International Journal of Progressive Sciences and Technologies (IJPSAT)
ISSN: 2509-0119.
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https://ijpsat.org/

Vol. 59 No. 2 October 2026, pp. 933-951

Volatile Compound Profiles And Chemical Variation Of Origanum Onites L. From Denizli, Türkiye

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Abstract: This study aimed to characterize the volatile compound profiles of *Origanum onites* L. collected from natural habitats across different localities and elevations in Denizli, Türkiye, and to evaluate the chemical diversity among the collected samples. Field surveys identified 110 localities where the species occurred, from which seven sample groups (O1–O7) representing different geographical locations and elevation ranges were selected for chemical analysis. The volatile compound profiles of the aboveground plant material were determined using headspace solid-phase microextraction coupled with gas chromatography–mass spectrometry (HS-SPME/GC–MS). The resulting data were evaluated according to chemical classes, while similarities and differences among samples were examined using heatmap visualization and principal component analysis (PCA). A total of 63 volatile compounds were identified. Carvacrol was the predominant compound in samples O1–O5, accounting for 25.38–49.20% of the volatile profiles, whereas linalool predominated in samples O6 and O7, reaching 67.92% and 53.28%, respectively. Oxygenated monoterpenes (36.80–76.93%) and sesquiterpene hydrocarbons (16.06–51.68%) represented the major chemical classes. Sample O5 was particularly distinguished by its high sesquiterpene hydrocarbon content (51.68%). The first two principal components explained 87.82% of the total variance, revealing differences in chemical composition among the investigated samples. The findings demonstrated that the examined *O. onites* samples exhibited distinct carvacrol- and linalool-dominant volatile profiles and that the observed chemical variation could not be explained by elevation alone. This study contributes to documenting the local chemical diversity of *O. onites* in Denizli and provides baseline information for future ecological, phytochemical, and biological activity investigations.

Keywords: Carvacrol; linalool; HS-SPME/GC–MS; phytochemical variability; intraspecific variation; aromatic plants

1.INTRODUCTION

The genus Origanum L., belonging to the family Lamiaceae, represents an important component of the aromatic plant diversity of the Mediterranean Basin and includes species widely used as culinary herbs, herbal teas, and raw materials in the cosmetic and pharmaceutical industries. Among its economically important members, *Origanum onites* L., commonly known as Denizli oregano, İzmir oregano, or Turkish oregano, is an aromatic species naturally distributed in Türkiye and Greece and commercially valued particularly for its essential oil composition. Its traditional uses, phytochemical characteristics, and biological activities have encouraged investigations into its potential applications in various fields (Tepe et al., 2016; Stefanaki et al., 2016). In

Türkiye, both natural populations and cultivated areas in Denizli, Aydın, İzmir, and surrounding regions contribute to the production and economic significance of this species (Tonk et al., 2010; Demirci et al., 2022).

The essential oil of *O. onites* contains various volatile constituents, including carvacrol, thymol, p-cymene, γ-terpinene, and linalool, whose relative proportions may vary considerably among samples. Previous studies have reported high carvacrol concentrations ranging from 76.8% to 88.71%, while values between 65.5% and 91.0% have been documented in other samples (Baydar et al., 2004; Altıntas et al., 2013; Erenler et al., 2018; Demirci et al., 2022). Similarly, the reported variation in linalool content, ranging from 0.3% to 17.9%, indicates substantial diversity in the volatile composition of this species (Demirci et al., 2022). Differences in the relative abundance of major constituents, particularly carvacrol and thymol, suggest that the chemical diversity of *O. onites* should be evaluated on the basis of its overall volatile composition rather than individual compounds alone (Tekin et al., 2025).

The chemical diversity of *O. onites* is not restricted to carvacrol-rich samples, as volatile profiles dominated by linalool have also been reported (Özkan and Erdoğan, 2011; Taşdemir et al., 2019). The identification of carvacrol- and thymol-dominant chemical types in selected clones further supports the occurrence of distinct compositional profiles within the species. However, the lack of consistent correspondence between chemical differentiation and genetic markers suggests that chemical diversity cannot always be adequately explained by a single criterion (Tonk et al., 2010). These findings emphasize the importance of considering not only the dominant constituents but also the relative distribution of other volatile compounds when evaluating chemical differentiation among *O. onites* samples.

Essential oil yield and composition in aromatic plants may be associated with several factors, including phenological stage, harvesting time, and growing conditions. Studies on *O. onites* have demonstrated that seasonal variation, time of day at harvest, and plant developmental stage may be associated with changes in essential oil composition (Yaldiz et al., 2005; Toncer et al., 2009; Özkan et al., 2010). Nevertheless, investigations conducted across localities representing different habitats, elevations, geological substrates, and bioclimatic conditions have shown that relationships between environmental variables and essential oil yield or constituent proportions are not always clearly established (Stefanaki et al., 2016). Therefore, differences in volatile composition should be interpreted by considering elevation alongside other habitat characteristics and sampling conditions.

The analytical method, extraction conditions, and plant organs examined are also important factors affecting the comparability of volatile compound profiles. Differences in the dominant constituents of leaf- and flower-derived essential oils highlight the influence of plant organs on chemical composition (Özer, 2020). Similarly, extraction methods and extraction duration have been reported to affect the relative distribution of volatile constituents (Altıntas et al., 2013; Demirci et al., 2022). Accordingly, essential oil compositions obtained by hydrodistillation and headspace volatile profiles determined using headspace solid-phase microextraction coupled with gas chromatography–mass spectrometry (HS-SPME/GC–MS) should be interpreted in light of their methodological differences and should not be considered directly equivalent. This distinction is essential for accurately comparing chemical profiles reported in different studies.

The compositional diversity of *O. onites* has also stimulated interest in its potential biological and technological applications. Previous investigations have examined the antibacterial, antifungal, antioxidant, and antiparasitic activities of its essential oil (Baydar et al., 2004; Altıntas et al., 2013; Özkan and Erdoğan, 2011; Taşdemir et al., 2019; Karan et al., 2021; Kubiliene et al., 2023). Furthermore, the evaluation of its essential oil and major constituents in experimental biological models and various technological applications has contributed to increasing scientific interest in the phytochemical properties of this species (Spyridopoulou et al., 2019; Kılınç et al., 2021; Becer et al., 2022; Aydın et al., 2025). However, the biological activities reported in these studies are beyond the direct scope of the present investigation. Instead, the characterization of volatile compound profiles provides chemical data that may serve as a basis for future studies on biological activity.

Although several studies have investigated the essential oil composition, chemical diversity, and biological properties of *O. onites*, a comparative assessment of samples collected from different localities and elevation ranges in Denizli Province using a standardized HS-SPME/GC–MS approach provides an opportunity to investigate regional variation in volatile composition. In particular, examining samples characterized by different relative abundances of carvacrol and linalool, together with other volatile

constituents and chemical classes, may provide further insight into local chemical heterogeneity within the species. Moreover, multivariate analysis of compound-level variation enables chemical similarities and differences among samples to be evaluated within a broader compositional framework rather than solely on the basis of dominant constituents.

The present study aimed to characterize the volatile compound profiles of seven *O. onites* sample groups (O1–O7) collected from different localities in Denizli Province, Türkiye, across an elevation range of 200–1600 m, using HS-SPME/GC–MS, to evaluate the relative distribution of chemical classes, and to investigate chemical differentiation among samples. For this purpose, the distribution of volatile compounds was examined using heatmap visualization and principal component analysis (PCA), while variations in dominant constituents, particularly carvacrol and linalool, and major chemical classes were compared among samples. The study is expected to contribute to the documentation of volatile chemical diversity in naturally occurring *O. onites* populations in Denizli Province and to provide baseline data for future ecological and phytochemical investigations. Elevation was considered an environmental variable in the comparison of samples; however, no causal relationship between elevation and the observed chemical differences was assumed.

2.MATERIAL AND METHODS

2.1. Study Area and Plant Material

This study was conducted to investigate the natural distribution of *O. onites* throughout Denizli Province, Türkiye, and to characterize its occurrence across different elevation ranges. For this purpose, extensive field surveys were carried out to identify the natural habitats of the species. The surveys covered areas representing diverse habitat and environmental conditions within the administrative boundaries of Denizli Province.

Field surveys identified a total of 110 localities where *O. onites* naturally occurred. The distribution of these localities across elevation ranges revealed that 5 localities were situated at 200–400 m, 8 at 401–600 m, 21 at 601–800 m, 33 at 801–1000 m, 21 at 1001–1200 m, 19 at 1201–1400 m, and 3 at 1401–1600 m above sea level. The highest number of recorded localities occurred within the 801–1000 m elevation range, while the majority were distributed between approximately 600 and 1400 m (Figure 1).

To obtain plant material for chemical analysis, seven sampling localities were selected from the 110 identified localities to represent different elevation ranges and habitat characteristics. The selected samples were designated O1–O7 and used for comparative evaluation of volatile compound profiles. Detailed information on the sampling localities, elevation ranges, and sample codes is presented in Table 1.

At each of the seven selected localities, aboveground plant material was collected from ten individual *O. onites* plants growing under natural conditions. Plant material collected from individuals within the same locality was pooled to obtain a single composite sample representing the pooled plant material collected at that locality. Accordingly, seven composite samples, designated O1–O7, were prepared and analyzed using headspace solid-phase microextraction coupled with gas chromatography–mass spectrometry (HS-SPME/GC–MS) to characterize their volatile compound profiles. The resulting data were comparatively evaluated based on the volatile compositions of the composite samples representing the seven sampling localities.

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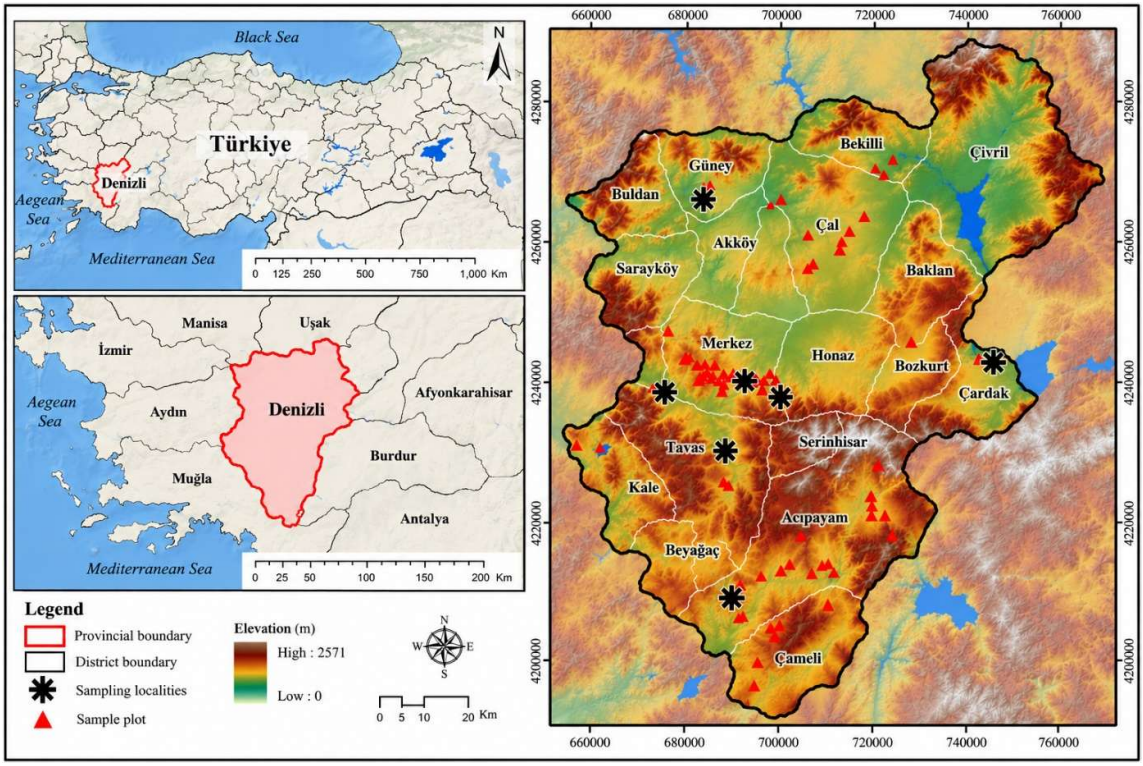


Figure 1. Geographic location of Denizli Province in Türkiye and distribution of sampling localities and sample plots within the study area.

Table 1. Sample codes, collection localities, habitat characteristics, and elevation ranges of *O. onites* samples used for chemical analyses.

Sample code	**District / Region**	**Sampling locality and habitat characteristics**	**Elevation (m)**
O1	Merkezefendi / Pamukkale	Central Denizli; open habitats associated with *Quercus coccifera* communities	600–800
O2	Tavas	Pınarlar Village; openings within *Pinus brutia* forests	1000–1200
O3	Tavas	Karahisar neighborhood; forest openings associated with *Pinus brutia* and J*uniperus* spp. communities	1400–1600
O4	Güney	Güney region; openings within *Pinus brutia* forests	200–400
O5	Çardak	Çardak Village; openings within *Juniperus* spp. stands	800–1000
O6	Acıpayam	Alcı Village; open habitats among *Quercus coccifera* communities	1000–1200
O7	Honaz	Central Honaz; openings within *Pinus nigra* forests	1200–1400

The aboveground parts (flowers, leaves, and shoots/stems) of *O. onites* plants collected during field surveys were placed in airtight bags and transported to the Herbarium of the Faculty of Forestry, Isparta University of Applied Sciences. Prior to chemical analysis, the plant material was air-dried at room temperature in a shaded, well-ventilated environment without exposure to direct sunlight. Following drying, the samples were stored in a refrigerator at 4 °C until analysis. The dried plant materials were subsequently used for chemical analyses to characterize and compare the volatile compound profiles of samples collected from different localities.

2.2. Determination of Volatile Compounds by HS-SPME/GC–MS

The volatile compound profiles of *O. onites* samples were determined using headspace solid-phase microextraction (HS-SPME) coupled with gas chromatography–mass spectrometry (GC–MS). For HS-SPME analysis, 2 g of dried plant material was weighed into a 10 mL vial and incubated at 60 °C for 30 min. Volatile compounds released into the headspace were extracted using a fused-silica fiber coated with 75 µm Carboxen/Polydimethylsiloxane (CAR/PDMS). Following extraction, the fiber was immediately introduced into the injection port of a GC–MS system (Shimadzu GCMS-QP2010 Plus) equipped with a Restek Rxi-5Sil MS capillary column (30 m × 0.25 mm i.d., 0.25 µm film thickness).

The GC oven temperature was initially maintained at 40 °C for 2 min and subsequently increased to 250 °C at a heating rate of 4 °C/min. The injector and detector temperatures were set at 250 °C. Mass spectrometric detection was performed using electron impact ionization (EI) at an ionization energy of 70 eV. Helium was used as the carrier gas at a flow rate of 1.61 mL/min. Volatile compounds were tentatively identified by comparing their mass spectra with reference spectra available in the Wiley, NIST, Tutor, and FFNSC mass spectral libraries.

2.3. Statistical Analyses

2.3.1. Heatmap Analysis

Heatmap analysis was performed to visualize variations in volatile compound profiles among the samples identified by GC–MS. A data matrix was constructed using the relative percentage abundances of 63 volatile compounds detected across seven *O. onites* samples (O1–O7). To facilitate comparisons of relative variations among samples, the data for each compound were independently standardized using Z-score normalization. For each compound, the mean value across the seven samples was subtracted from its value in each sample, and the resulting difference was divided by the corresponding standard deviation.

The heatmap was generated from the standardized dataset, with rows representing individual volatile compounds and columns representing the seven samples. In the color scale, red tones indicated standardized values above the mean abundance of a given compound across the seven samples, whereas blue tones represented values below the corresponding mean. Compounds with values below the detection limit or absent from the data matrix were assigned a value of zero for visualization purposes. This approach enabled a comparative visualization of the relative distribution of volatile compounds and differences in chemical profiles among samples.

2.3.2. Principal Component Analysis (PCA)

The volatile compounds identified by GC–MS were classified into six chemical groups: monoterpene hydrocarbons (MH), aromatic hydrocarbons (AH), oxygenated monoterpenes (OM), sesquiterpene hydrocarbons (SH), oxygenated sesquiterpenes (OS), and other compounds (OC). Principal component analysis (PCA) was performed using the relative percentage abundances of these six chemical classes in the seven samples (O1–O7).

Because the percentage compositions of the chemical classes represent compositional data subject to a constant-sum constraint, a centered log-ratio (CLR) transformation was applied prior to PCA. PCA was subsequently performed on the CLR-transformed data matrix to evaluate differences in chemical composition among samples and to identify the chemical classes contributing to these differences. The resulting principal component scores and variable loadings were visualized using a two-dimensional PCA biplot.

International Journal of Progressive Sciences and Technologies (IJPSAT)
ISSN: 2509-0119.
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https://ijpsat.org/
Vol. 59 No. 2 October 2026, pp. 933-951

3. RESULTS

3.1. Volatile Compound Profiles Determined by HS-SPME/GC–MS

A total of 63 volatile compounds were identified across the seven *O. onites* samples (O1–O7) collected from different localities and elevation ranges in Denizli Province, Türkiye. Oxygenated monoterpenes (OM) and sesquiterpene hydrocarbons (SH) were generally the predominant chemical classes. The relative abundance of oxygenated monoterpenes ranged from 36.80% to 76.93%, representing the dominant chemical class in all samples except O5, collected from Çardak (800–1000 m).

Carvacrol was the predominant individual compound in samples O1–O5, collected from central Denizli (600–800 m; O1), Pınarlar Village in Tavas (1000–1200 m; O2), Karahisar neighborhood in Tavas (1400–1600 m; O3), Güney (200–400 m; O4), and Çardak (800–1000 m; O5), with relative abundances ranging from 25.38% to 49.20%. In contrast, linalool was the dominant compound in samples collected from Alcı Village in Acıpayam (1000–1200 m; O6) and central Honaz (1200–1400 m; O7), accounting for 67.92% and 53.28% of the volatile profiles, respectively.

The relative abundance of sesquiterpene hydrocarbons ranged from 16.06% to 51.68%, with the highest proportion recorded in sample O5 from Çardak. Overall, the results showed marked differences in relative abundance in volatile compound composition among the investigated localities (Table 2).

3.2. Distribution of Volatile Compounds by Chemical Class

The percentage distribution of volatile compounds among chemical classes in samples O1–O7 is presented in Figure 2. The identified compounds were classified into six groups: monoterpene hydrocarbons (MH), aromatic hydrocarbons (AH), oxygenated monoterpenes (OM), sesquiterpene hydrocarbons (SH), oxygenated sesquiterpenes (OS), and other compounds (OC). Examination of the chemical class distributions revealed that oxygenated monoterpenes generally constituted the predominant group, although their relative abundances varied among samples.

The relative abundance of oxygenated monoterpenes ranged from 36.80% to 76.93%, with the highest proportion recorded in O6 (76.93%) and the lowest in O5 (36.80%). The corresponding proportions in O1, O2, O3, O4, and O7 were 57.49%, 63.02%, 57.02%, 52.27%, and 63.59%, respectively. Sesquiterpene hydrocarbons represented another major chemical class, accounting for 16.06–51.68% of the volatile profiles, with the highest proportion observed in O5 (51.68%). Unlike the other samples, O5 was characterized by a higher proportion of sesquiterpene hydrocarbons than oxygenated monoterpenes. Relatively high proportions of sesquiterpene hydrocarbons were also recorded in O4 (35.29%) and O7 (32.17%).

Monoterpene hydrocarbons accounted for 2.79–16.67% of the volatile profiles, with the highest proportions observed in O2 (16.67%) and O3 (16.12%) and the lowest in O7 (2.79%). Aromatic hydrocarbons ranged from 0.55% to 4.42%, reaching their highest proportion in O3 (4.42%) and their lowest in O7 (0.55%). Oxygenated sesquiterpenes constituted a relatively minor fraction of the total volatile profiles, ranging from 0.15% to 0.79%. The highest proportion was recorded in O1 (0.79%), whereas the lowest was observed in O6 (0.15%). In O7, oxygenated sesquiterpenes accounted for 0.60% of the volatile profile. The proportion of other compounds ranged from 0.15% to 0.61%, with the highest value recorded in O7 (0.61%) and the lowest in O1 (0.15%).

Overall, oxygenated monoterpenes were the predominant chemical class in O1, O2, O3, O4, O6, and O7, whereas sesquiterpene hydrocarbons predominated in O5. Sample O6 was distinguished by its high proportion of oxygenated monoterpenes (76.93%), while O5 exhibited the highest proportion of sesquiterpene hydrocarbons (51.68%). Samples O2 and O3 were characterized by relatively higher proportions of monoterpene hydrocarbons than the other samples. Furthermore, the high proportions of oxygenated monoterpenes accompanied by relatively low levels of monoterpene hydrocarbons in O6 and O7 distinguished these samples in terms of their chemical class distributions. Collectively, these findings demonstrate considerable variation in the relative distribution of chemical classes among the volatile compound profiles of *O. onites* samples.

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ISSN: 2509-0119.
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https://ijpsat.org/
Vol. 59 No. 2 October 2026, pp. 933-951

Table 2. Volatile compound profiles of *O. onites* samples (O1–O7) determined by HS-SPME/GC–MS.

No.	RT (min)	Compound	O1	O2	O3	O4	O5	O6	O7	Molecular Formula	Chemical Class
1	8.421	α-Thujene	0.48	0.75	0.88	0.61	0.41	0.20	0.18	$C_{10}H_{16}$	MH
2	8.656	α-Pinene	0.24	0.28	0.26	0.29	0.15	0.09	0.09	$C_{10}H_{16}$	MH
3	9.235	Camphene	0.15	0.11	0.07	0.10	0.05	0.10	0.10	$C_{10}H_{16}$	MH
4	10.133	Sabinene	0.11	0.08	0.08	0.22	0.14	0.15	0.11	$C_{10}H_{16}$	MH
5	10.277	β-Pinene	0.07	0.08	0.07	0.10	0.05	0.03	0.04	$C_{10}H_{16}$	MH
6	10.519	Octen-3-ol	0.15	0.31	0.18	0.24	0.21	0.20	0.26	$C_{8}H_{16}O$	OC
7	10.834	β-Myrcene	2.48	3.22	3.62	2.58	1.95	1.68	1.30	$C_{10}H_{16}$	MH
8	11.404	Phellandrene	0.18	0.30	0.32	0.19	0.15	0.06	0.04	$C_{10}H_{16}$	MH
9	11.499	Δ-3-Carene	0.05	0.09	0.10	0.07	0.05	-	-	$C_{10}H_{16}$	MH
10	11.825	α-Terpinene	0.74	1.85	1.70	0.70	0.75	0.18	0.10	$C_{10}H_{16}$	MH
11	12.134	o-Cymene	2.55	3.73	4.42	3.87	2.98	0.63	0.55	$C_{10}H_{14}$	AH
12	12.315	Limonene	0.21	0.36	0.38	0.31	0.25	0.35	0.24	$C_{10}H_{16}$	MH
13	12.329	β-Phellandrene	0.25	0.35	0.37	0.32	0.18	-	-	$C_{10}H_{16}$	MH
14	12.405	1,8-Cineole	0.03	0.03	0.03	0.03	0.02	-	-	$C_{10}H_{18}O$	OM
15	12.638	cis-Ocimene	0.04	0.06	-	0.05	0.08	0.16	0,12	$C_{10}H_{16}$	MH
16	13.031	trans-β-Ocimene	0.21	0.32	0.27	-	0.19	0.29	0.20	$C_{10}H_{16}$	MH
17	13.464	γ-Terpinene	2.79	8.63	7.80	2.16	3.23	0.31	0.20	$C_{10}H_{16}$	MH
18	13.926	trans-Sabinene hydrate	0.98	0.71	0.80	1.13	1.21	0.24	0.64	$C_{10}H_{20}O$	OM
19	14.504	α-Terpinolene	0.15	0.19	0.20	0.21	0.15	0.10	0.07	$C_{10}H_{16}$	MH
20	14.601	trans-Linalool oxide	-	-	-	-	-	-	0.31	$C_{10}H_{18}O_2$	OM
21	15.128	Linalool	0.91	17.76	2.54	3.59	0.37	67.92	53.28	$C_{10}H_{18}O$	OM
22	16.097	Camphenol	0.03	0.09	0.20	0.05	0.06	-	-	$C_{10}H_{16}O$	OM
23	17.848	endo-Borneol	1.04	0.80	0.63	0.44	0.34	0.43	0.59	$C_{10}H_{18}O$	OM
24	18.180	Terpinen-4-ol	0.32	0.34	-	0.32	0.20	0.05	0.07	$C_{10}H_{18}O$	OM
25	18.983	α-Terpineol	-	-	0.03	-	-	-	-	$C_{10}H_{18}O$	OM
26	20.364	Thymyl methyl ether	0.11	0.08	0.09	0,17	0.08	-	-	$C_{11}H_{16}O$	OM
27	18.649	(E)-3-Hexenyl butyrate	-	-	-	-	-	-	0.11	$C_{10}H_{18}O_2$	OC

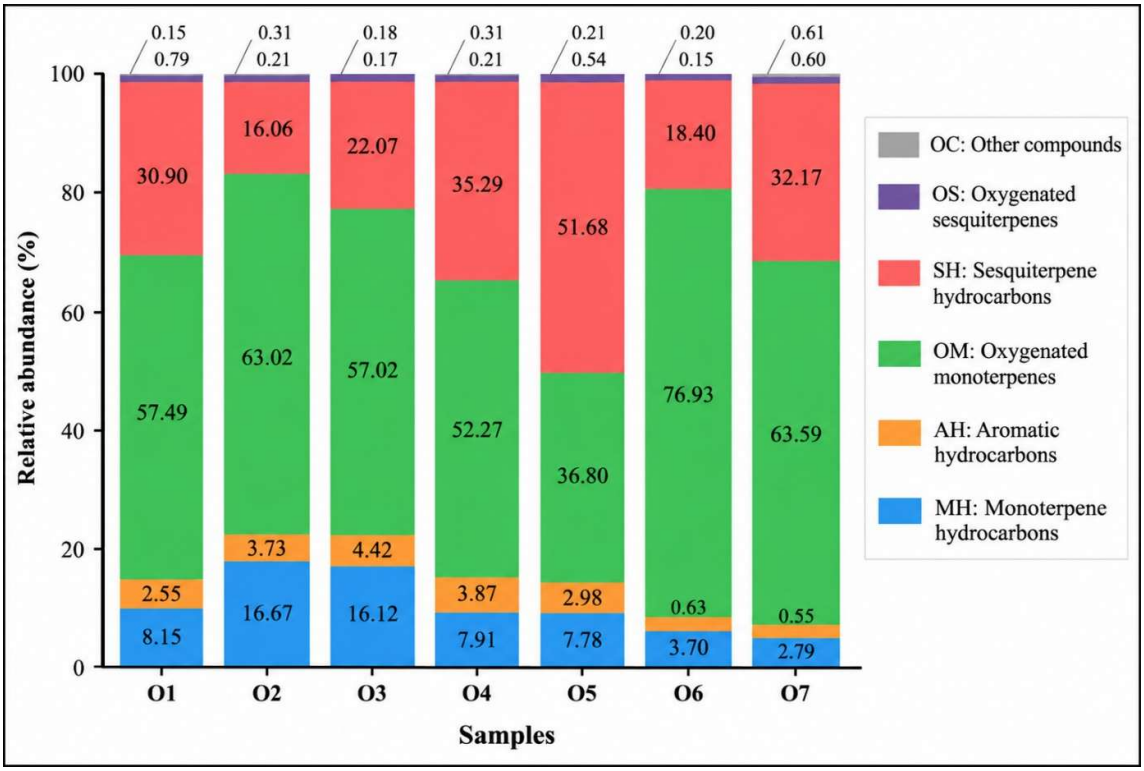
28	20.592	Carvone	-	-	-	-	-	0.12	0.08	$C_{10}H_{14}O$	OM
29	20.082	Butanoic acid	-	-	-	0.07	-	-	0.24	$C_4H_8O_2$	OC
30	20.808	Linalyl acetate	7.62	3.22	2.8	9.04	8.85	0.73	2.85	$C_{12}H_{20}O_2$	OM
31	22.370	Thymol	0.21	1.44	0.26	0.16	0.08	0.07	0.02	$C_{10}H_{14}O$	OM
32	22.964	Carvacrol	46.08	38.40	49.2	37.25	25.38	7.37	5.75	$C_{10}H_{14}O$	OM
33	23.717	Δ-Elemene	-	-	-	-	-	0.08	-	$C_{15}H_{24}$	SH
34	21.744	Terpendiol II	-	-	-	-	-	-	0.13	$C_{15}H_{28}O_2$	OS
35	24.254	α-Cubebene	0.03	0.04	0.05	0.14	0.16	0.09	0.04	$C_{15}H_{24}$	SH
36	24.872	Carvacryl acetate	0.13	0.15	0.44	0.03	0.14	-	-	$C_{12}H_{16}O_2$	OM
37	25.226	α-Copaene	0.03	0.06	0.07	0.19	0.26	0.10	0.05	$C_{15}H_{24}$	SH
38	25.354	Geranyl butyrate	0.03	-	-	0.06	0.07	-	-	$C_{14}H_{24}O_2$	OM
39	25.492	β-Bourbonene	0.05	0.18	0.14	0.49	0.69	0.22	0.07	$C_{15}H_{24}$	SH
40	25.715	β-Elemene	0.03	-	0.05	0.18	0.28	0.08	0.03	$C_{15}H_{24}$	SH
41	26.761	Caryophyllene	7.81	5.41	7.14	7.04	6.88	5.77	7.28	$C_{15}H_{24}$	SH
42	26.960	Alloaromadendrene	0.05	0.04	0.06	-	-	-	-	$C_{15}H_{24}$	SH
43	27.043	β-Cubebene	0.04	0.06	0.08	0.20	0.24	0.11	0.03	$C_{15}H_{24}$	SH
44	27.162	α- trans-Bergamotene	0.37	0.27	0.29	1.60	1.49	0.35	1.03	$C_{15}H_{24}$	SH
45	27.331	Aromadendrene	0.91	0.82	1.04	0.63	0.37	0.14	0.04	$C_{15}H_{24}$	SH
46	27.393	β-Cederene	-	-	-	0.15	0.22	-	0.12	$C_{15}H_{24}$	SH
47	27.561	Cadina-1(6)	0.22	0.10	0.13	0.18	0.39	0.08	0.23	$C_{15}H_{24}$	SH
48	27.815	β-Farnesene	0.15	-	0.11	0.39	0.96	-	0.49	$C_{15}H_{24}$	SH
49	27.880	α-Humulene	0.46	0.34	0.39	0.42	0.28	0.39	0.39	$C_{15}H_{24}$	SH
50	28.098	Bicyclosesquiphellandrene	0.30	0.08	0.12	0.24	0.62	0.15	0.32	$C_{15}H_{24}$	SH
51	28.523	γ-Muurolene	0.05	0.09	0.13	0.34	0.45	0.24	0.09	$C_{15}H_{24}$	SH
52	28.722	Germacrene D	1.03	1.31	1.9	5.81	8.03	3.11	1.48	$C_{15}H_{24}$	SH
53	29.058	Viridiflorene	0.49	0.45	0.57	0.52	0.57	0.25	0.09	$C_{15}H_{24}$	SH
54	29.191	Bicyclogermacrene	0.17	0.32	0.23	0.16	-	1.04	0.33	$C_{15}H_{24}$	SH
55	29.287	α-Muurolene	0.05	0.04	0.06	0.21	0.28	0.11	0.08	$C_{15}H_{24}$	SH
56	29.703	β-Bisabolene	16.46	5.83	8.57	14.58	26.98	5.07	17.51	$C_{15}H_{24}$	SH
57	29.783	γ-Cadinene	1.22	0.21	0.28	0.43	-	0.32	0.97	$C_{15}H_{24}$	SH

International Journal of Progressive Sciences and Technologies (IJPSAT)
ISSN: 2509-0119.
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58	29.955	Δ-Cadinene	0.19	0.18	0.25	0.54	0.73	0.43	0.52	$C_{15}H_{24}$	SH
59	30.095	β-Sesquiphellandrene	0.41	0.12	0.22	0.49	0.99	0.12	0.51	$C_{15}H_{24}$	SH
60	30.610	α-Caryophyllene	0.38	0.11	0.19	0.36	0.81	0.15	0.47	$C_{15}H_{24}$	SH
61	31.735	Spathulenol	0.05	0.04	0.03	0.04	0.03	0.03	0.02	$C_{15}H_{24}O$	OS
62	31.887	Caryophyllene oxide	0.16	0.12	0.11	0.17	0.10	0.12	0.10	$C_{15}H_{24}O$	OS
63	33.697	α-Muurolol	0.58	0.05	0.03	-	0.41	-	0.35	$C_{15}H_{26}O$	OS
Total			100.00	100.00	100.00	100.00	100.00	100.00	100.00	–: Indicates relative abundances below 0.01%..	
MH: Monoterpene hydrocarbons			8.15	16.67	16.12	7.91	7.78	3.70	2.79		
AH: Aromatic hydrocarbons			2.55	3.73	4.42	3.87	2.98	0.63	0.55		
OM: Oxygenated monoterpenes			57.49	63.02	57.02	52.27	36.80	76.93	63.59		
SH: Sesquiterpene hydrocarbons			30.90	16.06	22.07	35.29	51.68	18.40	32.17		
OS: Oxygenated sesquiterpenes			0.79	0.21	0.17	0.21	0.54	0.15	0.60		
OC: Other compounds			0.15	0.31	0.18	0.31	0.21	0.20	0.61		

O1: Denizli, Central Region (600–800 m); O2: Tavas, Pınarlar Village (1000–1200 m); O3: Tavas, Karahisar Neighborhood (1400–1600 m); O4: Güney, Pinus brutia forest openings (200–400 m); O5: Çardak, Çardak Village (800–1000 m); O6: Acıpayam, Alcı Village (1000–1200 m); O7: Honaz, Central Region (1200–1400 m).

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Vol. 59 No. 2 October 2026, pp. 933-951



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Figure 2. Relative abundance (%) of volatile compound classes in *O. onites* samples (O1–O7).

3.3. Heatmap Analysis of Volatile Compound Profiles

The Z-score-based heatmap of the relative abundances of 63 volatile compounds identified in samples O1–O7 revealed considerable variation in volatile composition among the samples. In the heatmap, red tones indicate values above the mean abundance of a given compound across the samples, whereas blue tones represent values below the corresponding mean. Therefore, color intensities reflect relative variations among samples rather than the absolute percentage abundances of individual compounds.

Regarding monoterpene hydrocarbons, samples O2 and O3 exhibited similar compositional patterns. These samples showed relatively higher abundances of α-thujene, β-myrcene, α-terpinene, o-cymene, and γ-terpinene compared with most other samples. In particular, γ-terpinene accounted for 8.63% and 7.80% of the volatile profiles in O2 and O3, respectively, whereas substantially lower proportions were recorded in O6 (0.31%) and O7 (0.20%). Similarly, o-cymene reached its highest proportion in O3 (4.42%), compared with 0.63% and 0.55% in O6 and O7, respectively. These findings indicate that O2 and O3 were distinguished from the other samples by their relatively higher abundances of certain monoterpene hydrocarbons.

Among oxygenated compounds, linalool and carvacrol exhibited particularly pronounced variation across the samples. Linalool was highly abundant in O6 (67.92%) and O7 (53.28%), whereas considerably lower proportions were recorded in O1 (0.91%) and O5 (0.37%). In contrast, carvacrol was present at relatively high proportions in O1 (46.08%), O2 (38.40%), O3 (49.20%), and O4 (37.25%), but occurred at substantially lower levels in O6 (7.37%) and O7 (5.75%). These contrasting patterns indicate distinct volatile compositional profiles, characterized predominantly by carvacrol in O1–O5 and by linalool in O6 and O7.

Regarding sesquiterpene hydrocarbons, O4 and particularly O5 exhibited relatively high abundances of several compounds. β-Bisabolene reached its highest proportion in O5 (26.98%) and was also present at considerable levels in O1 (16.46%), O4 (14.58%), and O7 (17.51%). Similarly, germacrene D was more abundant in O4 (5.81%) and O5 (8.03%) than in the other samples. Other sesquiterpene hydrocarbons, including β-bourbonene, β-elemene, α-copaene, and γ-muurolene, also exhibited relatively high abundances in O4 and O5, further distinguishing these samples in terms of their sesquiterpene composition.

Overall, the heatmap revealed distinct compositional patterns among the seven samples. Samples O2 and O3 were characterized by relatively high abundances of several monoterpene hydrocarbons, whereas O4 and O5 exhibited higher proportions of various sesquiterpene hydrocarbons. Samples O6 and O7 were distinguished by their high linalool content, while O1 was characterized by relatively high proportions of carvacrol and β-bisabolene. These findings demonstrate that the volatile compound profiles of the investigated *O. onites* samples were heterogeneous, with different compounds predominating across sampling localities. Nevertheless, heatmap analysis provides a descriptive visualization of compositional similarities and differences and does not, by itself, establish the statistical significance of the observed variations (Figure 3).

3.4. Principal Component Analysis (PCA) of Volatile Compound Classes

Principal component analysis (PCA) was performed on centered log-ratio (CLR)-transformed data to evaluate variation in the relative distribution of volatile compound classes and compositional differences among samples O1–O7 (Figure 4). The first principal component (PC1) explained 64.57% of the total variance, while the second principal component (PC2) accounted for 23.25%. Together, the first two principal components explained 87.82% of the total variance, indicating that a substantial proportion of the variability in chemical class composition was represented in the two-dimensional PCA space.

Examination of the PCA biplot revealed that samples O2 and O3 were positioned close to each other along the positive PC1 axis, whereas O6 and O7 were separated in the negative PC1 direction. The positioning of O2 and O3 was associated with the relative contributions of monoterpene hydrocarbons (MH) and aromatic hydrocarbons (AH). Monoterpene hydrocarbons accounted for 16.67% and 16.12% of the volatile profiles in O2 and O3, respectively, while aromatic hydrocarbons represented 3.73% and 4.42% in the corresponding samples.

Samples O6 and O7 were positioned along the negative PC1 axis, indicating compositional differentiation from O2 and O3. Oxygenated monoterpenes (OM) accounted for 76.93% and 63.59% of the volatile profiles in O6 and O7, respectively, representing the predominant chemical class in both samples. In contrast, monoterpene hydrocarbons were present at relatively low proportions of 3.70% and 2.79%, while aromatic hydrocarbons accounted for 0.63% and 0.55% in O6 and O7, respectively. These differences reflect distinct relative distributions of chemical classes in these samples.

International Journal of Progressive Sciences and Technologies (IJPSAT)
ISSN: 2509-0119.
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Vol. 59 No. 2 October 2026, pp. 933-951

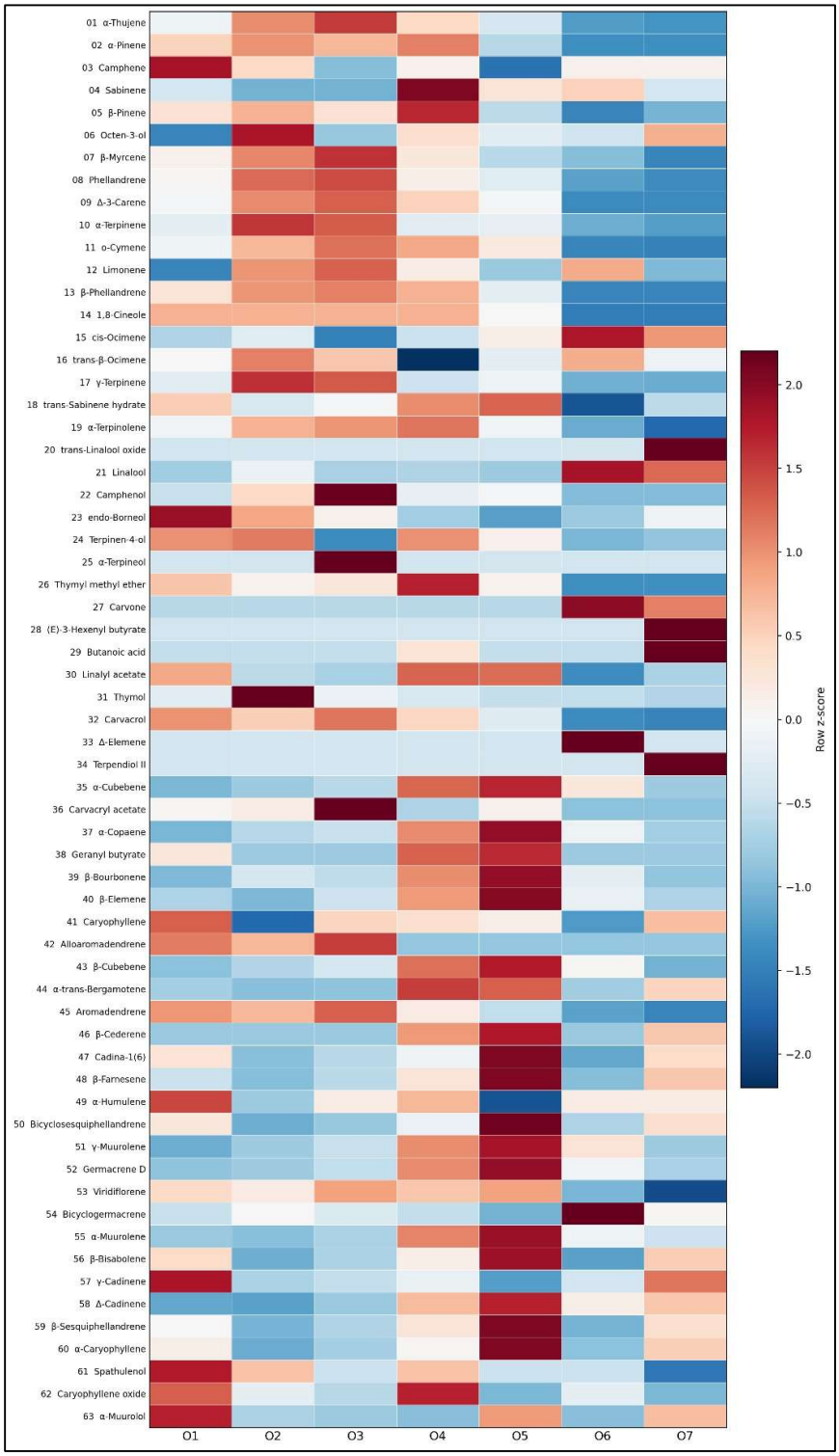
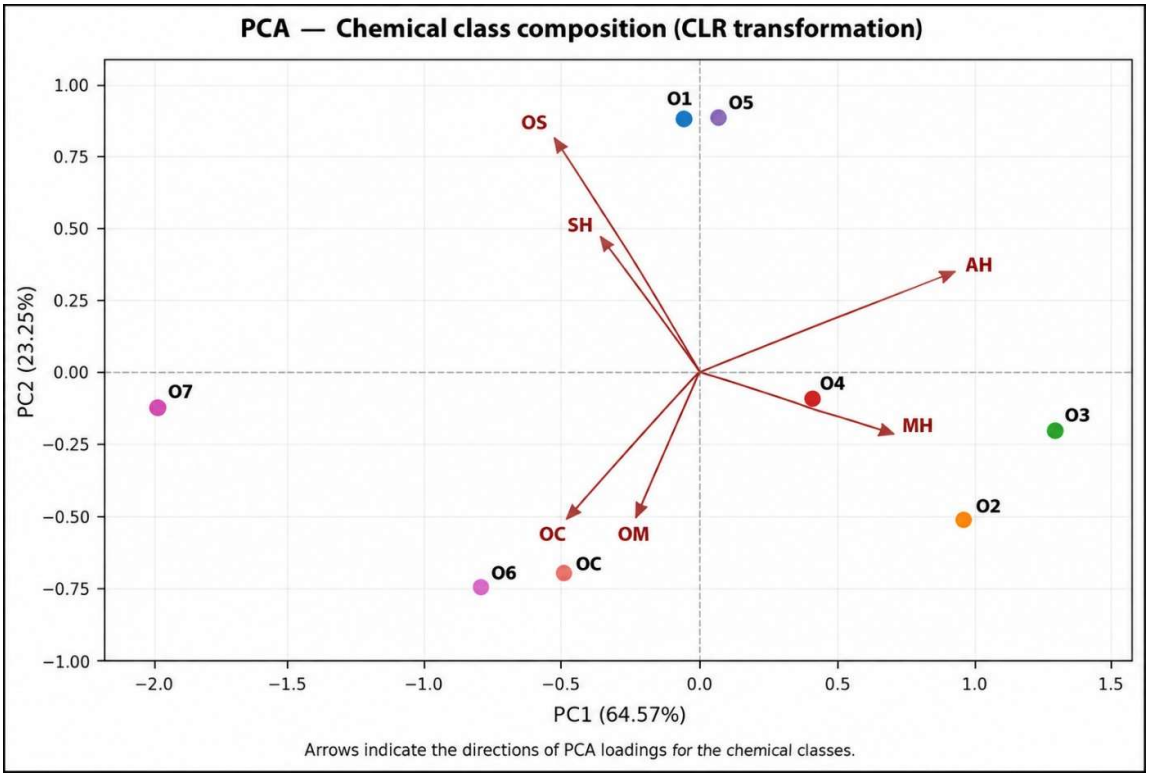


Figure 3. Z-score-standardized heatmap of the relative abundances of 63 volatile compounds in *O. onites* samples (O1–O7).

International Journal of Progressive Sciences and Technologies (IJPSAT)
ISSN: 2509-0119.
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Vol. 59 No. 2 October 2026, pp. 933-951

Along the second principal component (PC2), samples O1 and O5 were positioned relatively close to each other on the positive side of the axis. Sesquiterpene hydrocarbons (SH) accounted for 30.90% and 51.68% of the volatile profiles in O1 and O5, respectively. Notably, O5 exhibited a higher proportion of sesquiterpene hydrocarbons (51.68%) than oxygenated monoterpenes (36.80%), distinguishing its chemical class composition from that of the other samples. Furthermore, oxygenated sesquiterpenes (OS) accounted for 0.79% and 0.54% in O1 and O5, respectively, suggesting that this chemical class may have contributed to their positioning in the PCA space.

Overall, the PCA results revealed variation in the relative distribution of volatile compound classes among the seven *O. onites* samples. Samples O2 and O3 were characterized by relatively higher proportions of monoterpene hydrocarbons and aromatic hydrocarbons, whereas O6 and O7 exhibited a predominance of oxygenated monoterpenes. Sample O5 was particularly distinguished by its high proportion of sesquiterpene hydrocarbons. These findings indicate distinct chemical class profiles among the investigated samples, as reflected by their relative proximity or separation in the PCA biplot.



O1: Denizli, Central Region (600–800 m); O2: Tavas, Pınarlar Village (1000–1200 m); O3: Tavas, Karahisar Neighborhood (1400–1600 m); O4: Güney, Pinus brutia forest openings (200–400 m); O5: Çardak, Çardak Village (800–1000 m); O6: Acıpayam, Alcı Village (1000–1200 m); O7: Honaz, Central Region (1200–1400 m).

Figure 4. Principal component analysis (PCA) biplot of six volatile compound classes in *O. onites* samples (O1–O7) based on centered log-ratio (CLR)-transformed data.

4. DISCUSSION

A total of 63 volatile compounds were identified by HS-SPME/GC–MS analysis in *O. onites* samples collected from seven sampling localities across an elevation range of 200–1600 m in Denizli Province, Türkiye. The variation in the relative

abundances of individual compounds among samples revealed considerable chemical heterogeneity across the investigated localities. Carvacrol was the predominant compound in samples O1–O5 (25.38–49.20%), whereas linalool predominated in O6 and O7, accounting for 67.92% and 53.28%, respectively. These findings indicate two contrasting volatile compositional profiles, primarily characterized by carvacrol or linalool dominance. Such differentiation reflects not only the diversity of identified compounds but also differences in the relative distribution of major constituents among samples.

The identification of carvacrol as a major constituent is consistent with previous investigations of *O. onites*. Baydar et al. (2004) reported a carvacrol content of 86.9% in the essential oil of this species, while Altıntaş

et al. (2013) reported values of 76.8% and 79.2% in essential oils obtained by hydrodistillation and microwave-assisted hydrodistillation, respectively. Economou et al. (2011) documented carvacrol proportions ranging from 72.3% to 89.2% in samples from Ikaria Island, whereas Stefanaki et al. (2016) reported values of 69.0–92.6% in samples from Chios Island. Similarly, cultivation studies conducted in Türkiye reported carvacrol proportions ranging from 68.64% to 81.32% (Katar and Katar, 2020) and from 77.16% to 84.59% (Can et al., 2021), depending on harvesting periods. In the present study, the relative abundance of carvacrol in O1–O5 (25.38–49.20%) was lower than most values reported in these hydrodistillation-based studies. However, this difference should not be interpreted as evidence of a biological reduction in carvacrol production. The present investigation characterized headspace volatile profiles using HS-SPME, whereas most previous studies analyzed essential oils obtained through hydrodistillation. Differences in the plant organs examined, extraction techniques, and analytical basis of the reported percentages limit direct quantitative comparisons between these approaches.

One of the most notable findings of the present study was the predominance of linalool in samples O6 (Alcı Village, Acıpayam District; 1000–1200 m) and O7 (Honaz District Center; 1200–1400 m), where its relative abundance reached 67.92% and 53.28%, respectively. In these samples, carvacrol accounted for only 7.37% and 5.75% of the volatile profiles. Although *O. onites* is commonly characterized as a carvacrol-rich species, Özkan and Erdoğan (2011) reported an essential oil profile containing 50.53% linalool, 24.52% carvacrol, and 15.66% thymol. Therefore, the predominance of linalool observed in the Denizli samples should not be regarded as entirely exceptional within this species. Nevertheless, the definitive classification of O6 and O7 as a linalool chemotype would require confirmation of consistent chemical profiles across different years, comparable phenological stages, and sufficient independent biological replicates, preferably supported by genetic evidence. Tonk et al. (2010) identified carvacrol- and thymol-dominant chemical differentiation among *O. onites* clones and reported that chemical profiles did not consistently correspond to genetic structure. These observations support the view that chemical differentiation within the species cannot be attributed exclusively to a single environmental or hereditary factor.

Regarding chemical classes, oxygenated monoterpenes (OM) accounted for 36.80–76.93% of the volatile profiles, whereas sesquiterpene hydrocarbons (SH) represented 16.06–51.68%, indicating that variation at the individual compound level was also reflected in the relative distribution of chemical classes. Sample O6 exhibited the highest proportion of oxygenated monoterpenes (76.93%), followed by O7 (63.59%). In contrast, sesquiterpene hydrocarbons constituted the predominant chemical class in O5 (Çardak Village, Çardak District; 800–1000 m), reaching 51.68%. In this sample, β-bisabolene (26.98%) and germacrene D (8.03%) together accounted for 35.01% of the volatile profile, indicating that O5 differed from the other samples not only in its carvacrol and linalool proportions but also in its sesquiterpene composition. Monoterpene hydrocarbons (MH) ranged from 2.79% to 16.67%, with the highest proportions recorded in O2 (16.67%) and O3 (16.12%) and the lowest in O7 (2.79%). The relative abundance of γ-terpinene was higher in O2 (8.63%) and O3 (7.80%) than in O6 (0.31%) and O7 (0.20%), indicating that this compound was more abundant in the carvacrol-rich samples examined. Correspondingly, carvacrol accounted for 38.40% and 49.20% in O2 and O3, respectively, compared with 7.37% and 5.75% in O6 and O7. These patterns highlight differences in the relative distribution of individual monoterpene hydrocarbons and oxygenated monoterpenes among the investigated samples.

Elevation, temperature, solar radiation, moisture availability, soil properties, and plant developmental stage are among the factors that may influence secondary metabolite profiles in aromatic plants. However, no clear linear trend in carvacrol or linalool abundance across elevation ranges was evident in the present samples. For example, O2 (Pınarlar Village, Tavas District) and O6 (Alcı Village, Acıpayam District) were both collected within the 1000–1200 m elevation range, yet O2 exhibited a carvacrol-rich

profile, whereas O6 was dominated by linalool. Similarly, O3 (Karahisar Neighborhood, Tavas District), collected from the highest elevation range (1400–1600 m), was characterized by carvacrol predominance, while O7 (Honaz District Center; 1200–1400 m) exhibited a linalool-rich profile. Thus, the observed chemical differentiation did not show a consistent relationship with elevation in the sampled localities. Stefanaki et al. (2016) likewise reported no clear relationships between essential oil yield or major constituent proportions and habitat characteristics, geological substrate, elevation, or bioclimatic variables across 42 *O. onites* localities on Chios Island. In contrast, Kocabaş Oğuz and Kaplan (2023) demonstrated variation in the essential oil constituents of flowers and leaves among three natural habitats in Antalya, Türkiye. These findings suggest that relationships between environmental conditions and chemical composition may depend on geographical context and sampling design.

Studies involving closely related species have also reported contrasting findings regarding the influence of elevation on volatile composition. Öner and Yeşil (2023) reported that linalool reached 79.84% at lower elevations in Origanum majorana, whereas certain other constituents increased at higher elevations. Huamán-Castilla et al. (2020) investigated variation in volatile compounds associated with elevation and taxonomic differences in two Origanum taxa from Peru using HS-SPME/GC–MS and PCA. However, because these investigations did not specifically examine *O. onites*, their findings cannot be directly generalized to the Denizli samples. In a separate ecological investigation, Özdemir and Özkan (2016) identified elevation, solar radiation, topographic position, and temperature index as important variables associated with the potential distribution of *O. onites* on Ovacık Mountain in Antalya. Similarly, Gülsoy and Negiz (2014) reported relationships between the occurrence of this species and soil texture and species richness in the Lakes Region of Türkiye. Although these ecological studies provide valuable information on the habitat preferences of *O. onites*, they did not directly quantify volatile compound composition and therefore cannot independently explain the chemical variation observed in the present study.

Phenological stage and harvesting time should also be considered when interpreting differences in volatile composition among samples. Kızıl et al. (2008) reported that developmental stage influenced essential oil yield and composition in *O. onites*. Katar and Katar (2020) documented variation in carvacrol and γ-terpinene proportions across flowering stages, while Can et al. (2021) demonstrated associations between ontogenetic and diurnal variation and essential oil composition. In the present study, phenological stage, time of collection, exposure conditions, and genetic background were not investigated as independently controlled experimental factors. Consequently, the relative contributions of these variables to the observed differences among localities could not be determined. Future investigations incorporating independent biological replicates, repeated sampling across years at comparable phenological stages, microclimatic measurements, and soil analyses would provide a more robust basis for evaluating the factors associated with chemical differentiation.

Heatmap analysis revealed differences in the relative distribution of 63 volatile compounds among the seven *O. onites* samples. Samples O2 and O3 exhibited relatively higher abundances of certain monoterpene hydrocarbons, O4 and O5 were characterized by several sesquiterpene hydrocarbons, and O6 and O7 were distinguished particularly by their high linalool proportions. These patterns indicate that chemical differentiation among samples cannot be adequately described by a single dominant constituent. Nevertheless, because the heatmap was based on compound-wise Z-score standardization, color intensities represent deviations from the mean abundance of each compound rather than directly comparable absolute abundances across different compounds. Principal component analysis (PCA), performed on centered log-ratio (CLR)-transformed chemical class compositions, showed that the first principal component (PC1) explained 64.57% of the total variance, while the second principal component (PC2) accounted for 23.25%. Together, the first two components explained 87.82% of the total variance. In the PCA biplot, O2 and O3 were positioned along the positive PC1 axis in association with the relative contributions of monoterpene hydrocarbons and aromatic hydrocarbons, whereas O6 and O7 were separated along the negative PC1 axis. This distribution was consistent with differences in the relative proportions of chemical classes, particularly the predominance of oxygenated monoterpenes in O6 (76.93%) and O7 (63.59%). Along PC2, O1 and O5 were positioned on the positive side of the axis, showing differentiation associated with their sesquiterpene compositions. In particular, the high proportion of sesquiterpene hydrocarbons in O5 (51.68%) contributed to its distinctive chemical class profile. Collectively, the heatmap and PCA findings indicate that the investigated samples differed in both individual volatile compound abundances and the relative distribution of chemical classes.

Considering the economic and biological significance of volatile constituents in *O. onites*, the chemical profiles identified in this study may provide a basis for further investigations into potential applications. The antimicrobial properties of carvacrol-rich *O. onites* material have previously been investigated by Baydar et al. (2004) and Canlı et al. (2023). However, because antimicrobial, antioxidant, and other biological activity assays were not performed in the present study, no direct conclusions can be drawn regarding the biological activities of samples O1–O7. Likewise, although linalool-rich samples may have different potential applications in aroma-related or industrial contexts, confirmation would require further sensory evaluation, quality assessment, and biological activity studies. Furthermore, because plant materials collected from individuals within each locality were pooled into composite samples, variation in chemical composition among individual plants within the same locality could not be evaluated.

5. CONCLUSIONS

This study demonstrated variation in headspace volatile composition in the volatile compound profiles of the aerial parts of *O. onites* collected from different localities and elevation ranges in Denizli Province, Türkiye. HS-SPME/GC–MS analysis identified a total of 63 volatile compounds, with carvacrol (25.38–49.20%) being the predominant constituent in samples O1–O5, whereas linalool dominated in O6 (67.92%) and O7 (53.28%). Regarding chemical classes, oxygenated monoterpenes accounted for 36.80–76.93% of the volatile profiles, while sesquiterpene hydrocarbons represented 16.06–51.68%. Sample O6 was distinguished by its high proportion of oxygenated monoterpenes (76.93%), O5 by the predominance of sesquiterpene hydrocarbons (51.68%), and O2 and O3 by their relatively high proportions of monoterpene hydrocarbons (16.67% and 16.12%, respectively).

The Z-score-standardized heatmap and principal component analysis (PCA) performed on centered log-ratio (CLR)-transformed data further supported the observed differences among samples in both individual volatile compound profiles and the relative distribution of chemical classes. The first and second principal components explained 64.57% and 23.25% of the total variance, respectively, with a cumulative explained variance of 87.82%. Samples O2 and O3 were characterized by relatively higher proportions of monoterpene hydrocarbons and aromatic hydrocarbons, O6 and O7 by the predominance of oxygenated monoterpenes, and O5 by its high sesquiterpene hydrocarbon content. These findings indicate distinct patterns of chemical class composition among the investigated samples.

Overall, *O. onites* samples from Denizli exhibited distinct volatile profiles characterized by differences in carvacrol and linalool predominance, as well as variation in sesquiterpene composition. These findings contribute to documenting the local chemical diversity of the species and provide a basis for selecting candidate plant material for future investigations involving standardized sampling, multi-year monitoring, genetic characterization, and biological activity assessments.

EXPLANATION

This article is derived from the doctoral dissertation entitled “Elevation-Dependent Variation in Volatile Compounds and Distribution Modeling of *Origanum onites* L. in Denizli Province,” conducted in the Department of Forest Engineering, Graduate School of Isparta University of Applied Sciences, Türkiye.

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