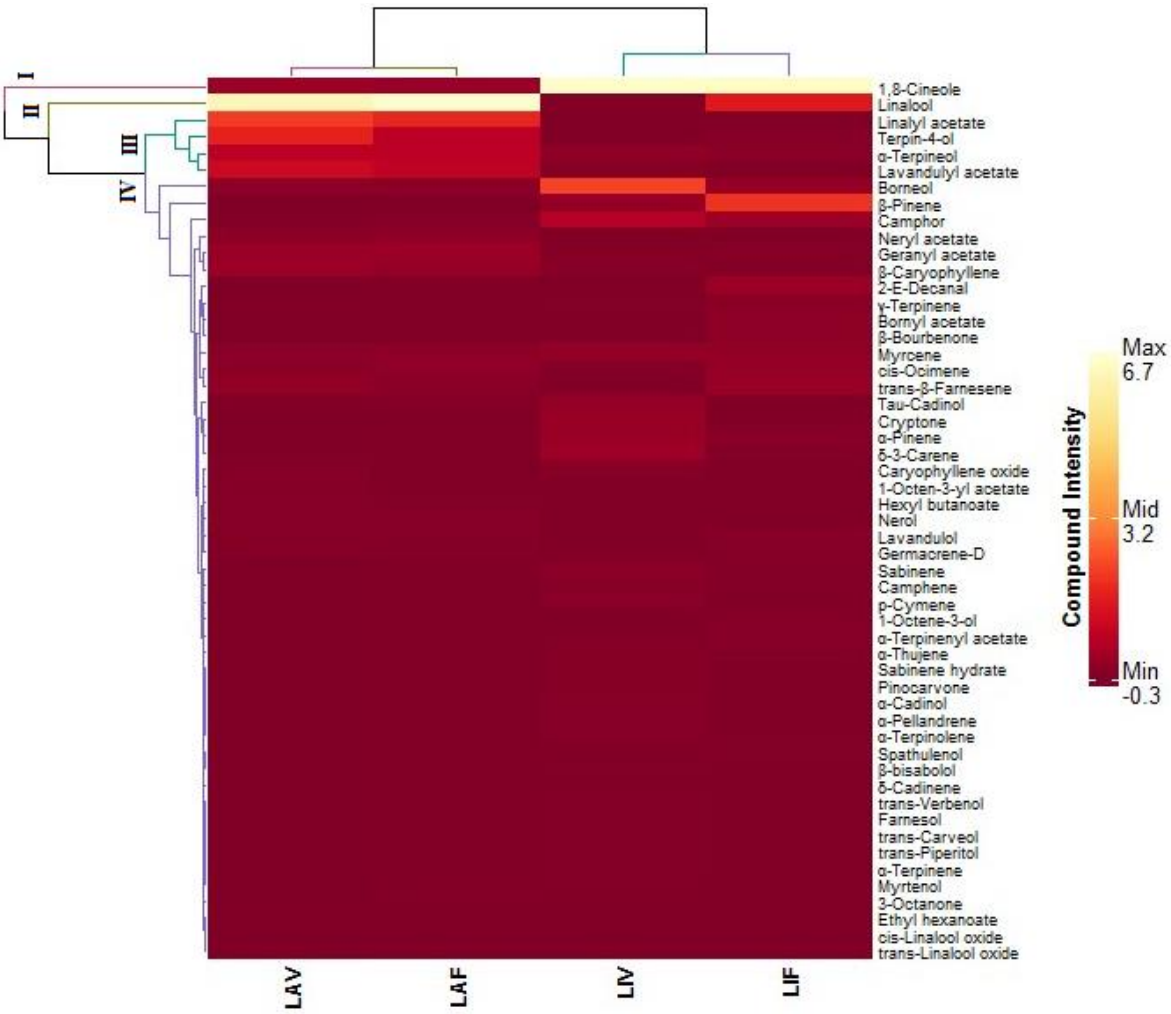

Fig. 2. Hierarchical heatmap of essential oil constituents in *Lavandula angustifolia* Mill. and *Lavandula* × *intermedia* Emeric ex Loisel. at two phenological stages: vegetative (LAV and LIV) and flowering (LAF and LIF).

Principal Component Analysis (PCA) (Fig. 3) provided additional insights into the relationships between samples and compounds. The first two components (PC1 and PC2) explained 97.5% of the total variation. *L. angustifolia* samples (LAV and LAF) were clearly separated along PC1, driven by the abundance of linalool, linalyl acetate, and lavandulyl acetate, reflecting a linalool-rich chemotype ideal for perfumery. In contrast, *L.* × *intermedia* samples (LIV and LIF) were separated along PC2, associated with high levels of 1,8-cineole, borneol, and β-pinene—indicative of a medicinal chemotype. This chemotypic divergence aligns with known genetic distinctions and differential enzymatic activities regulating monoterpene biosynthesis.

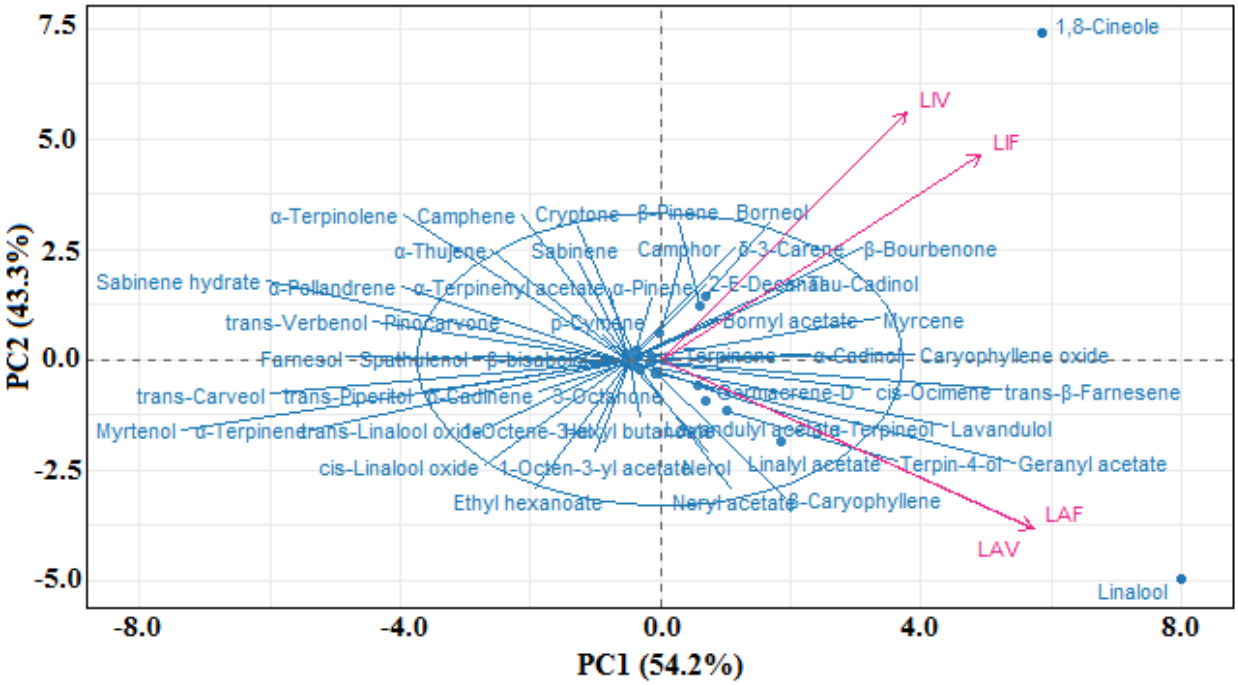

Fig. 3. Principal component analysis (PCA) of essential oil profiles in *Lavandula angustifolia* Mill. and *Lavandula* × *intermedia* Emeric ex Loisel. across two phenological stages: vegetative (LAV and LIV) and flowering (LAF and LIF). The biplot displays sample distribution and compound loadings based on the first two principal components, highlighting chemotypic differentiation between species and developmental stages.

Together, the heatmap and PCA results emphasize the dual influence of species and phenological stage on essential oil profiles. *L. angustifolia* in the flowering stage emerged as a superior source of oxygenated monoterpenes with commercial relevance for fragrance industries, while *L.* × *intermedia*, especially at the vegetative stage, exhibited profiles more suited to therapeutic applications. These findings support the use of chemometric tools not only for species authentication but also for optimizing harvest timing and industrial utilization (27, 28).

Importantly, the observed metabolic shifts along the vegetative-to-flowering transition underscore the plasticity of secondary metabolism in *Lavandula* species. This plasticity is shaped by complex genotype × environment × development (G × E × D) interactions. Environmental factors such as solar radiation, temperature, and soil nutrients can fine-tune gene expression patterns, thereby influencing essential oil yield and composition. Understanding these dynamic regulatory networks is essential for strategic cultivation, breeding, and selection of *Lavandula* chemotypes tailored to specific industrial or therapeutic demands.

Lavender essential oils have a long history of use in cosmetics and medicinal formulations dating back to the Greek and Roman eras. In recent years, their applications have expanded to include fields such as alternative medicine, food preservation, and pest management. While most research has primarily concentrated on the two dominant constituents—linalool and linalyl acetate—other minor components, including camphor, 1,8-cineole, and carvacrol, have also been investigated for their potential biological activities (29).

Linalool and linalyl acetate are extensively used as fragrance ingredients in perfumes, colognes, soaps, lotions, shampoos, and other personal care products due to their pleasant floral scent, volatility, and fixative properties. Linalool imparts a fresh, sweet, and citrusy-floral aroma, while linalyl acetate adds a softer, fruity note, enhancing fragrance complexity and longevity (30, 31). These compounds also exhibit various pharmacological properties, including anxiolytic, sedative, analgesic, anti-inflammatory, and antimicrobial effects. Linalool, in particular, has been studied for its ability to modulate the central nervous system and promote relaxation, making it a promising agent in aromatherapy and topical therapeutic formulations (32, 33).

The comparative analysis of essential oil profiles from *L. angustifolia* and *L.* × *intermedia* cultivated in a semi-arid temperate region of Iran reveals significant qualitative and quantitative variations across phenological stages. These variations are crucial in determining the suitability of each essential oil for pharmaceutical, perfumery, cosmetic, and aromatherapy applications (Fig. 4).

According to the literature survey, for medicinal and therapeutic uses—especially anti-inflammatory, antimicrobial, and wound-healing purposes—the content of oxygenated monoterpenes such as linalool, 1,8-cineole, borneol, and camphor is of primary importance due to their bioactivity (32-34). *L. angustifolia* at full flowering shows the highest linalool (50.2%) and α-terpineol (6.0%), both recognized for antimicrobial and calming effects. *L.* × *intermedia* in the vegetative stage contains high 1,8-cineole (52.6%) and borneol (18.1%), contributing to respiratory and anti-inflammatory applications. For pharmaceutical use in topical formulations and respiratory treatments, *L.* × *intermedia* at the vegetative stage is more suitable due to its high cineole and borneol levels. For neurocalming and antimicrobial products, *L. angustifolia* at full flowering is ideal.

In perfumery, the desirable profile includes high levels of linalool, linalyl acetate, lavandulyl acetate, and terpene esters, which contribute to floral, sweet, and fresh scents (30, 31). *L. angustifolia* (especially at full flowering) presents an ideal profile with linalool (50.2%), linalyl acetate (13.7%), and lavandulyl acetate (6.7%), making it a classic source for high-quality lavender oil. *L.* × *intermedia*, while more camphoraceous and sharper in aroma, contains lower esters and is less valued in fine perfumery. For luxury perfumes and high-grade aromatic blends, *L. angustifolia* at full flowering is strongly preferred due to its rich ester and alcohol content.

Aromatherapy focuses on compounds with anxiolytic, sedative, and uplifting effects. Linalool, linalyl acetate, α-terpineol, and lavandulol are key contributors to calming and mood-enhancing properties (29). *L. angustifolia* again dominates here, especially at full flowering, with high concentrations of calming components. *L.* × *intermedia*, due to its higher camphor and cineole, may be too stimulating for some aromatherapy uses. For stress relief, anxiety reduction, and relaxation in aromatherapy, *L. angustifolia* at full flowering offers the most desirable chemical profile.

Fig. 4. Pharmaceutical, perfumery, cosmetic, and aromatherapy applications of essential oils from *Lavandula angustifolia* Mill. and *Lavandula* × *intermedia* Emeric ex Loisel.

Conclusion

This study highlights distinct chemotypic differentiation between *L. angustifolia* and *L.* × *intermedia* across vegetative and flowering stages, revealing how species-specific genetic factors and phenological development shape essential oil profiles. The predominance of linalool and linalyl acetate in *L. angustifolia* and the enrichment of 1,8-cineole and borneol in *L.* × *intermedia* underscore the metabolic divergence between the two taxa. The dominance of oxygenated monoterpenes, particularly during the flowering stage of *L. angustifolia*, reflects enhanced biosynthetic activity likely driven by transcriptional regulation. These findings offer valuable insights into the dynamic regulation of secondary metabolism in lavender species and provide a biochemical foundation for optimizing cultivation and harvest strategies tailored to industrial demands in perfumery, cosmetics, and phytopharmaceutical sectors. Moreover, the integration of metabolomic profiling with phenological monitoring supports the development of genotype-specific cultivation models aligned with desired aromatic traits.

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Authors' Contributions

Mansoureh Tavan: Conceptualization, Supervision, Investigation, Formal analysis, Writing-original draft. **Maryam Moradi:** Formal analysis, Writing-review and editing.

Declaration of Interest

The authors of this article declared no conflict of interest.

Ethical Considerations

All ethical principles were adheried in conducting and writing this article.

Transparency of Data

In accordance with the principles of transparency and open research, we declare that all data and materials used in this study are available upon request.

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