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A screening analysis of foliar terpene emissions of 36 rainforest tree species in French Guiana and their relationships with seasonality

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Abstract

Key message **Inventory and Seasonal Variation of Terpene Emissions from Tropical Trees in French Guiana: Implications for Environmental and Ecological Roles.**

Abstract A limited understanding of foliar terpene emissions from different tree species is prominent in diverse tropical forests. We conducted a study in French Guiana, screening BVOC emissions from 36 tropical woody species. We focused on 32 species in the dry season and 33 in the wet season, documenting terpene emissions for the first time in some of these tree species. Our findings show that 93.8% emitted terpenes in the dry season, while only 33.3% did so in the wet season. Terpene emissions ranged from 0.01-80.9 µg g-1 h-1 in the dry season and 0-11.7 µg g-1 h-1 in the wet season, consistent with previous reports. We identified and quantified 23 terpene compounds, including 19 monoterpenes and 4 sesquiterpenes. Additionally, 2 non-terpenoid compounds were detected: 2,2,4,6,6-pentamethylheptane (with no detected emissions in the dry season) and toluene. Among the monoterpenes, the most abundant were α-terpinolene, limonene, α-pinene, β-ocimene, and sabinene. As for sesquiterpenes, β-caryophyllene, α-caryophyllene, and α-copaene were observed during the dry season, while during the wet season, α-terpinolene predominated, followed by limonene, α-pinene, sabinene, β-caryophyllene, and α-copaene. Isoprene was detected in most of the species studied in both seasons.

Sesquiterpene emissions displayed a notable phylogenetic pattern, whereas total terpenes and monoterpenes did not; however, total terpenes and monoterpenes exhibited a significant seasonal influence.

Our study demonstrates that seasonality strongly influences BVOC production in tropical trees, with higher emissions in the dry season. These findings imply that various factors and conditions influence tree emissions in this tropical forest, affecting their ecological, environmental, and climatic roles, as well as the implementation of atmospheric chemistry models.

Keywords biogenic volatile organic compounds (BVOCs) emissions · chemical diversity · monoterpenes · sesquiterpenes · tropical forest · seasonality

Introduction

Biogenic Volatile Organic Compounds (BVOCs), which include a variety of organic compounds, are emitted by various organisms such as bacteria, fungi, marine life, plants, and even humans (Wheatley 2002; Morath et al. 2012; Bourtsoukidis et al. 2018; Lawson et al. 2020; Edtbauer et al. 2021). On the other hand, phyllospheric emissions, originating from the leaf surface, also contribute to BVOC emissions, with processes like oxidation and adsorption/desorption playing significant roles (Kembel et al. 2014; Koskella 2020; Farré-Armengol et al. 2016; Kesselmeier et al. 1999; Rundell et al. 2015). These compounds range from short-chain methanol (with C1) to longer-chain hemiterpenes like isoprene (with C5), terpenes like monoterpenes (MTs, with C10), sesquiterpenes (SQTs, with C15), and diterpenes (DTs, with C20) exhibiting a wide array of functional groups (Kesselmeier and Staudt 1999; Heiden et al. 1999; Guenther 2013; Yáñez-Serrano et al. 2020). Among BVOCs, terpenoids, including hemiterpenes, have garnered considerable attention in ecophysiology studies (Llusià and Peñuelas 2000; Peñuelas et al. 2005; Owen and Peñuelas 2005; Yáñez-Serrano et al. 2018; Misztal et al. 2015).

The production and release of BVOCs are influenced by both biotic and abiotic factors. Biotic factors involve interactions with other organisms (Kegge and Pierik 2010), while abiotic factors include environmental conditions like air temperature, humidity, light intensity, water availability, and seasonal variations (Dement et al. 1975; Tingey et al. 1980; Hansted et al. 1994; Llusià and Peñuelas 1999; Staudt and Seufert 1995; Loreto et al. 1996; Seufert 1997; Jardine et al. 2020; Peñuelas and Llusià 1997, 1999). Air temperature, particularly crucial for regulating BVOC emissions, affects enzymatic reactions involved in BVOC biosynthesis and their diffusion in biological tissues (Llusià and Peñuelas 2000). Temperature not only influences the emission rates of MTs but also affects their composition, acting as a "thermometer" to measure these changes. Changes in monoterpene composition, especially the increase in β-ocimenes and the decrease in α-pinene, may reflect the response of plants to thermal stress and their ability to adapt to warmer conditions (Jardine et al. 2017). Additionally, air humidity, light intensity and quality, water availability, and seasonal changes contribute to the complex dynamics of BVOC production and emission (Kuhn et al. 2002; Holzinger et al. 2000; Jardine et al. 2015, 2020).

The impacts of these factors on BVOCs can vary depending on the specific climatic zone and the plant species present. Notably, even within the same plant species, different populations or individuals can display adaptations to thrive in diverse climatic conditions, showcasing their capacity to adjust BVOC production and emission in response to environmental changes (Kigathi et al., 2019; Picazo-Aragonés et al., 2020).

BVOCs play essential ecological roles, including plant defense mechanisms, plant-insect interactions, and ecosystem biodiversity maintenance (Raguso 2008; Farré-Armengol et al. 2015; Borges et al. 2008; Peñuelas and Llusià 2001; Pichersky and Gershenzon 2002; Vickers et al. 2009). They can act as antioxidants, protect against oxidative stress, and aid in coping with environmental stressors like heat damage (Sharkey and Singsaas 1995; Peñuelas and Llusià 2002; Loreto et al. 2004; Munné-Bosch et al. 2004; Copolovici et al. 2005; Peñuelas et al. 2005; Medori et al. 2012; Centrito et al. 2014; Salomon et al. 2016; Dumanovic et al. 2021), protecting cell membranes from peroxidation and reactive oxygen species (Loreto and Velikova 2001; Loreto et al. 2004; Munné-Bosch et al. 2004; Llusià et al. 2005; Peñuelas and Munné-Bosch 2005; Salomon et al. 2016; Dumanovic et al. 2021), providing a competitive advantage in harsh environments. This protective capacity of BVOCs would explain that, despite the adverse environmental conditions that negatively affect photosynthesis and transpiration, it does not result in a reduction in the production and emission rates of BVOCs. Isoprene, for instance, plays a crucial role in tropical forest survival under climatic stress (Taylor et al. 2018), underscoring the ecological importance of BVOC emissions. The opportunistic emissions hypothesis sees these functions as evolved from these volatile compounds once they are byproducts of primary metabolism (Peñuelas and Llusià 2004; Owen and Peñuelas 2005).

Moreover, BVOC emissions significantly affect atmospheric chemistry and climate by influencing aerosol formation, cloud formation, precipitation patterns, and temperature regulation (Andreae and Crutzen 1997; Singh and Zimmerman 1992; Kulmala et al. 2009; Peñuelas and Staudt 2010). They also have implications for air quality, reacting with other pollutants to form secondary pollutants like tropospheric ozone formation and particulate matter (Laothawornkitkul et al. 2009).

In tropical forests such as French Guiana's, terpene production and emission rates are likely to vary seasonally in response to temperature and water availability fluctuations. Considering their ecological significance in tropical forests and their influence on atmospheric chemistry and climate, coupled with the scarcity of information regarding their emissions from tropical plant species (Courtois et al., 2009, 2016; Alves et al., 2016; Mu et al., 2022; Bourtsoukidis et al., 2024), our study was prompted.

Thus, our objective is twofold: (i) to analyze terpene emissions from various tree species in French Guiana, including those that have not been previously studied (Table S8), and (ii) to investigate the influence of seasonality on the production and emission rates of any BVOCs, specifically comparing the dry and wet seasons.

Materials and methods

Site description and sampling

The screening campaign was conducted in French Guiana on the Guiana Shield, one of three South American cratons (Gibbs and Barron 1993) (Fig. 1) and part of the Amazonian rainforest, one of the largest undisturbed areas of tropical forest in the world (Hansen et al. 2013). This tropical region rests on a Precambrian geological substrate that is particularly low in phosphorus content, especially if compared to the generally younger, nutrient-rich soils of western Amazonia (Hammond 2005; Grau et al. 2017). Fieldwork was performed at two research stations, Nouragues (Bongers 2001) (04°05´N, 52°40´W) and Paracou (Gourlet-Fleury et al. 2004) (05°18´N, 52°53´W) in well-conserved old-growth tropical forests. Sampling was conducted in 2015 on May 28–June 11 in Paracou and June 14–July 1 in Nouragues (wet season), and on October 5–22 in Paracou and October 24–November 8 in Nouragues (dry season).

Mean annual air temperature is 26°C (Bongers 2001; Gourlet-Fleury et al. 2004), and precipitation is similar, although slightly lower in Paracou (annual average of 2990 and 3100 mm in Paracou and Nouragues, respectively; Bongers 2001; Aguilos et al. 2019).

The tropical climate of French Guiana is characterized by important interannual variability in the short dry seasons, with the amount of precipitation between August and November varying from 102.2 to 532.0 mm, and long wet seasons lasting from December to July, with cumulative annual rainfall varying from 1900 to 2800 mm (Aguilos et al. 2018). This is due to the north/south movement of the Inter-Tropical Convergence Zone (Aceituno et al. 2009).

Soil water content and nutrient availabilities vary with topographical position in this French Guianese tropical forests (Epron et al. 2006; Ferry et al. 2010; Stahl et al. 2011; Allié et al. 2015). Local spatial variation (less than 200 m) creates specific habitats that differ in terms of soil characteristics, aboveground vegetation (Sabatier et al. 1997) and forest structure (Baraloto et al. 2007; Allié et al. 2015) and dynamics (Ferry et al. 2010; Courtois et al. 2018).

Nouragues has sandy soils of variable depth originating from weathered granite (van der Meer and Bongers 1996), while Paracou has shale floors with pegmatite veins of a Precambrian metamorphic formation known as the Bonidoro series (Epron et al. 2006). The soils of both sites are classified as nutrient-poor Acrisols (FAO-ISRIC-ISSS 1998) (Nachtergaele et al. 2000).

The selected trees were among the most abundant and mature tree species in the two studied areas (Table S1, Verryckt et al. 2022). We also used a fully resolved and dated Bayesian phylogeny, previously derived at the sampling sites (Baraloto et al. 2012). In addition to the previously mentioned selection criteria, it was taken into account that they were adult trees and of a similar diameter depending on the species. Thirty-six tree species were included in the sampling. Among these, 32 species were sampled during the dry season, while 33 species were sampled during the wet season (Figures 2 and 3; Table S1 and S7). The number of samples per species is indicated in Table S7. Certain species could not be sampled during specific seasons. In the dry season, *Carapa surinamensis*, *Dipteryx odorata*, *Pouteria eugeniifolia*, and

Vochysia sabatieri were not sampled. In the wet season, *Tetragastris panamensis*, *Moronobea coccinea*, and *Symphonia globulifera* could not be sampled. This discrepancy arises because the leaves of these species were not in ideal conditions to be sampled (Table S7). Additionally, the species names were verified based on the list published in Stegee et al. (2019) (see Table S8). It should be noted that in this list, *Aniba roseaodora* appears as *A. rosiodora*, *Eugenia culcullata* as *E. cucullata*, and *Tetragastris panamensis* is not included.

To obtain the branches that were used for perform gas exchange measurements and collect BVOC samples, we collaborated with expert tree climbers to collect sunlit branches between 1 and 2 meters long. Two branches were cut from each sampled tree. To avoid cavitation, we immediately immersed approximately 20 cm of the cut end in water, cutting about 7 cm of the branch into the water. For transport to the laboratory, we carefully placed the harvested branches in plastic bags with damp paper (Verryckt et al. 2020ab). Throughout the sampling process, the branches remained submerged in water. Transport time from the forest to the laboratory varied depending on the location. In Nouragues it ranged between 20 and 30 minutes, while in Paracou it lasted between 1 and 2 hours. We studied the variation of the effects of branch excision and transport among branches at the different heights in the canopy. When the branch had acclimated to its new environmental conditions—which took on average 20 min—light-saturated leaf net photosynthetic rates did not significantly differ between the excised and intact branches. We therefore conclude that branch excision did not affect the measurement of gas exchange, provided that the branch is recut under water and is allowed sufficient time to acclimate to its new environmental conditions, as we did (Verryckt et al. 2020ab).

Upon arrival at the laboratory, we meticulously selected twigs with the seemingly healthiest leaves, following the procedure mentioned earlier. Subsequently, these selected twigs were recut underwater at the base to prevent cavitation and then immersed in plastic cups filled with water. To ensure stability during the acclimatization period, they were sealed inside transparent plastic bags for approximately 24 hours at 23-25 ºC (Niinemets et al. 2005, 2009; Llusià et al. 2010a, 2014). For VOC sampling, three twigs were collected from each branch as replicates. Thus, a total of 6 twigs per tree were sampled. All leaf handling steps were carried out with utmost care to avoid causing wounds or other alterations that could lead to artifacts in VOC emission determination. Tests were conducted to compare the response of leaves on cut branches with those on uncut branches, and it was observed that the differences in photosynthetic activity and transpiration were not significant (Verryckt et al. 2020a, 2021).

Furthermore, samples without leaves were taken, thus characterizing the contribution of VOCs from the sampling system. These samples obtained from the system were used as blanks, subtracted from those obtained with leaves in the calculations described later on.

Soil water content and soil temperature

Soil water content and temperature were measured in the same BVOC sampling period, at a depth of 10 cm at five points in the 50x50 m tree sample plots. Soil moisture was measured with an HH2 soil moisture meter connected to an ML2x soil moisture sensor (Delta-T Devices Ltd, Cambridge, England), while soil temperature was measured with a digital soil thermometer (TO 15, Jules Richard instruments, Argenteuil, France) (Table S2).

Sampling of BVOC emissions

Measurements of BVOC emissions were conducted in the laboratory on a pre-cut branch with attached leaves, as previously mentioned. These measurements were carried out using a Licor-6400XT gas-exchange system coupled with a leaf chamber equipped with environmental control capabilities.

All tubes and accessories used for BVOC sampling were constructed of PFA Teflon (Cole Parmer, USA). Hydrocarbon-free ambient air was delivered to the gas inlet of the LI-6400XT using a capillary-grade hydrocarbon trap (Restek, USA). BVOC emissions were measured at a quantum flux density of 1000 μmol m^{-2} s^{-1} under standard temperature conditions (30ºC) with controlled CO_2 concentrations of 400 ppm. Given that, all tree species had leaves with a surface area greater than that of the chamber surface; the leaves were clamped on an area of the limb without prominent ribs. The 6400-40 is designed with a uniform, integrated LED light source and PAM fluorimeter that easily attaches to the LI-6400XT sensor head, giving the user complete control of the environment surrounding the 2-cm^2 leaf area. The flow in the cuvette was an average of 675 ml min^{-1} in the two seasons.

The air exiting the cuvette was pumped through custom-made sampling tubes, comprised of stainless steel tubes (89 mm in length and 6.4 mm in external diameter), which were equipped with adsorbents (115 mg of Tenax® TA and 230 mg of SulfiCarb®). These tubes were separated by sorbent-retaining springs, fixed using gauze-retaining springs, and sealed with airtight caps (Markes International Inc., Wilmington, USA). Air samples were collected using a Q_{max} air-sampling pump (Supelco, Bellefonte, Pennsylvania). The flow was measured with a Bios Defender 510 flowmeter (Bios International Corporation, Butler, USA) and adjusted with a valve. The sampling time was 20 min and the flow was 360 ± 3 mL min^{-1}. The hydrophobic properties of the activated adsorbents minimized any sample displacement by water. The terpenes were not chemically transformed in these tubes, as demonstrated by reference to trapped standards (α-pinene, β-pinene, camphene, myrcene, *p*-cymene, limonene, sabinene, camphor, α-humulene and dodecane). Prior to terpene sampling, the tubes were conditioned twice for 30 min at 350°C with a stream of 100 mL min^{-1} of purified helium. The trapping and desorption efficiency of standards such as α-pinene, β-pinene and limonene was 99%. Blank samples of air with no plants in the cuvette were collected in the tubes for 20 min immediately before each measurement. The terpene content of the blank samples was subtracted from the samples collected from plants in order to calculate the rates of terpene emission.

All the leaves used for VOC sampling were collected and the specific leaf area (SLA) was obtained by dividing the fresh leaf area by its dry weight. Leaf area was measured with the LI-3100C Leaf Area Meter (LI-COR, Lincoln, NE, USA), after which the leaves were dried for at least 48 h and weighed.

BVOC analysis

The emitted BVOCs trapped in the sorbent tubes were sampled using an automatic sample processor (TD Auto sampler, Series 2 Ultra, Markes International Inc. Wilmington, USA) and thermally desorbed using a coupled injector with a cryotrap (Unity, Series 2, Markes International Inc. Wilmington, USA) connected to a Gas Chromatograph (7890A, Agilent Technologies, Santa Clara, USA) with a mass spectrometer detector (5975C inert MSD with Triple-Axis Detector, Agilent Technologies). A full-scan (between 35 to 350 m/z) method was used in the chromatographic analyses.

Pre-desorption conditions consisted of a pre-purge time of 0.1 min, with a split of 20 mL min^{-1}, and a dry purge of 2 min. Then, BVOCs were desorbed with a flow path temperature of 200 ºC, minimum carrier pressure of 0.5 KPa, and a GC cycle time of 30 min, optimal time to recover maximum sample; the standby split was 25 mL min^{-1}. Sample desorption time was 30 min at 320 ºC with the trap maintained in-line, with a flow rate of 50 mL min^{-1} and a split of 2 mL min^{-1}; the cryotrap low temperature was -25 ºC. Prior to heating, traps were held in a pre-cryotrap fire purge for 2 min. The cryotrap flow rate was 50 mL min^{-1}, with a split of 10 mL min^{-1}, and the heating rate was 40 ºC s^{-1} to a cryotrap high of 320 ºC maintained for 7 min, with a split of 5 mL min^{-1}.

Then, the cryofocused desorbed samples were injected into a GC column (Agilent Tech., HP 5MS, 30 m x 0.25 μm x 0.25 mm) using a transfer line at 250ºC. Following sample injection at 35 ºC (initial time: 3 min), the column temperature was increased stepwise by 15 ºC min^{-1} to 150 ºC, by 50 ºC min^{-1} to 250 ºC for 5 min, and by 30 ºC min^{-1} to 280 ºC for 5 min, and was maintained at each time for 5 min. The total run time was 30 min, the helium column flow rate was 1 mL min^{-1}.

Terpene identification and quantification

Terpene identification was performed by comparing the derived mass spectra with published results (Wiley275 and Nist05a libraries) and known standards such as those mentioned below for quantification. Quantification of peaks was conducted using the fragmentation product with mass 93 (Blanch et al. 2012; Llusià et al. 2012; Hellén et al. 2024), while calibration curves were prepared using commercial standards for some of the most abundant recorded compounds: four monoterpenes (α-pinene, 3-carene, β-pinene and limonene) and one sesquiterpene (α-caryophyllene) (Fluka Chemie AG, Buchs, Switzerland). These standards were adsorbed on cartridges similar to those used for the samples by means of a valve coupled to the chromatograph and a flow of Helium 5.0 like the one used for the flows generated by the Q_{max} pump. They were then desorbed and analysed following the same protocol as used for the samples. Terpene calibration curves for signals and concentrations were always highly correlated ($r^2 \geq 0.95$) and the sensitivity of the most abundant terpenes were similar (differences were < 5%). The response factor for the MTs was an average of the standard MTs and only that of the α-caryophyllene for the sesquiterpenes. We estimate a 5% error in the quantification given by the response variation of each standard with respect to each other. For isoprene, we used a Linde gas standard (1 ppm) of which we made three dilutions to obtain its calibration curve.

To prepare the liquid standards, three different dilutions were made: 1 μL of the pure standard was diluted in 1000 μL of pentane and then 100 μL of this standard were taken and diluted in another 1000 μL of pentane. From this second dilution another 100 μL were taken and diluted in 1000 μL of pentane.

In addition, we also prepared standards from a standard at 500 ppb of a 50-L bottle (Reimer Environmental, Inc., Miami, USA). We injected 15, 25 and 35 mL into three sampling tubes using the same valve as mentioned above. In each sequence (of 30 tubes) of analysis, a series of three standards (one for each concentration) of the gas standard were added at the beginning, and at the end of series 3 (one for each concentration) of the liquid standard (previously gassed). To avoid interference in samples due to contamination, the standards were arranged from lowest to highest concentrations. In addition, the analysis of the sequences always started with an empty tube followed by a tube with the same adsorbents taken from the field but not sampled to test for possible contamination during the process.

To calculate the micrograms (μg) of terpenes per gram (g) of dry matter and per hour, we used the following formula:

$$[(AUs / svs) - (AUb / svb)] \times [(rf \times Fch \times 60\ min) / (AUrf \times g\ d.m. \times st)] \qquad \text{Equ. 1.}$$

In this equation, the variables represent the following:

- AUs and Aub: Arbitrary units of area of the air sampled from the cuvette and of the blank air sample (area units).
- Svs and svb: Volume of air sampled from the cuvette with leaves and as blank (milliliters, mL).
- rf: Response factor calculated from the calibration curves (micrograms, μg).
- Fch: Flow rate in the sampling chamber (milliliters per minute, mL min^{-1}).
- AUrf: Arbitrary units of area corresponding to the response factor (arbitrary units).
- g d.m.: Grams of dry matter (g).
- st: Sampling time (minutes, min).

The Shapiro-Wilk test (N > 30) showed that the data of the variables (i.e. emissions of total BVOCs, monoterpenes and sesquiterpenes) were normally distributed (P > 0.05).

We used Bayesian phylogenetic linear mixed-effects models implemented in the MCMCglmm R package (Hadfield 2010) (Table S6) to test for the effects of season while controlling for the potential effects of intraspecific plasticity and phylogenetic ancestry on the foliar variables. In these analyses season was included as a fixed factor, and phylogenetic relationships and species identities as random factors. The phylogenetic term accounted for the variability related with shared ancestry, while the species term accounted for species-specific traits independent of shared ancestry. Thus, both random factors accounted for the variance explained by heritability and by the plastic expression of species' emission capacities.

We computed the phylogenetic signal as Pagel's λ to assess the importance of phylogenetic ancestry on the emission of BVOCs. The corresponding P-values were based on the variance in phylogenetically independent contrasts relative to tip-shuffling randomization, as implemented in the *phylosig* function in the R *phytools* package (Revell 2012). Pagel's λ (1999) provides a quantitative phylogenetic measure in which λ is a scaling parameter for the correlations between species in relation to the correlation expected under Brownian evolution. λ has a natural scale between zero (no correlation between species) and 1.0 (correlation between species equal to the expected Brownian correlation). λ itself is not a correlation but, rather, a scaling factor for a correlation, so $\lambda > 1.0$ is theoretically possible. However, depending on the structure of the tree, $\lambda >> 1.0$ is not usually defined.

Terpene emission rates were expressed as μg g^{-1} d.m. h^{-1}.

Results

Environmental conditions

The French Guiana monthly average rainfall in 2015 was 237 ± 44 mm during the wet season (December–August) and 47.5 ± 11.1 mm during the dry season (September–November), with the maximum rainfall falling in May (532 mm) and the minimum in October (33 mm). The field campaign during the dry season was conducted with 32.8 mm of rainfall. Mean air temperature during the rainy season was 27–28ºC, with a maximum of 28ºC in December. During the dry season the maximum temperatures were 28–28.5ºC, with minimum temperatures recorded in February (26.5ºC). The overall air temperature remains steady throughout the year in French Guiana.

Soil water content and temperature values correspond to measurements made in the experimental plots. The average soil water content was 20.2 ± 0.3% in the dry season and 32.3 ± 0.2% in the wet season (Fig. 1 and Table S2). The average soil temperature in the dry season was 26.5 ± 0.1ºC and in wet season 23.7 ± 0.01ºC (Fig. 1 and Table S2).

BVOC emission rates

Total BVOC emissions varied from 0.01 to 80.9 μg g^{-1} d.m. h^{-1} in the dry season and from 0 to 11.7 μg g^{-1} d.m. h^{-1} in the wet season, indicating considerable variation based on environmental conditions (Fig. 2, 3, 4, and S1, and Table S3 and S4). The values for total BVOCs they were 5.7 ± 0.6 and 1.3 ± 0.7 μg g^{-1} d.m. h^{-1} while, for total terpenes were 5.4 ± 0.6 and 0.5 ± 0.7 μg g-1 d.m. h-1, in dry and wet season respectively. The majority of both total BVOCs and terpenes were mainly emitted during the dry season (see Figs. 4 and S1). These differences were statistically significant, with ANOVA analysis showing $P < 0.0001$. Sample sizes were 285 in the dry season and 219 in the wet season. Of the monoterpenes, the most abundant were α-terpinolene, limonene, α-pinene, t-β-ocimene and sabinene. Of the sesquiterpenes, β-caryophyllene, α-caryophyllene and α-copaene were observed during the dry season, while during the wet season, α-terpinolene predominated, followed by limonene, α-pinene, sabinene, β-caryophyllene and α-copaene (Figs. 3A, 4 and Table S3). Isoprene was detected in most of the species studied in both seasons (Figs. 3B, 4 and S1, and Table S3). However, in three tree species (*Gustavia hexapétala* (1.8 ± 1.6 vs 0 ± 0 $\mu g\ g^{-1}$ d.m. h^{-1}), *Eugenia culcullata* (3.1 ± 1.1 vs 0.4 ± 0.1 $\mu g\ g^{-1}$ d.m. h^{-1}) and *Dycorinia guianensis* (1.2 ± 0.8 vs 0 ± 0 $\mu g\ g^{-1}$ d.m. h^{-1})) was significantly higher in the wet season than in the dry season ($P < 0.01$). Only *Aniba rosaeodora* emitted more isoprene in the dry season than in the wet season (2.2 ± 2.0 vs 0 ± 0 $\mu g\ g^{-1}$ d.m. h^{-1}) (Fig. 3B).

Among the BVOCs detected, the main non-terpenoid compounds were 2,2,4,6,6-pentamethyl heptane (with no detected emissions in the dry season and 0.3 ± 0.1 $\mu g\ g^{-1}$ d.m. h^{-1} in the wet season) and toluene (0.1 ± 0.02 $\mu g\ g^{-1}$ d.m. h^{-1} in the dry season and 0.012 ± 0.007 $\mu g\ g^{-1}$ d.m. h^{-1} in the wet season) (Fig. 4 and Table S4). Notably, 2,2,4,6,6-pentamethyl heptane exhibited a strong correlation with isoprene during the wet season ($r^2 = 0.23$, $P < 0.0001$, $N = 219$), while toluene showed a correlation with α-pinene during the dry season ($r^2 = 0.15$, $P < 0.01$, $N = 285$).

The emission rates of the terpenes and toluene followed a similar pattern to the total BVOCs, except for 2,2,4,6,6-pentamethyl heptane, which was primarily emitted during the wet season (Fig. 4 and Table S4). Among the emitted BVOCs, α-terpinolene, limonene, α-pinene, t-β-ocimene (MT), β-caryophyllene, and α-caryophyllene (SQT) were the most abundant, especially in the dry season (Fig. 3A and 4). Additionally, there was a group of unidentified sesquiterpenes emitted, collectively surpassing the previously mentioned BVOCs, also in the dry season (Fig. 3A).

Figure 2 displays all the tree species studied along with their average terpene emissions during both the dry and wet seasons. Among these species, 27.6% were classified as high terpene emitters, 51.7% as intermediate emitters, and 20.7% as low emitters. The remaining species were categorized as very low emitters (Fig. 2A). Notably, 90.6% of the species emitted terpenes during the dry season, whereas only 36.4% emitted terpenes during the wet season. The percentages for monoterpenes mirrored those of the total terpenes. However, sesquiterpenes were emitted by 75% of the species in the dry season and only by 15.6% in the wet season (Figs. 2 and 3).

Specifically, 2,2,4,6,6-pentamethyl heptane was emitted by 31.3% of the tree species exclusively during the wet season, while toluene was emitted by 37.5% of the species during the dry season and by 6.3% of the species during the wet season (Table S4). Monoterpenes generally predominated over sesquiterpenes, except in the case of the tree species *Eperua grandiflora* (Fig. 2B, C). Notably, a significant phylogenetic signal, as assessed by Pagel's λ, was observed only for sesquiterpenes (Table S5).

Discussion

Our results emphasized the species-specificity of BVOC emissions and the varying tree species responses to seasonal and environmental conditions (Gomes-Alves et al. 2022; Khun et al. 2002; Mishra and Sinha 2020). The majority of the species emitted terpenes, isoprene, and other BVOCs (Figs. 2 and 3; Table S3). However, the emitted quantities were relatively low compared to similar studies in other ecosystems such as the Mediterranean forests (Llusià et al. 2013) but comparable to those observed in analogous tropical environments (Llusià et al. 2010a, 2014). In the Amazon rainforest, various studies have explored BVOC emissions and their fluctuations. Jardine et al. (2015) studied the speciation of 12 monoterpenes and their vertically resolved ambient air mixing ratios in a central Amazon rainforest and their reactive potential of some of them. Specifically, they observed the highly reactive cis-β-ocimene (160 ppt), trans-β-ocimene (79 ppt) and terpinolene (32 ppt), which represented approximately 21% of the total monoterpene composition and 55% of the rate of ozonolysis of monoterpenes from the upper part of the canopy. Leaf-level emissions of highly reactive monoterpenes accounted for up to 1.9% of photosynthesis, confirming light-dependent emissions in several genera of Amazonian trees, corroborating the present study accounting the qualitatively results. Jardine et al. (2017) utilized monoterpenes as an indicator to gauge the central Amazon rainforest's response to climate warming and found that monoterpene emissions increase with temperature, especially β-ocymene, corroborating our results of higher emissions in the dry season (Figs. 3A, 4, S1 and Tables S3 and S4). And in another study (Yáñez-Serrano et al., 2018), conducted in the Amazon rainforest, the chemical speciation of monoterpenes, was investigated using samples collected during the dry season of October 2015 at the Amazon Tall Tower Observatory (ATTO). A distinct differentiation in chemical composition between day and night was found, with α-pinene being more abundant during the day and limonene predominating at night. Reactivity calculations revealed that higher abundance does not always correlate with greater reactivity, and modeling simulations indicated the need for further research to fully understand the processes of monoterpene exchange in the tropical forest canopy. This study highlights the importance of chemical speciation in understanding the role of monoterpenes in atmospheric chemistry and the carbon cycle in tropical forest ecosystems. Furthermore, Byron et al. (2022) investigated the chemical speciation of chiral monoterpenes in a tropical rainforest ecosystem, revealing distinct diel emission peaks and shifts in emissions in response to drought conditions. Their findings emphasize the importance of considering enantiomeric distribution in understanding monoterpene emission mechanisms and predicting atmospheric feedbacks in forest ecosystems, which complements our understanding of BVOC emissions.

Gomes-Alves et al. (2022) investigated the variability of isoprenoid emission patterns, including isoprene, in Amazonian ecosystems in response to ecophysiological and environmental factors. They conducted measurements of isoprenoid emission capacities across seasons and environmental gradients for three dominant tree species in the central Amazon. Contrary to the common perception that isoprene emissions predominantly occur under water stress and high temperatures, their results align with those of Gomes-Alves et al. (2022), who documented higher isoprene emissions during the wet season, challenging previous assumptions (Taylor et al. 2018) across all tree species. They suggested that the decreased emissions during the dry season could represent a plastic response to escalating abiotic stress, such as heat and drought, coupled with reduced substrate availability for isoprenoid synthesis. The study proposed that shifts in emission composition, characterized by elevated isoprene emissions during the wet season, might serve as a physiological adaptation to optimize plant performance under prevailing wet season conditions. These findings contrast with the higher terpene emissions observed in the driest and hottest seasons, indicating potential differences in emission behavior between isoprene and other isoprenoids, necessitating separate consideration in seasonal emission studies.

In their study, Gomes-Alves et al. (2022) noted a significant decrease in isoprenoid emission capacity during the transition from the wet to the dry season, coinciding with heightened abiotic stress due to heat and drought in the Amazon rainforest. Moreover, they observed an increase in emissions of heavier isoprenoids, such as monoterpenes and sesquiterpenes, during this seasonal transition, suggesting a plastic response of plants to changing conditions. This adaptation in the composition of isoprenoid emissions may represent a strategy to mitigate abiotic stress and sustain essential plant functions. Additionally, previous research has demonstrated the variability of plant responses in isoprenoid emission rates in relation to climatic and ecological factors (Staudt et al. 2017). It has also been observed that moderate drought can lead to an increase in isoprenoid emission rates as plants adapt to water stress (Dani et al., 2014). However, under conditions of extreme drought, these rates have been shown to decline substantially (Llusià and Peñuelas, 1998).

Furthermore, the study by Byron et al. (2022) examined the response of monoterpene emissions to drought in a tropical rainforest ecosystem. They found that, during a controlled drought experiment, monoterpene emissions exhibited distinct diurnal peaks and changes in the composition of α-pinene enantiomers. Additionally, as drought progressed, the emission source of (-)-α-pinene shifted towards storage pools, promoting cloud formation. This alteration in monoterpene emission composition may be linked to the plant's ability to adapt to water and thermal stress, supporting the hypothesis of a plastic response to drought.

In summary, these findings suggest that plants can adjust their terpene emissions, including isoprenoids, as an adaptive strategy to cope with abiotic stress during the dry season in tropical rainforests. The ability to modulate the composition of terpene emissions could have significant implications for atmospheric chemistry and climate feedback processes in these ecosystems.

Given the present climate change scenario with altered rainfall patterns (Dore 2005), and recognizing that moderate drought conditions amplify BVOC emissions (Niinemets 2010), a negative feedback effect might occur, particularly regarding increased aridity. During moderate drought conditions, heightened terpenes in the atmosphere could potentially enhance rainfall, alleviating, to some degree, the detrimental impacts of climate change in these areas (Llusià and Peñuelas 1998; Llusià et al. 2006, 2008, 2010b; Blanch et al. 2007, 2009).

It is noteworthy that non-terpene compounds like toluene and 2,2,4,6,6-pentamethyl heptane were detected (Heiden et al. 1999; Zhiqun et al. 2017; Misztal et al. 2015). α-Pinene emission rates also showed a correlation with these factors, especially during the dry season (Fig. 4). This study also presents the first report of 2,2,4,6,6-pentamethyl heptane emission from the leaves of several tropical tree species (Khun et al. 2002; Courtois et al. 2009). This BVOC is known to have allopathic effects, implying a role in plant defense (Zhiqun et al. 2017).

BVOC emissions are thus sensitive to taxonomy and environmental factors, including temperature, light, and moisture availability. Considering the increasing occurrence of drought periods in tropical areas due to climate change, understanding the potential implications for BVOC emissions is crucial. Drought stress can significantly affect plant physiology and metabolism, potentially altering the quantity and composition of BVOC emissions.

The findings of this study contribute to the characterization of BVOC emissions from some tropical tree species and, therefore, to our understanding of the complex interactions between climate change, drought, tree species and BVOC emissions. By considering the potential effects of drought on BVOC emissions and their implications for atmospheric chemistry and climate processes, we can develop a more comprehensive understanding of the role of BVOCs in the context of climate change and its impact on drought periods in tropical areas (Dore 2005; Fubao et al. 2018).

Conclusions and final remarks

This study reports the results of the emissions of different BVOCs by 36 tree species in the tropical forests of French Guiana and confirms that there are significant seasonal differences, on average, for BVOCs emitted. On average, emissions in the dry season were higher than in the wet season; as well, the proportion of each type of BVOCs in each season was found to be different. Species' shared ancestry had a significant effect on sesquiterpene (Liang et al. 2021) emissions but not on the total terpenes or monoterpenes.

This study provides strong evidence of higher rates of foliar terpene emissions from tropical trees in the dry season than in the wet season. Our results underscore the potential role of this variation in the capacity of terpene emissions to act as a buffer effect on climate change (Engelhart et al. 2008). More BVOC emissions under increased drought could partly counteract the severity of droughts by favoring cloud formation and precipitation (Jardine et al. 2020).

As these compounds have important roles in atmospheric chemistry, aerosol formation, and plant-atmosphere interaction, further research in this field will help improve our understanding of biogeochemical processes and address important issues related to climate change and air quality.

Authorship contribution statement

AG-G Manuscript review. **CS, DA, GP, LB** and **RO** Support in field work and manuscript review. **EC, IU, LVL** and **OG** Support in field work. **IAJ** Planning and development of the experiment, supervision of the collection of the samples. **IF**

Planning and development of the experiment. Manuscript review. **JLl** Collection of samples of BVOCs and their analysis and writing of the document. **JP** Planning and development of the experiment, supervision of the collection of the samples and analyses and manuscript review. **JS** Planning and development of the experiment, supervision of the collection of the samples. Analysis of the Bayesian phylogeny. Manuscript review. **LTV** Support in field and laboratory work, manuscript review. All authors read and commented on the paper.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could influence the work reported in this paper.

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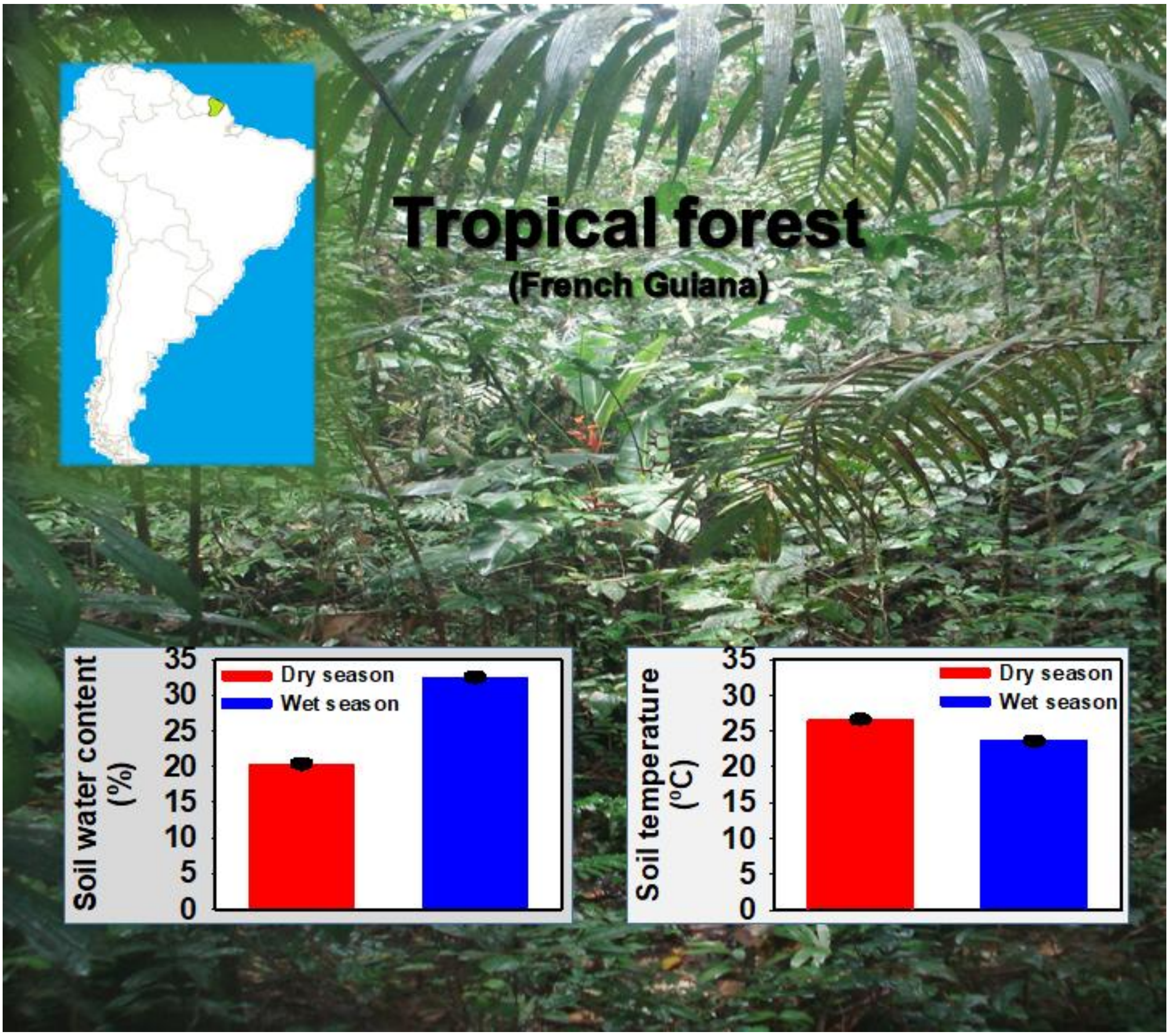

Fig. 1. Mean soil water content (%) and soil temperature (ºC) (± standard error) in French Guiana, South America. The picture was taken during the 2015 wet season at the Nouragues Ecological Research Station.

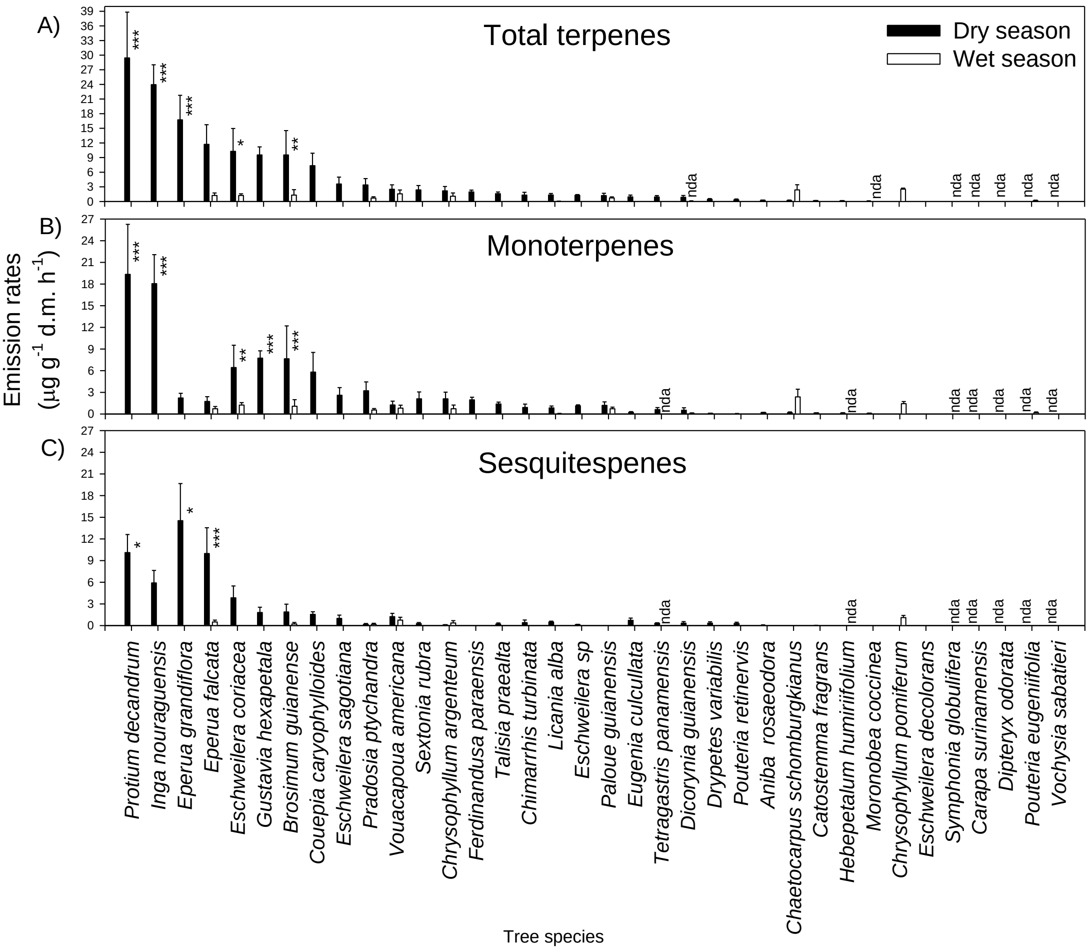

Fig. 2. Mean terpene emissions (± standard deviation) for A) total terpenes, B) monoterpenes and C) sesquiterpenes from 36 tropical tree species in French Guiana. Asterisks indicate significant differences between seasons, * P < 0.01, ** P < 0.001, *** P < 0.00001; N = 285 and 219 in the dry and wet season, respectively. Nda stands for no data available.

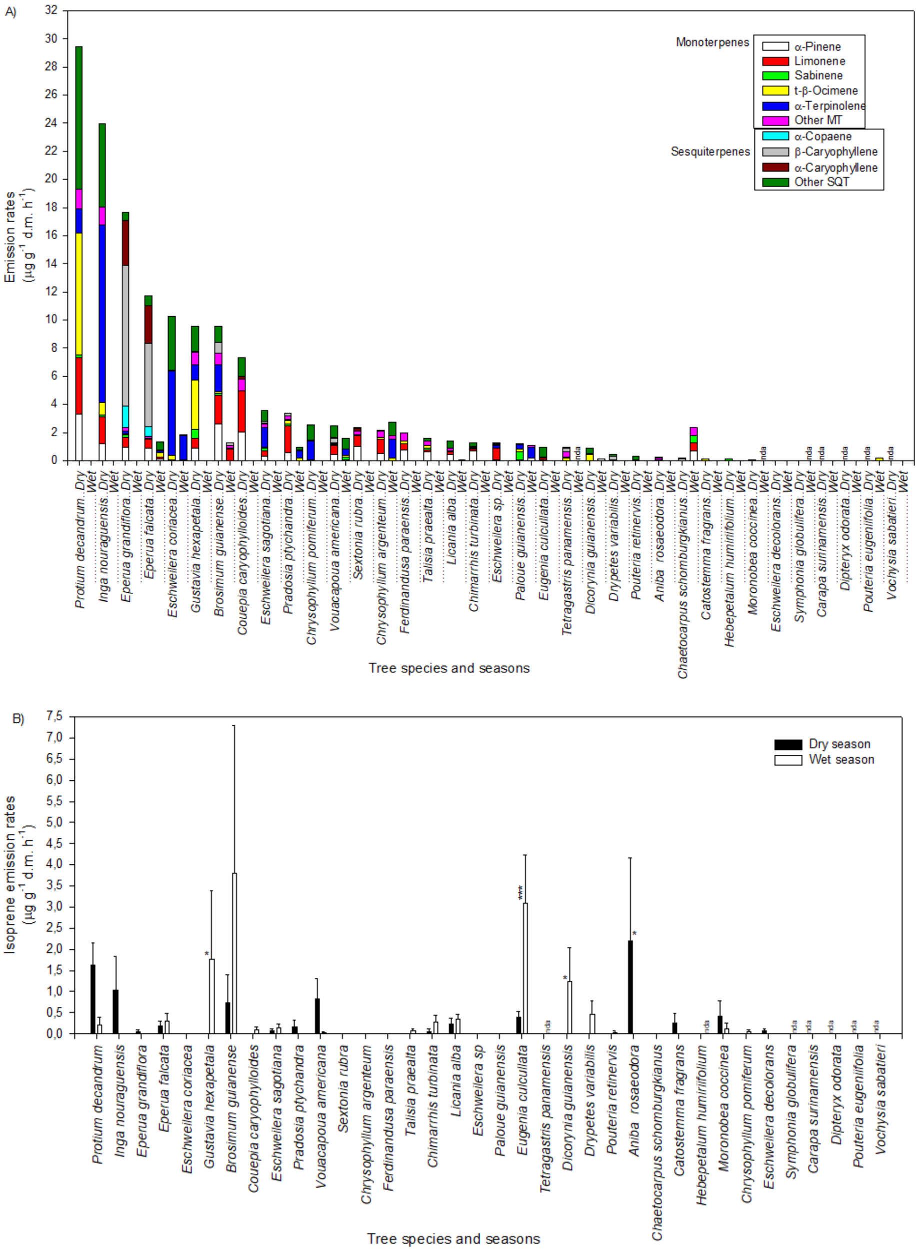

Fig. 3. Mean terpene emissions (± standard error) for A) Total terpenes and B) the isoprene group from 36 tropical tree species in French Guiana. Asterisks indicate significant differences between seasons, * $P < 0.01$, ** $P < 0.001$, *** $P < 0.00001$; N = 285 and 219 in the dry and wet season, respectively. "N" refers to the sample size, representing the number of observations available in each season. "Nda" stands for no data available.

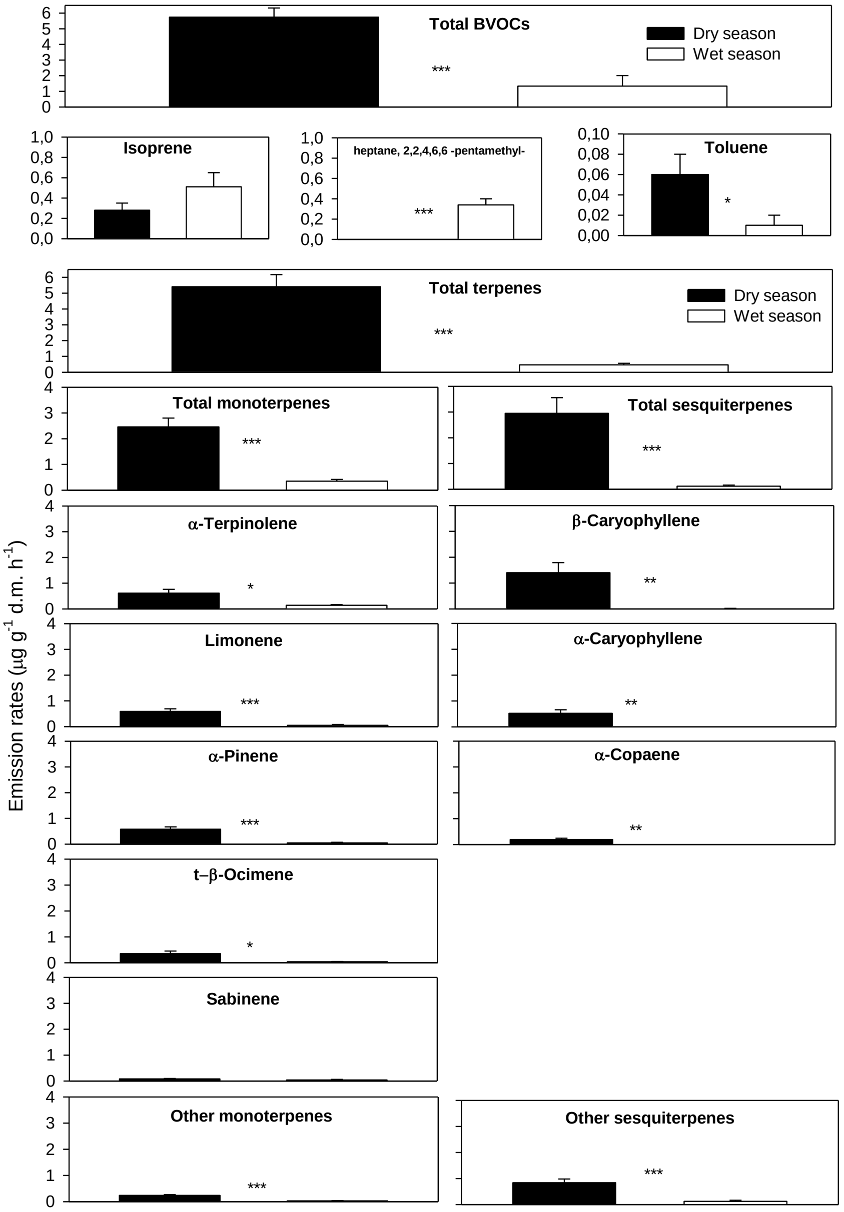

Fig. 4. Mean biogenic volatile organic compound (BVOC) emissions (± standard error) from 36 tropical tree species in French Guiana. Asterisks indicate significant differences between seasons: * $P < 0.01$, ** $P < 0.001$, *** $P < 0.00001$; $N = 285$ and 219 in the dry and wet seasons, respectively. In this context, "N" represents the sample size, indicating the number of observations available for each season.

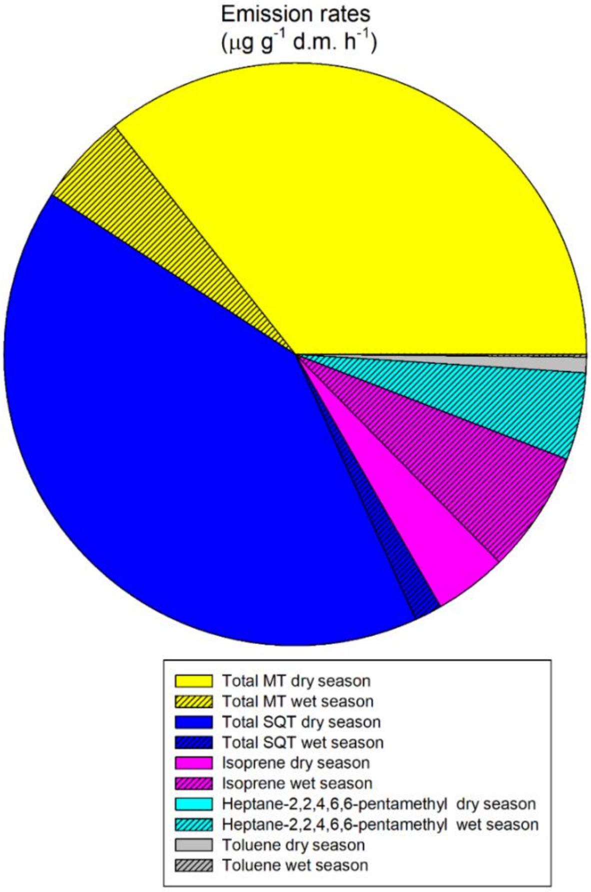

Fig. S1. Means of the different types of BVOCs emitted by 36 tropical tree species in French Guiana. MT: monoterpenes; SQT: sesquiterpenes.

Table S1. List of the different tropical tree species studied in the dry and wet seasons in the Nouragues Ecological Research Station and Paracou Experimental Field Station in French Guiana.

Season	Site	Species	Family
Dry	Nouragues	*Aniba rosaeodora*	Lauraceae
		Brosimum guianense	Moraceae
		Chimarrhis turbinata	Rubiaceae
		Chrysophyllum argenteum	Sapotaceae
		Couepia caryophylloides	Chrysobalanaceae
		Dicorynia guianensis	Fabaceae
		Eperua falcata	Fabaceae
		Eschweilera coriacea	Lecythidaceae
		Eschweilera decolorans	Lecythidaceae
		Eugenia culcullata	Myrtaceae
		Ferdinandusa paraensis	Rubiaceae
		Inga nouraguensis	Fabaceae
		Licania alba	Chrysobalanaceae
		Paloue guianensis	Fabaceae
		Pouteria retinervis	Sapotaceae
		Pradosia ptychandra	Sapotaceae
		Protium decandrum	Burseraceae
		Sextonia rubra	Lauraceae
		Talisia praealta	Sapindaceae
		Vochysia sabatieri	Vochysiaceae
		Vouacapoua americana	Fabaceae
	Paracou	*Carapa surinamensis*	Meliaceae
		Catostemma fragrans	Malvaceae
		Chaetocarpus schomburgkianus	Euphorbiaceae
		Chrysophyllum pomiferum	Sapotaceae
		Dipteryx odorata	Fabaceae
		Drypetes variabilis	Putranjivaceae
		Eperua falcata	
		Eperua grandiflora	Fabaceae
		Eschweilera sagotiana	Lecythidaceae
		Eschweilera sp	Lecythidaceae
		Gustavia hexapetala	Lecythidaceae
		Hebepetalum humiriifolium	Linaceae
		Licania alba	
		Moronobea coccinea	Clusiaceae
		Pouteria eugeniifolia	Sapotaceae
		Symphonia globulifera	Clusiaceae
		Tetragastris panamensis	Burseraceae
		Vouacapoua americana	
Wet	Nouragues	*Aniba rosaeodora*	Lauraceae
		Agonandra silvatica	
		Brosimum guianense	Moraceae
		Chimarrhis turbinata	Rubiaceae

	Chrysophyllum argenteum	Sapotaceae
	Couepia caryophylloides	Chrysobalanaceae
	Dicorynia guianensis	Fabaceae
	Eperua falcata	Fabaceae
	Eschweilera coriacea	Lecythidaceae
	Eschweilera decolorans	Lecythidaceae
	Eugenia culcullata	Myrtaceae
	Ferdinandusa paraensis	Rubiaceae
	Inga nouraguensis	Fabaceae
	Licania alba	Chrysobalanaceae
	Paloue guianensis	Fabaceae
	Pouteria retinervis	Sapotaceae
	Pradosia ptychandra	Sapotaceae
	Protium decandrum	Burseraceae
	Sextonia rubra	Lauraceae
	Talisia praealta	Sapindaceae
	Vochysia sabatieri	Vochysiaceae
	Vouacapoua americana	Fabaceae
Paracou	*Carapa surinamensis*	Meliaceae
	Catostemma fragrans	Malvaceae
	Chaetocarpus schomburgkianus	Euphorbiaceae
	Chrysophyllum argenteum *Chrysophyllum pomiferum*	Sapotaceae
	Dipteryx odorata	Fabaceae
	Drypetes variabilis	Putranjivaceae
	Eperua falcata *Eperua grandiflora*	Fabaceae
	Eschweilera sagotiana	Lecythidaceae
	Eschweilera sp	Lecythidaceae
	Gustavia hexapetala	Lecythidaceae
	Hebepetalum humiriifolium	Linaceae
	Licania alba *Moronobea coccinea*	Clusiaceae
	Pouteria eugeniifolia	Sapotaceae
	Symphonia globulifera	Clusiaceae
	Tetragastris panamensis	Burseraceae
	Vouacapoua americana	

Table S2. Mean (± STD) soil water content (%) and soil temperature (ºC) around the 36 tropical tree species in French Guiana. Letters indicate significant differences between seasons. N indicates the number of measurements.

Specific name	Season	Soil water content (%)	Soil temperature (ºC)	N
Protium decandrum	Dry	23.6 ± 0a	26.3 ± 0a	
	Wet	33.1 ± 0b	23.7 ± 0b	
Inga nouraguensis	Dry	23.6 ± 0a	26.3 ± 0a	
	Wet	33.1 ± 0b	23.7 ± 0b	
Eperua grandiflora	Dry	15.6 ± 1.1a	26 ± 0.4	
				20
	Wet	28.8 ± 1.5b	nda	
Eperua falcata	Dry	20.3 ± 0.6a	25 ± 0.07a	
				32
	Wet	34.2 ± 0.7b	23.7 ± 0b	
Eschweilera coriacea	Dry	20.2 ± 0a	26.2 ± 0a	
				6
	Wet	35.8 ± 0.3b	23.9 ± 0.05b	
Gustavia hexapetala	Dry	21.3 ± 0a	24.6 ± 0	
	Wet	30.7 ± 0b	nda	
				6
Brosimum guianense	Dry	18.7 ± 0a	28 ± 0a	
	Wet	35 ± 0b	23.7 ± 0b	
				6
Couepia caryophylloides	Dry	23.4 ± 0a	29.6 ± 0a	
	Wet	31.5 ± 0b	23.7 ± 0b	
Eschweilera sagotiana	Dry	19.9 ± 1.6a	27 ± 0.6	
	Wet	32.8 ± 0b	nda	
Pradosia ptychandra	Dry	20.3 ± 0.5a	28 ± 0a	
	Wet	36.4 ± 0b	23.6 ± 0b	
Chrysophyllum pomiferum	Dry	20.5 ± 0	25.1 ± 0	
				6
	Wet	nda	nda	
Vouacapoua americana	Dry	22.6 ± 0.5a	25.4 ± 0.1a	
				18
	Wet	32.1 ± 1b	23.7 ± 0.03b	
				17
Sextonia rubra	Dry	25.4 ± 0a	28.5 ± 0a	
				6
	Wet	33.4 ± 0b	23.7 ± 0b	

Chrysophyllum argenteum	Dry	20.2 ± 0a	26.2 ± 0a	
	Wet	32.7 ± 1.3b	23.9 ± 0b	
				6
Ferdinandusa paraensis	Dry	24.2 ± 0a	27.5 ± 0a	
	Wet	31.4 ± 0b	23.3 ± 0b	
Talisia praealta	Dry	25.4 ± 0a	29 ± 0a	
	Wet	36.3 ± 0b	23.5 ± 0b	
Licania alba	Dry	22.5 ± 0.7a	27.7 ± 0.3a	
	Wet	33 ± 0.5b	23.7 ± 0.02b	
				40
Chimarrhis turbinata	Dry	25.2 ± 0a	27.6 ± 0a	
	Wet	38.1 ± 0b	23.4 ± 0b	
Eschweilera sp	Dry	12.8 ± 0a	24.5 ± 0	
	Wet	27.9 ± 0b	nda	
Paloue guianensis	Dry	21.8 ± 0a	28 ± 0a	
	Wet	36.4 ± 0b	23.6 ± 0b	
				4
Eugenia culcullata	Dry	9 ± 0a	28.9 ± 0a	
	Wet	25.3 ± 0b	23.5 ± 0b	
Tetragastris panamensis	Dry	25.3 ± 0	25 ± 0	
	Wet	nda	nda	
Dicorynia guianensis	Dry	19 ± 0a	28 ± 0a	
	Wet	34.4 ± 0.5b	23.8 ± 0.02b	
Drypetes variabilis	Dry	22.2 ± 0a	24.8 ± 0	
	Wet	29.7 ± 0b	nda	
Pouteria retinervis	Dry	9 ± 0a	29 ± 0a	
	Wet	25.3 ± 0b	23.5 ± 0b	
Aniba rosaeodora	Dry	24.2 ± 0a	27.5 ± 0a	
	Wet	31.4 ± 0b	23.3 ± 0b	
Chaetocarpus schomburgkianus	Dry	13.7 ± 0a	25.4 ± 0	
	Wet	27.8 ± 0b	nda	
Catostemma fragrans	Dry	21.3 ± 0a	24.6 ± 0	
				6
	Wet	30.7 ± 0b	nda	
Hebepetalum humiriifolium	Dry	15 ± 0	24.7 ± 0	
	Wet	nda	nda	
Moronobea coccinea	Dry	9.9 ± 0a	24.9 ± 0	
	Wet	26.2 ± 0b	nda	
Symphonia globulifera	Dry	19.4 ± 0	24.6 ± 0	
	Wet	nda	nda	

Eschweilera decolorans	Dry	22.9 ± 0a	27.3 ± 0a
			6
	Wet	37.6 ± 0b	23.9 ± 0b
Capirona decorticans	Dry	nda	nda
	Wet	31.5 ± 0	23.7 ± 0
Caryocar glabrum	Dry	nda	nda
	Wet	33.4 ± 0	23.7 ± 0
Chrysophyllum sanguinolentum	Dry	nda	nda
	Wet	31.5 ± 0	23.7 ± 0
Helicostylis pedunculata	Dry	nda	nda
	Wet	36.4 ± 0	23.6 ± 0
Hirtella bicornis	Dry	nda	nda
	Wet	33.4 ± 0	23.7 ± 0
Hymanea courbaril	Dry	nda	nda
	Wet	35.5 ± 0	23.9 ± 0
Lecythis poiteaui	Dry	nda	nda
	Wet	38.1 ± 0	23.4 ± 0
Myrcia splendens	Dry	nda	nda
	Wet	25.3 ± 0	23.5 ± 0
Protium opacum	Dry	nda	nda
	Wet	36.4 ± 0	23.6 ± 0
Sloanea sp	Dry	nda	nda
	Wet	nda	nda
Sterculia pruriens	Dry	nda	nda
	Wet	30.7 ± 0	nda
Pouteria eugeniifolia	Dry	nda	nda
	Wet	27.8 ± 0	nda
Carapa surinamensis	Dry	nda	nda
	Wet	29.7 ± 0	nda
Dipteryx odorata	Dry	nda	nda
	Wet	30.7 ± 0	nda
Vochysia sabatieri	Dry	nda	nda
	Wet	33.4 ± 0	23.7 ± 0

Table S3. Mean (minimum, maximum ± standard deviation and standard error, in μg g^{-1} d.m. h^{-1}) biogenic volatile organic compounds (BVOCs) and *P-value* of the 36 tropical tree species studied in the dry and wet seasons in French Guiana. N = 285 and 219 for the dry and wet seasons, respectively. MTu: monoterpene unidentified; SQTsu: Sum of unidentified sesquiterpenes.

Season	Dry					Wet					
BVOCs	Mean	Min.	Max.	Std	Ste	Mean	Min.	Max.	Std	Ste	*P-value*
Total BVOCs	5,5	0	80,9	12,8	0,8	0,8	0	11,7	1,9	0,1	0.000010
Total terpenes	5,4	0	80,9	12,8	0,8	0,5	0	10,3	1,5	0,1	0.000010
Total monoterpenes	2,5	0	39,6	5,7	0,3	0,4	0	6,6	1	0,1	0.000010
Other monoterpenes	0,2	0	4,5	0,6	0	0	0	2	0,2	0	0.000010
Total sesquiterpenes	3	0	79,9	10,3	0,6	0,1	0	4,4	0,6	0	0.000100
Other sesquiterpenes	0,8	0	16,7	2,3	0,1	0,1	0	4,4	0,6	0	0.000010
Isoprene	0,3	0	13	1,2	0,1	0,5	0	22,9	2,1	0,1	ns
Heptane-2.2.4.6.6-pentamethyl	0	0	0	0	0	0,3	0	5,7	0,8	0,1	0.000010
Toluene	0,1	0	3,2	0,3	0	0	0	1,4	0,1	0	0.010000
MTu1	0	0	0	0	0	0	0	0,3	0	0	ns
MTu2	0	0	0,4	0	0	0	0	0	0	0	ns
MTu3	0	0	0	0	0	0	0	0	0	0	ns
α-Pinene	0,6	0	15,4	1,5	0,1	0,1	0	2,5	0,2	0	0.000010
MTu4	0	0	0,9	0,1	0	0	0	0,7	0,1	0	0.020000
MTu5	0	0	0,6	0,1	0	0	0	0,2	0	0	0.000026
MTu6	0	0	0,2	0	0	0	0	0	0	0	ns
MTu7	0,1	0	2	0,2	0	0	0	0,4	0	0	0.000010
MTu8	0,1	0	1,8	0,2	0	0	0	1,6	0,1	0	0.010000
Limonene	0,6	0	13,7	1,7	0,1	0,1	0	4,9	0,4	0	0.000010
Sabinene	0,1	0	2,4	0,3	0	0	0	2,2	0,2	0	ns
trans-β-Ocimene	0,4	0	19,8	1,8	0,1	0	0	1,8	0,2	0	0.010000
MTu9	0	0	0,8	0,1	0	0	0	0	0	0	0.010000
MTu10	0	0	0,7	0,1	0	0	0	0	0	0	0.001000
MTu11	0	0	0,5	0	0	0	0	0	0	0	ns
MTu12	0	0	1,7	0,1	0	0	0	0	0	0	ns
α-Terpinolene	0,6	0	19,7	2,6	0,2	0,1	0	3,6	0,5	0	0.010000
MTu13	0	0	0,4	0	0	0	0	0	0	0	ns
MTu14	0	0	0,5	0	0	0	0	0	0	0	ns
α-Copaene	0,2	0	8,8	0,9	0,1	0	0	0	0	0	0.002500
β-Caryophyllene	1,4	0	54,6	6,7	0,4	0	0	1,3	0,1	0	0.002000
α-Caryophyllene	0,5	0	19,3	2,4	0,1	0	0	0	0	0	0.001000
SQTsu	0,8	0	16,7	2,3	0,1	0,1	0	4,4	0,6	0	0.0001

Table S4. Mean emissions (± standard error) of the two main non-terpenic volatile compounds emitted by some tropical tree species in French Guiana. Letters indicate significant differences between seasons ($P < 0.05$).

Specific name	Season	Heptane-2.2.4.6.6-pentamethyl	Toluene
Protium decandrum	Dry	0 ± 0	0.1 ± 0.1a
	Wet	0 ± 0	0 ± 0a
Inga nouraguensis	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Eperua grandiflora	Dry	0 ± 0	0.04 ± 0.02a
	Wet	0 ± 0	0 ± 0a
Eperua falcata	Dry	0 ± 0a	0 ± 0
	Wet	1.1 ± 0.3b	0 ± 0
Eschweilera coriacea	Dry	0 ± 0a	0.03 ± 0.02a
	Wet	1 ± 0.3b	0 ± 0a
Gustavia hexapetala	Dry	0 ± 0	0.5 ± 0.3a
	Wet	0 ± 0	0 ± 0b
Brosimum guianense	Dry	0 ± 0a	0 ± 0
	Wet	4.1 ± 0.4b	0 ± 0
Couepia caryophylloides	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Eschweilera sagotiana	Dry	0 ± 0	0.03 ± 0.02a
	Wet	0 ± 0	0 ± 0a
Pradosia ptychandra	Dry	0 ± 0a	0.2 ± 0.1a
	Wet	0.7 ± 0.2b	0.1 ± 0.04a
Chrysophyllum pomiferum	Dry	0 ± 0	0.04 ± 0.03
	Wet	nda	nda
Vouacapoua americana	Dry	0 ± 0	0 ± 0a
	Wet	0 ± 0	0.1 ± 0.1a
Sextonia rubra	Dry	0 ± 0	0.1 ± 0.1a
	Wet	0 ± 0	0 ± 0a
Chrysophyllum argenteum	Dry	0 ± 0a	0.01 ± 0.01a
	Wet	0.6 ± 0.3b	0 ± 0a
Ferdinandusa paraensis	Dry	0 ± 0	0.1 ± 0.1a
	Wet	0 ± 0	0 ± 0a
Talisia praealta	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Licania alba	Dry	0 ± 0a	0.2 ± 0.1a
	Wet	0.3 ± 0.1b	0 ± 0b
Chimarrhis turbinata	Dry	0 ± 0	0.3 ± 0.3a
	Wet	0 ± 0	0 ± 0b
Eschweilera sp	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Paloue guianensis	Dry	0 ± 0a	0 ± 0
	Wet	0.6 ± 0.2b	0 ± 0
Eugenia culcullata	Dry	0 ± 0	0 ± 0

	Wet	0 ± 0	0 ± 0
Tetragastris panamensis	Dry	0 ± 0	0 ± 0
	Wet	nda	nda
Dicorynia guianensis	Dry	0 ± 0a	0 ± 0
	Wet	0.7 ± 0.1b	0 ± 0
Drypetes variabilis	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Pouteria retinervis	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Aniba rosaeodora	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Chaetocarpus schomburgkianus	Dry	0 ± 0a	0 ± 0
	Wet	0.2 ± 0.1b	0 ± 0
Catostemma fragrans	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Hebepetalum humiriifolium	Dry	0 ± 0	0 ± 0
	Wet	nda	nda
Moronobea coccinea	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Symphonia globulifera	Dry	0 ± 0	0 ± 0
	Wet	nda	nda
Eschweilera decolorans	Dry	0 ± 0	0 ± 0
	Wet	0 ± 0	0 ± 0
Pouteria eugeniifolia	Dry	nda	nda
	Wet	0.5 ± 0.3	0 ± 0
Carapa surinamensis	Dry	nda	nda
	Wet	0 ± 0	0 ± 0
Dipteryx odorata	Dry	nda	nda
	Wet	0 ± 0	0 ± 0
Vochysia sabatieri	Dry	nda	nda
	Wet	0 ± 0	0 ± 0

Table S5. Results of the phylogenetic analyses using Pagel's *λ* and the corresponding *P* values. Significant values ($P < 0.05$) are shown in bold.

	Total BVOCs	Total terpenes	Total monoterpenes	Total sesquiterpenes
Phylogenetic signal lambda	0.2	0.2	6.6	0.8
logL(lambda)	-104	-103	-825	-827
LR(lambda=0)	0.1	0.1	-0.001	673
P-value (based on LR test)	0.7	0.8	1	0.01

Table S6. Results of the Bayesian phylogenetic linear mixed models with season as fixed factor and phylogeny and species as random factors obtained with the R package *MCMCglmm*. The phylogeny term accounted for variability in the shared ancestry, while the species term accounted for species-specific traits independently of the shared ancestry. Significant values of fixed independent variables ($P < 0.05$) are shown in bold.

Variables	Fixed factors	R^2				
	Statistics Table	Fixed factors	Random			Total model
			R^2_f	R^2_s	R^2_r	
Total terpenes	post.mean l-95% CI u-95% CI eff.samp pMCMC	0.1	0.02	0.01	0.1	0.2
	(Intercept) 0.1 -0.2 0.4 1700 0.4					
	seasonWET -0.4 -0.6 -0.3 1700 <6e-04 ***					
MTu1	post.mean l-95% CI u-95% CI eff.samp pMCMC	0.01	0.0001	0.00004	0.01	0.02
	(Intercept) -0.1 -0.2 0.1 1413 0.5					
	seasonWET 0.1 -0.1 0.3 1863 0.3					
Hept-6en-3yn-1ol	post.mean l-95% CI u-95% CI eff.samp pMCMC	0.02	0.0001	0.0004	0.1	0.1
	(Intercept) -0.03 -0.3 0.2 2056 0.8					
	seasonWET 0.1 -0.1 0.3 1554 0.3					
Toluene	post.mean l-95% CI u-95% CI eff.samp pMCMC	0.01	0.0002	0.0003	0.02	0.04
	(Intercept) 0.1 -0.1 0.2 1700 0.3					
	seasonWET -0.2 -0.4 -0.1 1553 0.01 *					
MTu1	post.mean l-95% CI u-95% CI eff.samp pMCMC	0.0045	0.0001	0.00004	0.01	0.015
	(Intercept) -0.1 -0.2 0.1 1413 0.5					

	seasonWET 0.1 -0.1 0.3 1863 0.3					
MTu2	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.1 0.3 1700 0.4 seasonWET -0.2 -0.3 0.004 1700 0.1	0.01	0.002	0.003	0.1	0.1
MTu3	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.2 0.3 1700 0.5 seasonWET -0.1 -0.3 0.03 1700 0.2	0.006	0.003	0.004	0.08	0.1
α-Pinene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.2 -0.01 0.4 1700 0.1 seasonWET -0.4 -0.6 -0.3 1855 <6e-04 ***	0.1	0.001	0.001	0.04	0.1
MTu4	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.2 -0.2 0.5 1700 0.2 seasonWET -0.3 -0.4 -0.1 1700 0.002 **	0.02	0.01	0.07	0.2	0.3
MTu5	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.1 0.3 1700 0.2 seasonWET -0.4 -0.5 -0.2 1700 <6e-04 ***	0.03	0.002	0.003	0.1	0.1
MTu6	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.2 0.3 1519 0.5 seasonWET -0.2 -0.3 -0.01 1700 0.05 *	0.01	0.005	0.004	0.1	0.1
MTu7	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.2 -0.04 0.4 1824 0.1 seasonWET -0.4 -0.6 -0.3 1700 < 6e-04 ***	0.05	0.003	0.01	0.1	0.1
MTu8	post.mean l-95% CI u-95% CI eff.samp pMCMC	0.02	0.005	0.01	0.1	0.1

	(Intercept) 0.1 -0.3 0.4 1463 0.6 seasonWET -0.2 -0.4 -0.05 1700 0.01 **					
Limonene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.2 -0.1 0.4 1700 0.1 seasonWET -0.4 -0.6 -0.2 1700 < 6e-04 ***	0.04	0.003	0.006	0.1	0.1
Sabinene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.04 -0.1 0.2 1700 0.6 seasonWET -0.1 -0.3 0.1 1700 0.2	0.01	0.001	0.002	0.05	0.06
Trans-β-Ocimene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.2 0.5 1835 0.3 seasonWET -0.3 -0.4 -0.1 1700 0.001 **	0.03	0.02	0.1	0.2	0.3
MTu9	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.3 0.5 1392 0.4 seasonWET -0.2 -0.4 -0.04 1700 0.01 *	0.01	0.02	0.03	0.2	0.2
MTu10	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.2 0.5 2087 0.3 seasonWET -0.3 -0.4 -0.1 1700 0.005 **	0.02	0.02	0.1	0.2	0.3
MTu11	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.3 0.4 2120 0.6 seasonWET -0.1 -0.3 0.05 1700 0.1	0.01	0.01	0.01	0.1	0.1
MTu12	post.mean l-95% CI u-95% CI eff.samp	0.01	0.002	0.01	0.1	0.2

	pMCMC (Intercept) 0.1 -0.3 0.4 1700 0.6 seasonWET -0.1 -0.3 0.04 1700 0.2					
α-Terpinolene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.2 0.5 1700 0.3 seasonWET -0.3 -0.5 -0.1 2067 0.001 **	0.02	0.02	0.1	0.2	0.4
MTu13	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.1 0.3 1700 0.3 seasonWET -0.2 -0.4 -0.01 1700 0.1	0.01	0.0004	0.001	0.03	0.04
MTu14	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.04 -0.1 0.2 1700 0.6 seasonWET -0.1 -0.3 0.1 1333 0.2	0.01	0.0003	0.001	0.03	0.04
α-Copaene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.002 -0.4 0.3 1700 1 seasonWET -0.2 -0.3 0.01 1517 0.05 *	0.01	0.01	0.01	0.1	0.1
α-Caryophyllene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) -0.001 -0.3 0.3 1700 1 seasonWET -0.2 -0.4 -0.01 1806 0.02 *	0.01	0.01	0.003	0.1	0.1
SQTsu1	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.2 -0.1 0.5 1700 0.2	0.05	0.01	0.06	0.2	0.3

	seasonWET -0.5 -0.6 -0.3 1700 <6e-04 ***					
Isoprene	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) -0.03 -0.3 0.3 1700 0.8 seasonWET 0.1 -0.04 0.3 1700 0.2	0.04	0.003	0.001	0.06	0.1
Total Monoterpenes	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.3 0.001 0.5 1700 0.1 seasonWET -0.5 -0.7 -0.4 1700 <6e-04 ***	0.07	0.01	0.04	0.2	0.3
Total Sesquiterpenes	post.mean l-95% CI u-95% CI eff.samp pMCMC (Intercept) 0.1 -0.2 0.4 1700 0.6 seasonWET -0.3 -0.5 -0.2 1574 <6e-04 ***	0.03	0.01	0.002	0.1	0.1

Table S7. Number of mature trees sampled per species at each topographic level and weather station. Phenology indicates if trees are evergreen or deciduous in each season. For more information, see Verryckt et al. (2022).

		Number of trees sampled per species	
	Topographic level	Season	
Species		Dry	Wet
Aniba rosaeodora	Slope	1	1
Brosimum guianense	Bottom	1	1
Carapa surinamensis	Bottom		1
Catostemma fragrans	Bottom	1	1
Chaetocarpus schomburgkianus	Top	1	1
Chimarrhis turbinata	Top	1	1
Chrysophyllum argenteum	Top	1	1
Chrysophyllum pomiferum	Top	1	1
Couepia caryophylloides	Slope	1	1
Dicorynia guianensis	Bottom	1	1
Dipteryx odorata	Bottom		1
Drypetes variabilis	Bottom	1	1
Eperua falcata	Bottom	3	4
Eperua grandiflora	Slope	2	1
Eschweilera sp	Bottom	1	1
Eschweilera coriacea	Top	1	1
Eschweilera decolorans	Bottom	1	1
Eschweilera sagotiana	Slope	1	
Eugenia NA	Top	1	1
Ferdinandusa paraensis	Slope	1	1
Gustavia hexapetala	Bottom	1	1
Hebepetalum humiriifolium	Slope	1	
Inga nouraguensis	Slope	1	1
Licania alba	Bottom	2	3
Moronobea coccinea	Top	1	1
Paloue guianensis	Bottom	1	1
Pouteria eugeniifolia	Top		1
Pouteria retinervis	Slope	1	1
Pradosia ptychandra	Bottom	1	1
Protium decandrum	Slope	1	1
Sextonia rubra	Top	1	1
Symphonia globulifera	Bottom	1	
Talisia praealta	Top	1	1
Tetragastris panamensis	Slope	1	
Vochysia sabatieri	Top		1
Vouacapoua americana	Bottom	1	1

Table S8. List of species sampled in this work and sampled by other authors previously. We want to show that in the present work there are tree species not previously sampled for BVOCs. In the case of Jardine et al. 2020 only gives information about gender.

Species	**Present work**	**Courtois et al. 2009**	**Courtois et al. 2016**	**Jardine et al. 2020**
Aniba rosaeodora [a]	x			
Brosimum guianense	x	x	x	
Carapa surinamensis	x			
Catostemma fragrans	x		x	
Chaetocarpus schomburgkianus	x			
Chimarrhis turbinata	x	x	x	
Chrysophyllum argenteum	x	x	x	
Chrysophyllum pomiferum	x			
Couepia caryophylloides	x			
Dicorynia guianensis	x		x	
Dipteryx odorata	x		x	
Drypetes variabilis	x		x	
Eperua falcata	x		x	
Eperua grandiflora	x			
Eschweilera coriacea	x	x	x	
Eschweilera decolorans	x		x	
Eschweilera sagotiana	x		x	
Eschweilera sp	x			x
Eugenia culcullata [b]	x		x	
Ferdinandusa paraensis	x			
Gustavia hexapetala	x		x	
Hebepetalum humiriifolium	x		x	
Inga nouraguensis	x			x
Licania alba	x			x
Moronobea coccinea	x		x	
Paloue guianensis	x			
Pouteria eugeniifolia	x			x
Pouteria retinervis	x			x
Pradosia ptychandra	x		x	
Protium decandrum	x	x	x	x
Sextonia rubra	x	x	x	
Symphonia globulifera	x		x	
Talisia praealta	x			
Tetragastris panamensis [c]	x	x	x	
Vochysia sabatieri	x			
Vouacapoua americana	x	x	x	

All names verified in Steege et al. 2019, except for **a**: which appears as *Aniba rosiodora*; **b**: *Eugenia cucullata*; **c**: Does not appear in the list.