



Seasonal phytochemical variation of *Peumus boldus* and *Cryptocarya alba* and its impact on forest therapy

Nicolás R. Mac Kay^{1,2} · Martha Hernández de la Torre¹ · Karina Crisóstomo-Ayala³ · Mauricio Aguirre-Díaz⁴ · Darío Bagüés Castro^{5,6,7} · Fernando Teillier⁸ · Claudia Pérez Manríquez³

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Abstract

Key message Seasonal dynamics shape the antioxidant capacity and volatile composition of *Peumus boldus* and *Cryptocarya alba*, suggesting that the potential bioactive inputs for forest therapy may vary throughout the year.

Abstract Plants, in their interaction with the environment, synthesize organic compounds that are considered beneficial for human health in the practice of forest therapy. This study describes seasonal changes in the production and activity of volatile organic compounds in two emblematic southern Chilean trees. Phytochemical profiles were obtained by gas chromatography-mass spectrometry, total phenolic content was determined by the Folin–Ciocalteu method, and antioxidant capacity was measured by ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonate)) and DPPH (2,2-diphenyl-1-picrylhydrazyl) assays, in *Peumus boldus* and *Cryptocarya alba* leaves obtained from Nonguén National Park (Chile). Climatic data were recorded. The results show that the phytochemical richness of sampled *P. boldus* trees reached the highest value in autumn, while *C. alba* showed a slight decrease in summer. The four seasons presented a broad core of constitutive compounds including monoterpenes and monoterpenoids, in both species. ABTS assay showed that antioxidant capacity in *P. boldus* samples was markedly higher in autumn, while in *C. alba*, the highest value was reached in winter. DPPH assay showed highest antioxidant capacity in spring in *P. boldus* samples, and in *C. alba* it occurred in winter. The highest phenolic accumulation was observed in spring for *P. boldus*, and in autumn for *C. alba*. Here we provide an initial characterization of the dynamics of phytochemical variation associated with the seasonal changes occurring in two trees of the southern forest. Further investigation is required to fully understand the emission dynamics in response to seasonal changes, and their potential contribution to human health through the practice of forest therapy.

Keywords Phytochemical seasonality · Antioxidant capacity · Forest therapy · Terpenes

Introduction

Because they are sessile organisms, plants have evolved an extremely diverse repertoire of chemical compounds that enables them to adapt to the biotic and abiotic stresses imposed by their environment. Of these phytochemicals, those called biogenic volatile organic compounds (BVOCs), such as terpenes, play essential ecological roles ranging from direct defense to chemical plant-to-plant communication and between plants and animals (Peñuelas and Staudt 2010; Buchanan et al. 2015). In forest ecosystems, trees represent the main source of BVOC emissions, with leaves

acting as the most active structures in this function due to specialized structures such as oil glands and trichomes (Antonelli et al. 2020). The biochemical and molecular control of BVOC emissions in response to short-term environmental drivers such as temperature, light, CO₂, and O₂, as well as long-term factors such as circadian, seasonal, and developmental effects, has been discussed (Li and Sharkey 2013). Regarding biosynthesis, BVOCs in plants originate from three principal biosynthetic pathways: the methylerythritol phosphate (MEP) pathway located in plastids, the mevalonate (MVA) pathway operating in cytoplasmic compartments, and the lipoxygenase (LOX) pathway associated

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with peroxisomal membranes (Luo et al. 2025). Biosynthesis of BVOCs depends on the availability of carbon, nitrogen, and sulfur, as well as the energy provided by primary metabolism. Based on their biosynthetic origin, all BVOCs are divided into several classes, including terpenoids (Dudareva et al. 2013).

The biosynthesis of terpenes is strongly regulated by environmental conditions that affect the expression of key genes, such as those encoding the enzyme terpene synthase (TPS). High temperature and high radiation, common during summer, induce TPS expression and the emission of monoterpenes (Michael et al. 2020; Jan et al. 2021; Wei et al. 2023). In addition, water and salt stress can significantly affect terpene production (Lantz et al. 2019). Although the influence of each of these factors has been well characterized for some species (Hu et al. 2025), little is known about the dynamics of BVOC production and bioactivity in response to seasonal changes in trees growing in southern Chilean forests.

In parallel, trees produce a wide array of non-volatile secondary metabolites, such as phenolic compounds, which contribute to cellular protection against oxidative stress and account for many of their pharmacological and antioxidant properties (Zhang et al. 2022). Quantifying total phenolic content and antioxidant capacity through ABTS and DPPH (Miller et al. 1993; Brand-Williams et al. 1995) assays complements BVOC characterization, offering a holistic view of the seasonal metabolic adjustments and bioactive potential of forest species.

Beyond their ecological and biochemical importance, BVOCs have gained attention for their contribution to human well-being. Forest therapy—which involves immersive exposure to forest environments—has shown significant psychological and physiological benefits, largely attributed to the inhalation of phytoncides and multisensory stimulation by the forest atmosphere. Several studies have demonstrated positive effects on health, including stress reduction, cardiovascular improvement, and immune system strengthening (Franco et al. 2017; Antonelli et al. 2020; Kotera et al. 2022). In this context, the temperate deciduous forest of Concepción represents an ideal natural setting for studying the interplay between forest chemistry and human health. Nonguén National Park is located in the peri-urban area of the province of Concepción, Biobío Region, Chile. Covering an area of 3,056.96 ha in the Cordillera de la Costa (73°00'W–36°52'S), it protects the last remnant of the “Concepción deciduous forest”, hosting species such as *Peumus boldus* Mol. (boldo) and *Cryptocarya alba* (Mol.) Looser (peumo) (Bocaz-Torres et al. 2013). The area exhibits a Mediterranean temperate climate, characterized by marked seasons, with winter rainfall and a dry summer, and an average annual temperature of 13.1 °C, and it is increasingly

used for health practices such as forest bathing. Both species are structurally and functionally central to the forest community and are culturally recognized for their distinctive aroma and therapeutic properties (Magni et al. 2016; Fuentes-Barros et al. 2025).

In this context, the present study aimed to evaluate the influence of seasonality on the production and composition of essential oils, total phenolic content, and antioxidant capacity in the leaves of *P. boldus* and *C. alba*. Such knowledge not only deepens our understanding of the ecophysiological resilience of *P. boldus* and *C. alba* under changing climatic regimes but also provides valuable insights for optimizing forest therapy practices based on science-driven evidence.

Materials and methods

Environmental conditions

The meteorological data used in this study were obtained from the Dirección Meteorológica de Chile (DMC) (Cariel Sur station, code 3,600,019) and correspond to the year 2022. The following parameters were considered: monthly mean temperature (°C), mean maximum temperature (°C), mean minimum temperature (°C), total monthly precipitation (mm), and the UVB radiation index. The representative temperature for each season was obtained by averaging of the data from the three corresponding months: summer (January–March), autumn (April–June), winter (July–September) and spring (October–December).

Plant material

To obtain phytochemical profiles for both *P. boldus* and *C. alba*, leaves were collected in each season. Five healthy mature trees, with similar environmental exposure and accessible via authorized trails within the national park, were identified and used throughout the study. The same five individuals per species were sampled across all four seasons to ensure a consistent amount of material was obtained for each sampling event. Sampling was conducted in the early morning during each of the four seasons, taking into account the four cardinal directions and collecting material at a constant height (Ortiz et al. 2017). To prevent severe defoliation of the trees located along the public trails, and to ensure sufficient foliage remained on these specific individuals for the subsequent samplings throughout the year, only a limited amount of biomass was harvested from each tree. Consequently, the leaves collected from the five trees per species were pooled, resulting in a single composite sample per species per season (n = 1). While this pooling

strategy minimized the impact on the trees and provided a representative sample of the trail's environment, this design precludes the estimation of inter-individual variability and does not support inferential comparisons. The pooled material was then subjected to phytochemical analysis.

Essential oil extraction

Essential oils from *P. boldus* and *C. alba* were obtained by steam-assisted hydrodistillation using a Clevenger-type apparatus (Biobase, HM-I). A total of 300 g of fresh leaves were distilled with 2.6 L of distilled water for four hours. Residual water in the essential oil was removed using anhydrous sodium sulfate. Extracts were stored in amber glass bottles at room temperature (Ortiz et al. 2017).

Characterization of essential oils

The essential oils were analyzed using gas chromatography-mass spectrometry (GC-MS) (Agilent 7890A) equipped with an automatic injector (Agilent) and an HP-5MS capillary column (30 m × 0.25 mm i.d., 0.25 µm film thickness). The injection port temperature was set at 250 °C. The GC oven temperature program was as follows: initial temperature of 50 °C (held for 2 min), increased at 8 °C min⁻¹ to 200 °C (held for 5 min), and finally at 10 °C min⁻¹ to 250 °C (held for 10 min). Helium was used as the carrier gas at a constant flow rate of 1.0 mL min⁻¹. The mass detector (Agilent 5975C) was operated in electron ionization mode at 70 eV, with a scan range of 35–500 m/z. Component identification was achieved by comparing their mass spectra with those in the NIST library and confirming their identities through retention index (RI) comparisons with a homologous series of n-alkanes (C8–C20), based on literature values reported for similar non-polar columns. Relative quantification was performed by peak area normalization without correction factors.

Hierarchical cluster analysis of essential oils

To identify seasonal patterns and compound associations in the essential oils, Hierarchical Cluster Analysis (HCA) was performed on Z-score standardized data using Euclidean distances and Ward's D2 method. For the resulting trend plots, the shaded ribbons represent the dispersion of standardized abundances among the various chemical constituents grouped within each specific cluster at each time point, rather than biological variance. To reduce noise from trace compounds, a minimum abundance threshold of 1.0% was applied prior to clustering; only compounds reaching this value in at least one season were included. For this multivariate approach, analyses and visualizations were

conducted in R software (v. 4.5) using the *tidyverse* suite for data manipulation, *ComplexHeatmap* for visualization, and *patchwork* for figure integration.

Antioxidant capacity assays of essential oils

ABTS assay

The ABTS assay described by Miller et al. (1993) and modified by Crisóstomo-Ayala et al. (2021) was employed. Essential oil samples were diluted in chloroform as solvent. The free radical solution contained 3.5 mM ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonate)) and 1.22 mmol potassium persulfate. Both solutions were mixed in equal volumes and kept in the dark for 16 h at room temperature. Subsequently, 1 mL of the ABTS⁺ stock solution was diluted with 14 mL of distilled water to reach an absorbance of 0.70 ± 0.01 at 734 nm. For each seasonal assay, a fresh ABTS⁺ solution was prepared. Reaction mixtures contained 180 µL of ABTS⁺ radical solution and 20 µL of either Trolox at concentrations ranging from 0.01 to 0.2 mg mL⁻¹ or the oil samples (25–100 mg mL⁻¹), incubated for 60 min in the dark. Absorbance was read at 734 nm using a BioTek EpochTM microplate spectrophotometer. Trolox served as a positive control, and chloroform was used as a blank. All determinations were performed separately.

DPPH assay

Antioxidant capacity was evaluated according to the method proposed by Brand-Williams et al. (1995), with modifications by Crisóstomo-Ayala et al. (2021). A liquid-liquid extraction in methanol was performed for each sample. The reaction mixture contained 270 µL of a 0.06 mmol DPPH (2,2-diphenyl-1-picrylhydrazyl) radical solution prepared in methanol and 30 µL of either Trolox (0.01–0.2 mg mL⁻¹) or the oil samples (25–100 mg mL⁻¹). Each mixture was incubated in the dark at 37 °C for 20 min. Absorbance was measured at 517 nm using a BioTek EpochTM microplate spectrophotometer. Trolox served as a positive control, and methanol was used as a blank. All tests were performed in triplicate (technical replicates).

Antioxidant capacity calculations

The percentage of inhibition, corresponding to the amount of radicals (DPPH and ABTS) neutralized by the extract at a given concentration, was calculated using the equation:

$$\%_{\text{Inhibition}} = (A_c - A_s) / A_c \cdot 100\%$$

where A_c is the absorbance of the control and A_s is the absorbance of the sample. Antioxidant capacity for both ABTS and DPPH assays was expressed as IC_{50} , representing the sample concentration required to inhibit 50% of the free radicals (Mkaddem et al. 2009; Rubilar et al. 2011).

Total phenolic content (TPC)

Total phenolic content in each sample was determined using the Folin–Ciocalteu method (Folin and Ciocalteu 1927), with modifications by Crisóstomo-Ayala et al. (2021). A liquid–liquid extraction in methanol was performed, using sample concentrations of $100 \mu\text{g mL}^{-1}$. The calibration curve was prepared using gallic acid (0.01 – 0.2 mg mL^{-1}). Each reaction mixture contained $400 \mu\text{L}$ of distilled water, $20 \mu\text{L}$ of sample or gallic acid standard solution, $40 \mu\text{L}$ of Folin–Ciocalteu reagent, and $200 \mu\text{L}$ of 15% (w/v) sodium carbonate. The mixture was incubated at room temperature for 60 min in darkness, with agitation. All measurements were performed in triplicate (technical replicates). Absorbance was recorded at 765 nm using a BioTek Epoch™ microplate spectrophotometer. TPC was expressed as $\mu\text{g g}^{-1}$ gallic acid equivalents (GAE) on a dry weight basis.

Statistical analysis

Quantitative data from antioxidant capacity and TPC assays are presented as mean $\pm$ standard deviation (S.D.) derived from three technical replicates of composite seasonal samples. Given the pooled sampling design, univariate analysis focused on descriptive trends and the magnitude of change (percentage difference) rather than inferential hypothesis testing, avoiding pseudoreplication while highlighting observed variations. All data processing and descriptive analyses were conducted using R software (v. 4.5).

Results

Environmental conditions

Consistent with a warm temperate climate, the study area exhibited pronounced seasonal variation during the sampling period. Figure 1 shows the variations in temperature, precipitation and radiation that occurred throughout the year. Summer was the warmest season, with a mean maximum temperature of 21.5°C , an average temperature of 16.5°C , and a mean minimum of 12.0°C . In contrast, winter was the coldest season, with a mean maximum temperature of 14.0°C , an average temperature of 9.5°C , and a mean minimum of 6.0°C , while the transitional seasons, autumn and spring, exhibited intermediate values.

In terms of precipitation, the rainiest season was autumn, with total rainfall reaching around 420 mm. This was followed by winter, with around 360 mm of rainfall. Summer was the driest season, with only 25 mm of precipitation. Spring showed slightly higher values, at around 50 mm, as shown in Fig. 1b.

In accordance with seasonal sun exposure, the highest UV radiation levels were recorded in summer and spring, and the lowest in autumn (Fig. 1c).

Phytochemical profiles

P. boldus

The shift in dominance between eucalyptol and p-cymene was the most distinctive aspect of the chemical profile (Table 1). In summer, the season with the lowest chemical diversity, eucalyptol was the predominant compound, accounting for 56.38%, and it remained dominant in winter, accounting for 23.23% of the oil. In seasons showing the greatest chemical diversity, dominance shifted toward

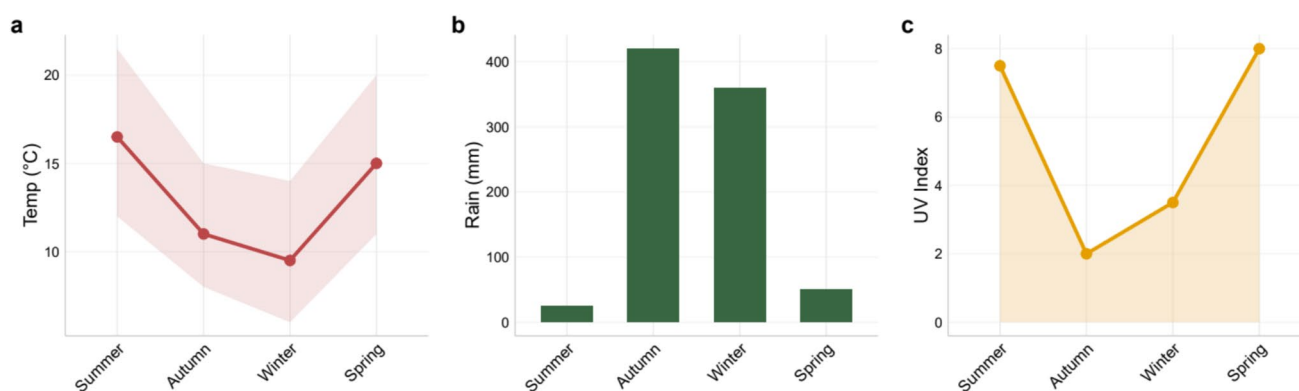
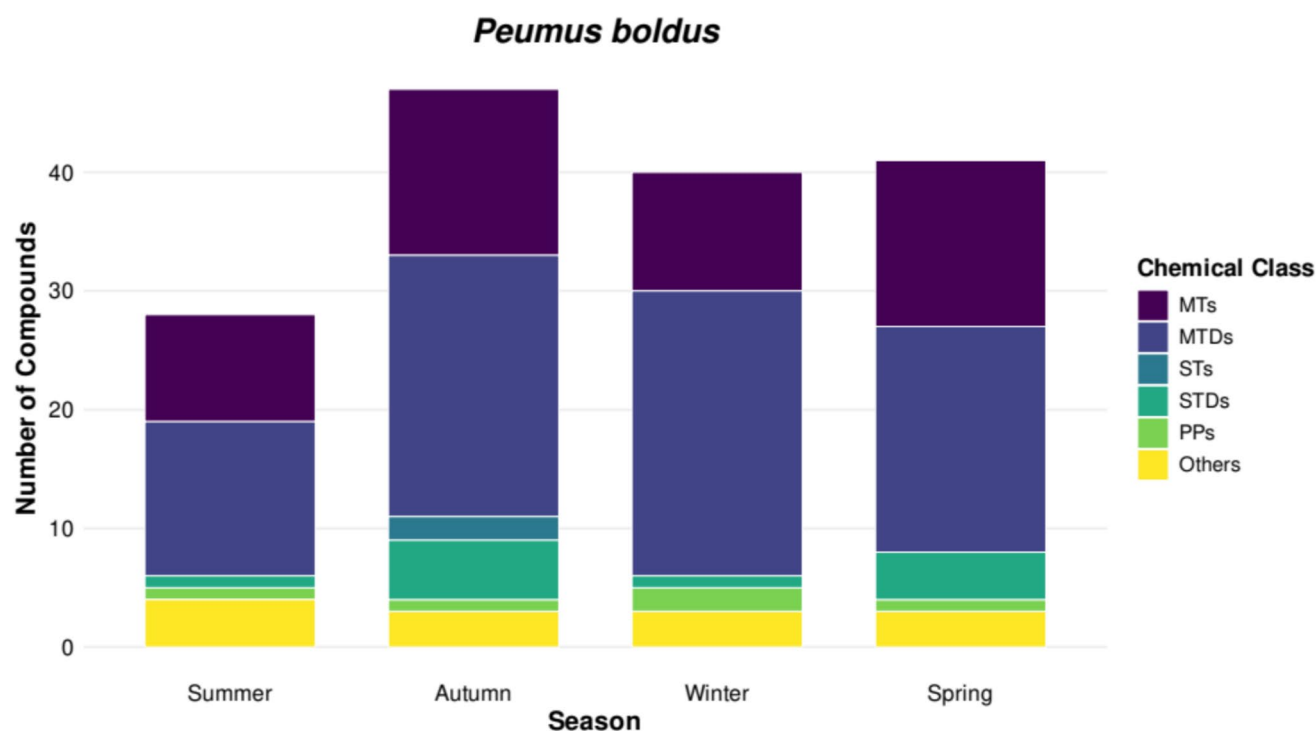


Fig. 1 Seasonal environmental dynamics in Nonguén National Park during the study period (2022). **(a)** Average seasonal temperature ($^\circ\text{C}$) represented by the red line, with the pink shaded region indicating the range between maximum and minimum recorded temperatures. **(b)**

Total accumulated precipitation (mm) shown as dark green bars. **(c)** Mean UV Radiation Index displayed by the yellow line. Data were retrieved from the Carriel Sur meteorological station (Dirección Meteorológica de Chile)

Table 1 Composition of the essential oil of *P. boldus* analyzed by gas chromatography-mass spectrometry (GC–MS). The concentration (%) values presented are relative to the total. The complete composition data are provided in the Supplementary Material

Fraction number	Retention time	Compounds	Concentration (%)			
			Summer	Autumn	Winter	Spring
2	5.916	α -Pinene	2.46	4.5	2.34	6.38
4	6.699	β -Phellandrene	3.55	2.73	1.88	2.22
5	6.761	β -Pinene	1.06	2.17	1.46	2.13
11	7.732	p-Cymene	6.7	15.21	10.34	19.71
12	7.830	cis-Geraniol	-	8.54	3.23	16.88
13	7.893	Eucalyptol	56.38	13.64	23.23	14.03
28	10.689	4-Terpineol	2.27	3.82	3.1	4.45
31	10.938	α -Terpineol	2.48	2.29	1.64	3.57
36	11.831	α -Terpinene	5.08	1.13	3.32	2.27
38	12.142	Ascaridole	1.56	5.66	1.03	3.04

**Fig. 2** Characterization of the number of compounds in the essential oil of *P. boldus* across four seasons using gas chromatography–mass spectrometry (GC–MS). Compound categories: MTs (monoterpenes),

MTDs (monoterpenoids), STs (sesquiterpenes), STDs (sesquiterpenoids), PPs (phenylpropanoids) and Others

p-cymene, which reached its highest levels in spring (19.71%) and remained relatively high in autumn (15.21%). The presence of significant amounts of other compounds, such as cis-geraniol in spring (16.88%), ascaridole in autumn (5.66%), and α -terpinene in summer (5.08%), complemented this dynamic.

In terms of phytochemical richness, the highest values (47 distinct compounds) were observed in autumn (Fig. 2), exhibiting also the highest diversity of monoterpenes (MTs; n=14), monoterpenoids (MTDs; n=22), and the largest variety of sesquiterpenoids (STDs; n=5) throughout the year. By contrast, summer showed the lowest metabolic

diversity (28 distinct compounds) and a strong dominance of MTs (n=9) and MTDs (n=13) in the phytochemical profile. Similar intermediate values of chemical richness (n=41) were obtained in spring and winter (n=40). The dynamic behavior of individual compounds (Table 1) can explain seasonal variation in chemical diversity. A core set of constitutive metabolites was present throughout the year, including the MTs α -pinene, p-cymene, and α -terpinene, as well as the MTDs eucalyptol and 4-terpineol.

To further elucidate the dynamic behavior of individual compounds and characterize the seasonal variation in diversity, a hierarchical clustering analysis based on normalized

relative abundances (Z-scores) was performed (Fig. 3). This analysis categorized the volatile constituents into four distinct clusters based on their temporal patterns. Cluster 1, the "Summer Phenotype," includes the major compound eucalyptol alongside β -phellandrene and α -terpinene, exhibiting maximal relative abundance exclusively during the summer, followed by a sharp decline in subsequent seasons. Cluster 2, the "Autumn Phenotype," is characterized by a peak in autumn and contains key oxygenated compounds such as ascaridole, ascaridole epoxide, and carvenone oxide, correlating with the high phytochemical richness and the diversification of oxidative products observed post-summer. Cluster 3, the "Winter Accumulation" group, represents the largest group ($n=10$), with compounds including methyleugenol, trans-pinocarveol, and nona-3,5-dien-2-ol showing a progressive accumulation tendency towards winter, suggesting a specific metabolic response to colder conditions. Finally, Cluster 4, the "Spring

Resurgence," contrasts with the summer and autumn profiles, maintaining low levels during the dormant seasons but experiencing a pronounced surge in spring. This group comprises constitutive MTs such as α -pinene, β -pinene, linalool, and γ -terpinene, with their higher relative abundance in spring coinciding with the recovery of MTs diversity and aligning with the increased levels of p-cymene observed at the onset of the growing season.

C. alba

The most distinctive feature of the chemical profile was the dominance of the MTDs 4-terpineol, reaching its peak (26.48% of the total compounds) in summer (Table 2). Although its relative abundance declined in the other seasons, it remained the most abundant compound throughout the year (15.94% in autumn, 16.14% in winter, and 15.51% in spring). Furthermore, an increase in the levels of two other MTs was observed, particularly during periods of

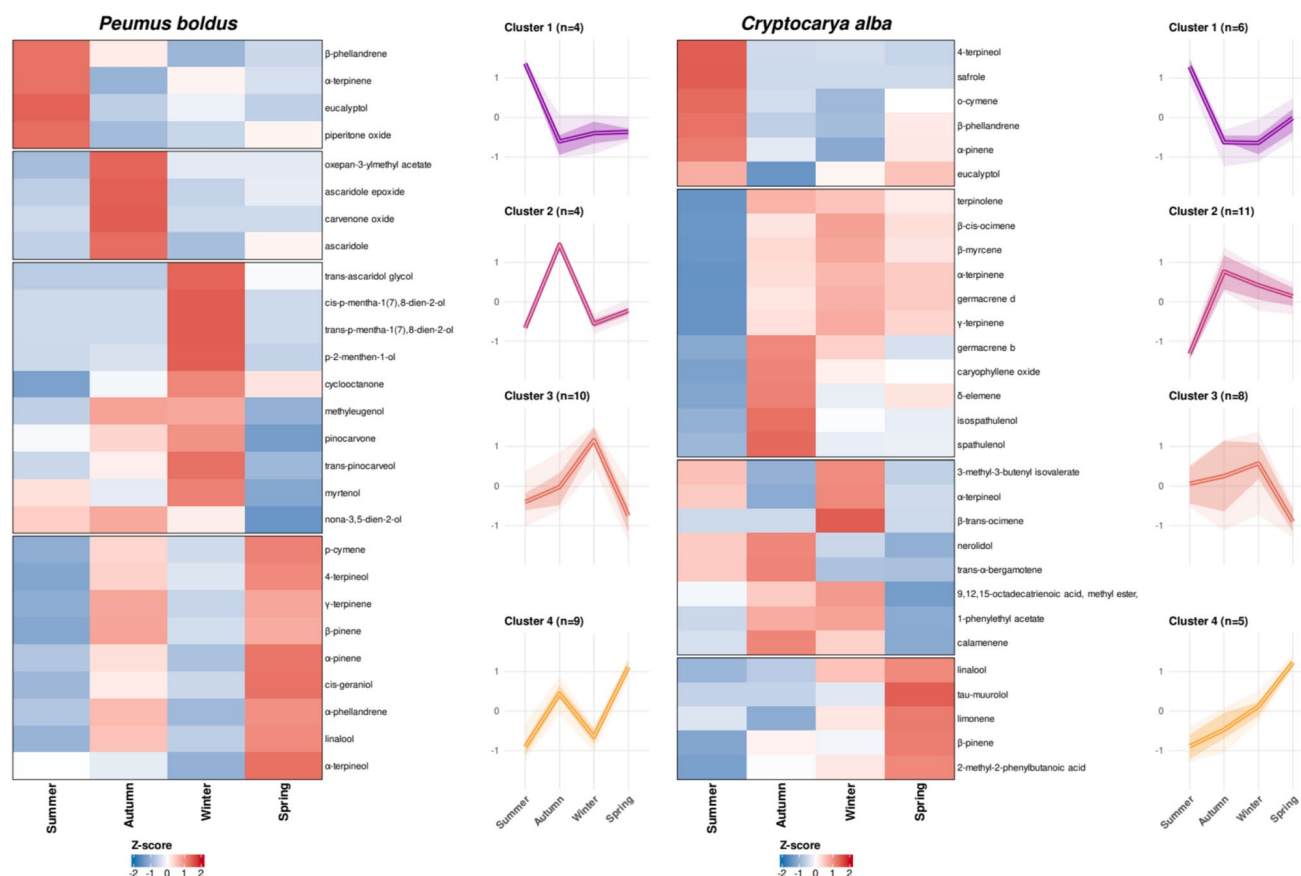
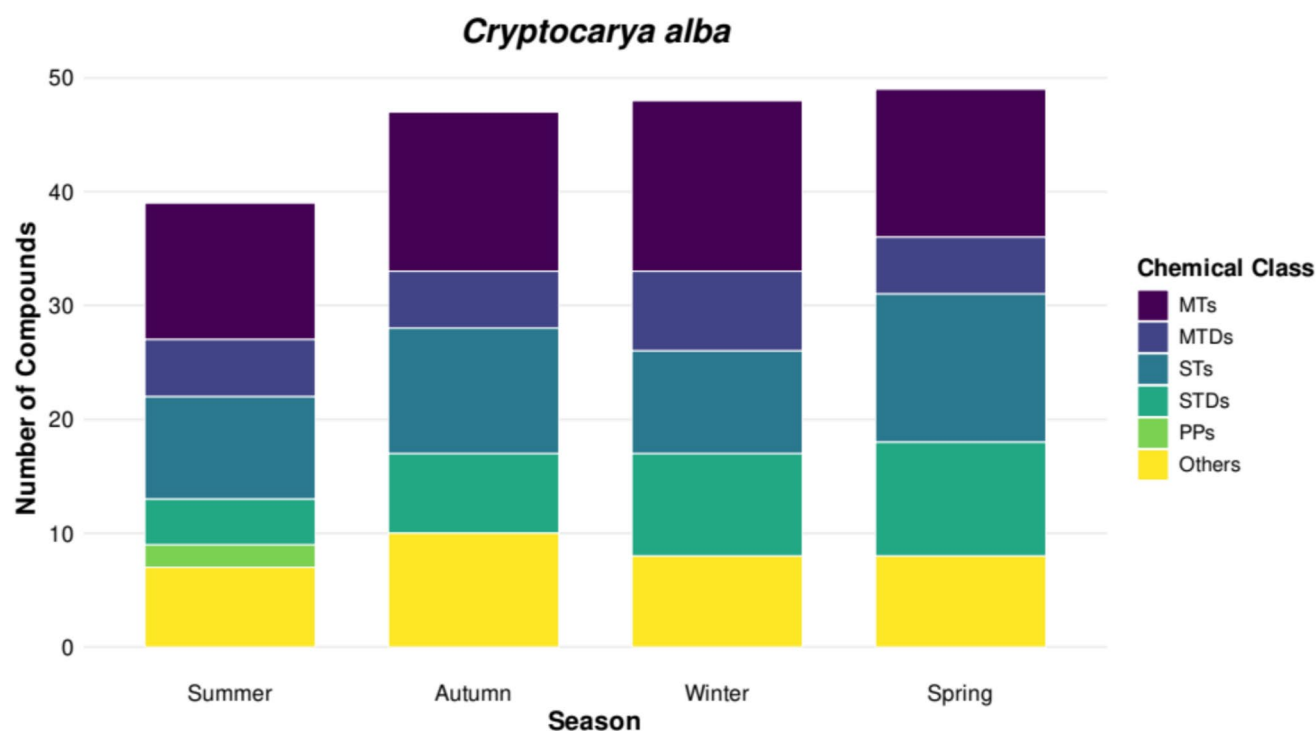


Fig. 3 Seasonal variation and clustering analysis of the volatile profiles of *P. boldus* and *C. alba* essential oils. The heatmaps display the normalized relative abundance (Z-score) of volatile compounds identified by GC–MS across four seasons (Summer, Autumn, Winter, and Spring). The color gradient ranges from dark blue (lowest abundance, -2) to dark red (highest abundance, +2). The trend plots to the right of each heatmap represent the aggregated seasonal profiles for each

cluster. The central solid line indicates the mean standardized abundance. The shaded ribbons represent the variation across the individual chemical constituents belonging to that cluster: the darker inner band denotes the interquartile range (25th–75th percentiles), while the lighter outer band captures the 90% distribution interval (5th–95th percentiles) of the compounds' Z-scores. The number of constituents (n) per cluster is indicated in each subplot

Table 2 Composition of the essential oil of *C. alba* analyzed by gas chromatography-mass spectrometry (GC–MS). The concentration (%) values presented are relative to the total. The complete composition data are provided in the Supplementary Material

Fraction number	Retention time	Compounds	Concentration (%)			
			Summer	Autumn	Winter	Spring
3	5.92	α -Pinene	6.62	5.6	4.99	5.93
5	6.71	β -Phellandrene	12.21	7.01	6.33	9.23
6	6.77	β -Pinene	5.22	6.2	6.02	7.01
10	7.55	α -Terpinene	1.49	3.45	3.83	3.62
11	7.72	o-Cymene	4.35	2.72	2.28	3.12
12	7.8	Limonene	2.21	1.74	2.55	3.15
13	7.86	Eucalyptol	9.38	5.47	8.19	9.03
16	8.38	γ -Terpinene	3.37	6.08	6.84	6.24
17	8.96	Terpinolene	1.13	2.31	2.22	2.02
23	10.75	4-Terpineol	26.48	15.94	16.14	15.51

**Fig. 4** Characterization of the number of compounds in the essential oil of *C. alba* across four seasons by gas chromatography–mass spectrometry (GC–MS). Compound categories: MTs (monoterpenes),

MTDs (monoterpenoids), STs (sesquiterpenes), STDs (sesquiterpenoids), PPs (phenylpropanoids) and Others

high temperatures and radiation. β -Phellandrene reached its maximum levels in summer (12.21%) and remained high in spring (9.23%). Similarly, eucalyptol was more abundant in summer (9.38%) and spring (9.03%).

This species showed only a slight decrease in phytochemical richness during the summer ($n=39$), with the rest of the year showing values around $n=48$ (Fig. 4). The overall chemical profile was characterized by a balance between MTs and MTDs and a substantial proportion of STs and STDs, which exhibited high diversity throughout most of the year. All four seasons presented a broad core of constitutive compounds that included the MTs α -pinene,

β -phellandrene, β -pinene, and γ -terpinene, as well as the MTDs eucalyptol and 4-terpineol, forming a complex and multifunctional chemical base (Table 2).

To further characterize the seasonal dynamics of these metabolites, hierarchical clustering defined four distinct groups based on normalized relative abundance (Z-scores) (Fig. 3). Cluster 1 ($n=6$) closely mirrored the behavior of the major compounds, grouping the dominant 4-terpineol with other key volatiles such as saffrole, eucalyptol, and β -phellandrene; these compounds exhibited their maximum expression exclusively during the summer, followed by a decline. As the season shifted, Cluster 2 ($n=11$) emerged

Table 3 Antioxidant capacity of *P. boldus* and *C. alba* across the four seasons of the year, expressed as IC_{50} , determined using the ABTS and DPPH free radical-scavenging assays. Each value represents the mean $\pm$ S.D. obtained from three technical replicates

Species	Assay	Summer	Autumn	Winter	Spring
<i>P. boldus</i>	ABTS	49.52 $\pm$ 8.55	10.17 $\pm$ 2.77	45.28 $\pm$ 4.35	20.34 $\pm$ 0.68
	DPPH	49.14 $\pm$ 5.98	45.64 $\pm$ 6.05	63.38 $\pm$ 4.42	20.56 $\pm$ 0.39
<i>C. alba</i>	ABTS	126.39 $\pm$ 4.90	183.50 $\pm$ 3.78	81.10 $\pm$ 1.86	165.82 $\pm$ 10.01
	DPPH	37.07 $\pm$ 4.43	128.19 $\pm$ 3.09	19.13 $\pm$ 0.49	20.80 $\pm$ 0.65

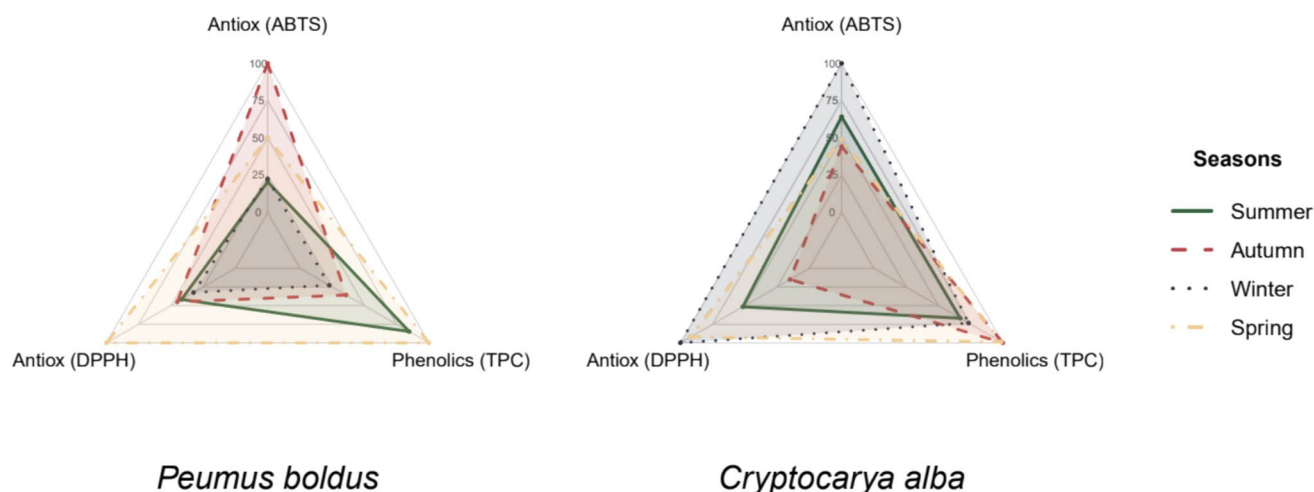


Fig. 5 Radar charts illustrating the seasonal profiles of antioxidant capacity and phenolic content in leaves of *P. boldus* and *C. alba*. The three axes represent the normalized standardized values (scaled 0–100) for Total Phenolic Content (TPC) and antioxidant capacity measured by ABTS and DPPH assays. Data points plotted further from the center

with a peak in autumn, characterized by an increased abundance of compounds like terpinolene, spathulenol, and germacrene D. A distinct accumulation trend was observed for Cluster 3 ($n=8$), which included oxygenated STs such as nerolidol; these compounds showed a progressive increase from summer to reach their maximum levels in winter. Finally, Cluster 4 ($n=5$) displayed a sharp resurgence in spring after remaining at minimal levels (negative Z-scores) during summer and autumn. This cluster was driven by the marked increase of specific MTs like linalool, limonene, and β -pinene, contributing to the maintenance of the high chemical diversity observed at the beginning of the vegetative cycle.

Antioxidant capacity from ABTS and DPPH Assays

Antioxidant capacity of *P. boldus*

ABTS assay showed that antioxidant capacity was markedly higher during autumn ($IC_{50}=10.17 \pm 2.77 \mu\text{g mL}^{-1}$) and spring ($IC_{50}=20.34 \pm 0.68 \mu\text{g mL}^{-1}$), with similar IC_{50} values observed between these two seasons. Antioxidant capacity was considerably lower during winter ($IC_{50}=45.28 \pm 4.35 \mu\text{g mL}^{-1}$) and summer ($IC_{50}=49.52 \pm 8.55 \mu\text{g mL}^{-1}$). On the

other hand, DPPH assay showed the highest antioxidant capacity in spring ($IC_{50}=20.56 \pm 0.39 \mu\text{g mL}^{-1}$). Autumn and summer exhibited comparable intermediate activities ($IC_{50}=45.64 \pm 6.05$ and $49.14 \pm 5.98 \mu\text{g mL}^{-1}$), respectively. Winter displayed the lowest DPPH radical-scavenging capacity, with the highest IC_{50} value ($63.38 \pm 4.42 \mu\text{g mL}^{-1}$) (Table 3, Fig. 5).

Antioxidant capacity of *C. alba*

As with the previous species, variations in antioxidant capacity were observed in accordance with seasonal changes in *C. alba*, showing marked differences between ABTS and DPPH assays (Fig. 5). ABTS assay scored the highest antioxidant capacity in winter ($IC_{50}=81.10 \pm 1.86 \mu\text{g mL}^{-1}$). This capacity decreased markedly in the other seasons in the following order: summer ($IC_{50}=126.39 \pm 4.90 \mu\text{g mL}^{-1}$), spring ($IC_{50}=165.82 \pm 10.01 \mu\text{g mL}^{-1}$), and autumn ($IC_{50}=183.50 \pm 3.78 \mu\text{g mL}^{-1}$). DPPH assay, in turn, revealed that the highest antioxidant capacity occurred in winter ($IC_{50}=19.13 \pm 0.49 \mu\text{g mL}^{-1}$) and spring ($IC_{50}=20.80 \pm 0.65 \mu\text{g mL}^{-1}$), with comparable values between them. Antioxidant capacity decreased in summer ($IC_{50}=37.07 \pm 4.43 \mu\text{g mL}^{-1}$) and dropped sharply in autumn,

Table 4 Total phenolic compound content of *P. boldus* and *C. alba* across the four seasons of the year, expressed as $\mu\text{g g}^{-1}$ of phenolics in dry mass equivalent to gallic acid (GAE). Each value represents the mean $\pm$ S.D. obtained from three technical replicates

Species	Summer	Autumn	Winter	Spring
<i>P. boldus</i>	141.31 $\pm$ 0.96	59.68 $\pm$ 1.01	37.94 $\pm$ 0.77	166.67 $\pm$ 16.40
<i>C. alba</i>	6.35 $\pm$ 0.23	9.48 $\pm$ 0.21	6.96 $\pm$ 0.13	9.36 $\pm$ 1.01

scoring the lowest levels with an IC_{50} of $128.19 \pm 3.09 \mu\text{g mL}^{-1}$ (Table 3).

Total phenolic content (TPC)

Phenolic content in *P. boldus*

Pronounced variations in the phenolic content of *P. boldus* were detected throughout the year (Fig. 5). The highest accumulation was scored in spring, with a value of $166.67 \pm 16.40 \mu\text{g g}^{-1}$ GAE. The second-highest level was observed in summer, at $141.31 \pm 0.96 \mu\text{g g}^{-1}$ GAE. Subsequently, phenolic content decreased sharply during the colder seasons. In autumn, the value dropped to $59.68 \pm 1.01 \mu\text{g g}^{-1}$ GAE and reached its minimum in winter, with only $37.94 \pm 0.77 \mu\text{g g}^{-1}$ GAE (Table 4). Regarding phenolic accumulation, all four seasons showed distinct concentration levels.

Phenolic content in *C. alba*

In contrast to the previous species, the phenolic content of *C. alba* remained considerably lower and more stable throughout the year (Fig. 5). Results indicated that the highest levels occurred in autumn ($9.48 \pm 0.21 \mu\text{g g}^{-1}$ GAE) and spring ($9.36 \pm 1.01 \mu\text{g g}^{-1}$ GAE), with similar concentrations among them, while the lowest values were scored in summer ($6.35 \pm 0.23 \mu\text{g g}^{-1}$ GAE) and winter ($6.96 \pm 0.13 \mu\text{g g}^{-1}$ GAE) (Table 4).

Discussion

During summer—the period of highest temperature and radiation, and lowest precipitation—the phytochemical diversity of the sampled *P. boldus* trees almost halved, coinciding with a massive production of the MTD eucalyptol. Previous studies have identified eucalyptol as one of the main components of *P. boldus* essential oils (Herrera-Rodríguez et al. 2015; Ortiz et al. 2017). This compound has been reported to exert a protective effect in plants against high temperatures and radiation by reducing reactive oxygen species (ROS), increasing pigment content, and enhancing photosynthetic capacity (Zuo et al. 2017; Xu et al. 2022). Therefore, the higher proportion of this compound observed in summer

suggests an adaptive response to heat stress. From the therapeutic perspective, in concordance with forest therapy, it has been reported that eucalyptol provides neuroprotection via glucose-lowering, antioxidant, anti-inflammatory, and neurotrophic actions (Juergens et al. 2020; Naseem et al. 2025). These pharmacological properties suggest that if eucalyptol is emitted into the forest air in sufficient amounts, it could theoretically be relevant to forest therapy. During the intermediate seasons of spring and autumn, the dominant BVOC in the analyzed samples was the MT p-cymene and a greater presence of STs and STDs was also detected. p-Cymene is a naturally occurring MT found in the essential oils of various medicinal plants, where it plays an antioxidant role (Pyo and Jung 2024). Interestingly, in vitro studies have demonstrated that p-cymene, exhibits considerable anti-inflammatory and anticancer activities, making it a promising candidate for cancer therapy, since preliminary research suggests that it can induce apoptosis in cancer cells by modulating key signaling pathways involved in tumor progression (Anwar et al. 2025). Similarly to eucalyptol, p-cymene represents a potential source for health-promoting effects associated with forest-based therapeutic environments. The production of STs has been previously associated with mechanical stress from herbivores and exposure to cold in conifers (Beton et al. 2010), implying that their increased production in these trees might be linked to similar triggers.

The findings in *C. alba* show a very different landscape, as the diversity of compounds remained stable throughout the year. The response to summer conditions in these trees appeared to rely on the overproduction of 4-terpineol rather than a reduction in diversity. Comparisons with other studies confirm that eucalyptol remains a predominant component of *C. alba*'s essential oil (Telascrea et al. 2008; Touma et al. 2020), likely serving a similar protective role in the foliage as in *P. boldus*. In other species, this compound increases in response to drought stress (Erdoğan et al. 2024) and it has also been reported to possess strong insecticidal activity (Huang et al. 2022). From a biomedical perspective, in addition to its antioxidant and anti-inflammatory properties, its anticancer potential has been recently highlighted since this MTDs presented a cytostatic effect against six cell lines, especially for breast adenocarcinoma and chronic myeloid leukemia (Bicas et al. 2011). It is important to note, however, that these bioactivities are based on direct administration in pharmacological models. Further research is needed to determine whether ambient inhalation exposure during forest therapy can elicit comparable physiological responses in humans.

A particularly noteworthy finding in this study is the inverse relationship observed between total phenolic content (TPC) and antioxidant capacity, which may indicate that the sampled *P. boldus* and *C. alba* exhibited fundamentally

different antioxidant defense mechanisms based on the seasonal modulation of their terpene profiles. To provide a robust evaluation of these mechanisms, the simultaneous use of ABTS and DPPH assays was crucial, as these methods possess distinct chemical principles and target different antioxidant profiles. The ABTS radical is highly reactive and soluble in both aqueous and organic solvents, making it suitable for evaluating both hydrophilic and lipophilic antioxidants across a wide range of pH levels (Cano et al. 2002; Bibi Sadeer et al. 2020). In contrast, the DPPH radical is strictly soluble in organic media, showing higher affinity for lipophilic antioxidants, and is known to be significantly more susceptible to steric hindrance from larger molecules, which can restrict its access to the radical site (Xie and Schaich 2014; Bibi Sadeer et al. 2020). Therefore, using both methods captures the full scavenging spectrum of complex extracts containing both bulky phenolic compounds and highly volatile lipophilic terpenes.

In the *P. boldus* samples, antioxidant defense appeared to rely on the synergistic interactions within a complex mixture of terpenes rather than phenolic compounds, whose accumulation did not directly correlate with the peak antioxidant capacity observed in autumn and spring (Bakkali et al. 2008; Touma et al. 2020). The highest diversity and antioxidant capacity in autumn are likely driven by the combined action of MTs such as p-cymene and eucalyptol, whose synergistic effects enhance free radical neutralization (Pyo and Jung 2024). Phenolic content showed an association with rainfall, reaching maxima in summer and spring, which contrasts with the classic drought-stress-phenolic hypothesis and points to UV radiation and temperature as potential drivers in this species (Sun et al. 2023; Qaderi et al. 2023). UV radiation emerges as a key regulator of secondary metabolism in both *P. boldus* and *C. alba*, potentially driving metabolic specialization in summer with the dominance of eucalyptol, a compound with established photoprotective and antioxidative roles (Zuo et al. 2017; Xu et al. 2022).

When considering TPC individually, precipitation appeared to be strongly associated with phenolic content in *P. boldus*, increasing its value. This trend contrasts with the classic “drought-stress-phenolic” hypothesis, which associates water deficit with phenolic accumulation (Sun et al. 2023). In the deciduous forest of Concepción, the data suggest that limited water availability may not be a major stress factor; instead, reduced precipitation coincides with higher UV radiation and temperatures, both of which could co-induce phenolic synthesis (Qaderi et al. 2023).

In *C. alba*, the observed antioxidant capacity appeared to reflect a specialized response to winter stress. This species maintained consistently low TPC levels, supporting the notion that its antioxidant capacity resides primarily in its

terpene components. The highest capacity was observed during winter in both assays, under temperatures ranging from 6 °C to 14 °C and high rainfall, suggesting adaptation to cold-induced oxidative stress. Low temperatures are known triggers of ROS overproduction in plants (Zhao et al. 2020; Raza et al. 2022). In response, plants activate defense mechanisms, including antioxidant secondary metabolite synthesis, to protect cell membranes and proteins from oxidative damage (Batra 2021). Importantly, maximum antioxidant capacity did not coincide with maximum production of the dominant compound 4-terpineol, indicating that the plant’s response likely involves the targeted synthesis of specific minor compounds highly effective in counteracting cold stress.

Conclusion

The observed seasonal phytochemical variation in sampled *P. boldus* and *C. alba* suggests distinct metabolic patterns: *P. boldus* exhibited high eucalyptol levels during summer, while *C. alba* maintained year-round diversity with 4-terpineol dominance. Antioxidant defense in both species appeared to be primarily terpene-driven and likely influenced by UV radiation, temperature, and precipitation. Our findings suggest that autumn and spring may provide the most diverse and bioactive phytochemical atmospheres for forest therapy in these ecosystems, characterized by a higher richness of therapeutic compounds such as p-cymene and eucalyptol. The data suggest that autumn and spring leaves contain a higher richness of potential therapeutic compounds such as p-cymene and eucalyptol. If these phytochemicals are emitted into the air at proportional rates, this could theoretically translate into more diverse and bioactive atmospheres for forest therapy. This study provides valuable initial insights into the dynamics of BVOC accumulation associated with seasonal changes in two emblematic trees of the southern Chilean forest. However, our methodology did not directly assess atmospheric BVOC concentrations, actual human exposure, or clinical outcomes. Therefore, further investigation is required to fully understand actual emission dynamics and their specific physiological contributions to human health through the practice of forest therapy.

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Data availability The datasets generated and/or analyzed during the current study are available in the Electronic Supplementary Material. Additionally, the raw data supporting the findings of this study are available in the Zenodo repository, <https://doi.org/10.5281/zenodo.18890793>.

Declarations

conflicts of interest The authors declare that they have no known financial or non-financial conflicts of interest that could have influenced the results or interpretation of the findings presented in this manuscript. All authors have read and approved the final version of the paper and agree with its submission.

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Authors and Affiliations

Nicolás R. Mac Kay^{1,2}  · Martha Hernández de la Torre¹  · Karina Crisóstomo-Ayala³  · Mauricio Aguirre-Díaz⁴  · Darío Bagüés Castro^{5,6,7}  · Fernando Teillier⁸  · Claudia Pérez Manríquez³ 

✉ Nicolás R. Mac Kay
rivasnicolas@uniovi.es

✉ Martha Hernández de la Torre
marhernandez@udec.cl

Karina Crisóstomo-Ayala
karicrisostomo@udec.cl

Mauricio Aguirre-Díaz
maguirred2017@udec.cl

Darío Bagüés Castro
dario.b.c@csic.es

Fernando Teillier
fernandoteillier@gmail.com

Claudia Pérez Manríquez
claudiaperez@udec.cl

¹ Centro de Biotecnología, Facultad de Ciencias Forestales, Universidad de Concepción, Barrio Universitario, Victoria 631, 4030000 Concepción, Chile

² Departamento de Biología de Organismos y Sistemas, University of Oviedo, Calle Catedrático Valentín Andrés Álvarez S/N, 33006 Oviedo, Asturias, Spain

³ Laboratorio de Química de Productos Naturales, Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Barrio Universitario, 4030000 Concepción, Chile

⁴ Facultad de Ciencias Forestales, Universidad de Concepción, Barrio Universitario, Victoria 631, 4030000 Concepción, Chile

⁵ Centro de Investigación en Nanomateriales y Nanotecnología (CINN-CSIC), Epigenética del Cáncer y Nanomedicina, San Martín del Rey Aurelio, Avenida de La Vega 4-6, 33940 El Entrego, Asturias, Spain

⁶ Instituto de Investigación Sanitaria del Principado de Asturias (ISPA), Avenida Hospital Universitario S/N, 33011 Oviedo, Asturias, Spain

⁷ Fundación Para La Investigación y La Innovación Biosanitaria del Principado de Asturias (FINBA), Avenida Hospital Universitario S/N, 33011 Oviedo, Asturias, Spain

⁸ Facultad de Salud y Ciencias Sociales, Universidad de Las Americas, Av. Pdte. Jorge Alessandri Rodríguez 1160, 4030000 Concepción, Chile