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Screening study of leaf terpene concentration of 75 Borneo rainforest plant Species: relationships with leaf elemental concentrations and morphology

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Abstract: Terpenes confer advantage in plant protection against abiotic stresses such as heat and drought and biotic stresses such as herbivore and pathogen attack. We conducted a screening of leaf mono- and sesquiterpene concentrations in 75 common woody plant species in the rainforest of Danum Valley (Borneo). Terpene compounds were found in 73 out of the 75 analysed species. Similar or lower proportions have been reported in other parts of the world. To our knowledge, this study reports for the first time the foliar concentration of mono- and/or sesquiterpene for 71 species and 39 genera not previously analyzed. Altogether 80 terpene compounds were determined across the species, and out of these only linalool oxide and (*E*)-γ-bisabolene had phylogenetic signal. A significant negative relationship between leaf monoterpene concentration and leaf length was observed, but leaf mono- and sesquitepene concentration were not related to any other leaf morphological trait nor to leaf elemental composition. Functions such as temperature protection, radiation protection or signaling and communication could underlie the high frequency of terpene-containing species of this tropical ecosystem which has multiple and very diverse interactions among multiple species.

Keywords: Borneo; herbivory; leaf morphology; LMA; nutrients; rain forest; sesquiterpenes; monoterpenes.

1. Introduction

Protection, defence and infochemical function have been highlighted as possible role of terpenes [1-5]. Examples of these roles are photoprotection [6], thermotolerance) [7-11], protection against drought [12, 13] and non-specific antioxidative capacity, whereby terpenes protect photosynthetic membranes against peroxidation and reactive oxygen species such as singlet [9, 14-17]. Terpenes also have a role in plant defence, acting as deterrents, toxins or modifiers of insect development [18]. They are effective against non-adapted specialist herbivores [19], and generalist herbivores [20-22].

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The dosage dependence for a successful deterrent function can change among terpene compounds [23, 24]. Moreover, terpenes have several other protective properties such as defence against fungi and [25]. All these physiological and ecological functions are likely to play a fundamental role in the tropical ecosystems with multiple and diverse interactions among multiple species. Although there are recent efforts to characterize terpene content of the wide diversity of tropical plant species [26], their terpene content is mostly unknown.

Tropical ecosystems are characterized by frequent nutrient limitations and intense herbivore pressures [27-30]. Both stresses are known to strongly influence plant terpene concentration [1, 8, 21, 22, 31-34]. Some studies have already shown multiple terpene ecological functions in tropical ecosystems such as insect nest building [35], or insect attraction [36-38].

Considering the abiotic factors, low terpene production in plants with low nutrient concentration and photosynthetic rates can be expected from the "nutrient-driven synthesis" hypothesis that predicts a large enzyme (including terpene synthase) production with greater cellular N and P availability. Higher nutrient availability is usually expected to translate into higher carbon fixation and activity of the enzymes involved in isoprenoid production [39, 40]. In contrast, a greater production of terpenes as carbon based secondary compounds under lower nutrient availabilities can be expected from the "carbon excess" hypotheses [41-44]. These hypotheses assert that plants allocate carbon to secondary metabolism only after growth requirements are met and that growth is constrained more by nutrients than by photosynthesis. Thereafter, these secondary metabolites can exert defensive functions.

From a biotic perspective the role of terpenes has been related to plant defensive capacity. Although there are several theories to explain defensive success in plants in different environmental situations such as those theories based on an evolutionary basis [45]. This hypothesis proposes that plant species adapted to high resource environments will be selected for growth allocation rather than for defense while plant species adapted to low resource environments will be selected for increased defense allocation, because with herbivore attack it is much more difficult to replace tissue in low resource environments than in high resource environments. Thus, there is a quite broad consensus on that the resource allocation hypothesis is a general framework in which to study the trade offs between growth and defense as a function of resources availability [42, 44-48]. Both "carbon excess" and "resource allocation" hypotheses expect higher terpene concentrations related to low nutrient concentrations, whereas contrarily, "nutrient-driven" hyphotesis predicts higher terpene concentrations related to high nutrient concentrations.

Several physical leaf properties have proved to be involved in defence mechanisms. Among them, LMA, plays a prominent role and has been proven to have a deterrent effect [49, 50]. On the other hand, costs for mechanical leaf support increase with increasing leaf size [51, 52], implying larger fractional investment in less-palatable veins [51]. Large diversity of leaf shapes and sizes are present in tropical forests, suggesting that trade-offs associated with leaf size-shape patterns can be important in modifying the linkages of leaf structure and chemistry to herbivory. At this regard higher C investment in leaf structures can suppose less allocation to terpenes production.

Few studies have investigated in a tropical rainforest the relationships between leaf terpene concentrations and other leaf traits related with defense and palatability such as leaf nutrient concentration, leaf phenolic concentration and leaf physical defenses, in a representative set of species in the field [53-55]. This type of study has been especially scarce comparing the relationships between leaf terpene concentrations and other leaf defensive traits. Moreover, there is a lack of terpene content screening studies in tropical forest.

Borneo is the third largest island of the world. It is located in South-eastern Asia and still has a great extent of tropical rain forest. Some studies have reported that nutrient availability is limiting for woody plant productivity in Borneo rainforest [56-60]. Previous studies have demonstrated that on average leaf nutrient concentrations of Borneo plants tend to be low [61] and some leaf nutrients concentrations, especially P, are in lower concentrations than in other tropical areas such as Hawaii [62]. In these nutrient limiting conditions, plant defence strategy against leaf herbivores might even be an evolutionary-acquired tool in order to avoid N and P losses such as predicted by “resource allocation” hypothesis [30, 46].

In this study, we conducted a screening of leaf terpene content in 75 common forest plant species of Borneo. Our aims were: (i) to characterize the mostly unknown terpene concentrations of these species and (ii) to study the relationships between the different terpene compounds and the concentrations of other carbon based defenses such as phenolics and with leaf morphological traits and C, N, P and K leaf concentrations. While studying these relationships, we also aimed to test the “nutrient-driven”, “carbon excess” and “resource allocation” hyphoteses.

2. Materials and Methods

2.1. Field site and studied species

The study was conducted in Danum Valley Field Centre located on the east coast of the Malaysian state of Sabah, Borneo Island (48.75' E and 5° 01' N). (See supplementary material for details).

A total of 75 common species were sampled (Figure 1, supplemetary material) and their basic ecological traits are shown in Table 1 (supplementary material).

2.2. Plant sampling

Plant sampling was conducted in medium to large gaps (10-100 m diameter). In all cases, leaves were sampled from at least three individual plants for each species. The plants were selected at random, with the condition that plants from a given species are at least 100 m apart. From each plant, even-aged mature non-senescent foliage, 6-12 months old was randomly sampled. (See supplementary material for plant sampling details).

2.3. Leaf structural traits

After sampling, the leaves were sealed in plastic bags with wet filter paper and immediately transported to the laboratory. In the laboratory, fresh and dry leaf mass, leaf area, leaf length, leaf mass area (LMA), compactness and leaf roundness of individual leaves were determined as described in supplementary information.

In the dataset, 6 species - *Caesalpina major, Cassia alata, Clausena excavata, Fordia splendidissima, Reinwardtiodendron humile* and *Sindora irpicina* - are compound-leaved. In the case of compound-leaved species, leaflets were considered as functional analogues of simple leaves, and all structural and chemical traits refer to leaflets.

2.4. Leaf elemental and phenolic analyses

See supplementary information for detailed explanation of chemical analyses of leaf elemental and phenolic concentrations. Briefly, for C and N sample determination, 1-2 mg of pulverized dried sample were mixed with 2 mg of V_2O_5 as oxidant and analysed by combustion coupled to gas chromatography using a Thermo Electron Gas Chromatograph model NA 2100 (C.E. instruments-Thermo Electron, Milan, Italy). For analyses of other elements, dried and ground samples were digested with concentrated HNO_3 and H_2O_2 (30%, w/v). Thereafter, the concentrations of As, Cd, Cr, Cu, Mo, Ni, Pb, V and Zn were determined using ICP-MS (Mass Spectrometry with Inductively Coupled Plasma) (Perkin-Elmer Corporation, Norwalk, USA) and Ca, Fe, K, Mg, Mn, Na and P were determined using ICP-OES (Optic Emission Spectrometry with Inductively Coupled Plasma) (Perkin-

Elmer Corporation, Norwalk, USA). For As analyses, we firstly generated arsenic hydrides and analyzed them with ICP-MS. Total phenolic concentration of leaves was determined by the improved Folin-Ciocalteu assay [63].

2.5. Leaf terpene extraction and analysis

We sampled three plants per species and 10-20 leaves in each plant. Samples were ground in liquid N_2 1-12 hours after sampling. In each sampled plant we took three samples that were mixed and used in a unique extraction. The leaves were crushed in liquid nitrogen with a Teflon pestle in a Teflon tube until a homogeneous fine powder was obtained. After homogenization, 1 mL of pentane was added before the pulp defrosted. The tubes were maintained at 25°C during 24 h, and after this period a sample of each extract was put into a 300 μL glass vial. The samples were extracted in the proportion 20 mg leaf powder: 1 mL of pentane. After extraction, samples were automatically injected into the GC-MS. The column was HP-5 crosslinked 5% PH Me Silicone (Supelco Inc.). The initial temperature of 40ºC was immediately increased with a ramp of 30 ºC min^{-1} to 60ºC. The second ramp was 10ºC min^{-1} to 150ºC which was maintained for 3 min. The third ramp was 70ºC min^{-1} to 250ºC which was maintained for 5 min. The carrier gas was helium at 0.7 mL min^{-1}. The mass detector was used with an electron impact of 70 eV. Identification of monoterpenes and sesquiterpenes was conducted by GC-MS and comparison with standards from Fluka (Buchs, Switzerland), literature spectra, and NIST and Wiley libraries. Calibration with common terpenes α-pinene, δ-3-carene, β-pinene, β-myrcene, p-cymene, limonene, sabinene (monoterpenes) and α-humulene (sesquiterpenes) standards was carried out once every five analyses. The standards were purchased from Sigma Aldrich (Gilingham, Dorset, UK) and analysed following the same process than for the sample extracts. Terpene calibration curves (each one with 4 different terpene concentrations; 0, 0.01, 0.1 and 0.83 mg mL^{-1}) were always highly significant ($r^2 > 0.99$ for the relationships between signal and terpene concentrations). The most abundant terpenes had similar sensitivity (differences were generally less than 5%). To link a peak with a determined compound using standard libraries (NIST and Wiley), we established the threshold value of a 95% or more of the percentage of security that the peak should correspond to a determined compound. All sampling and analytical procedures were applied in the same way for all species.

2.6. Phylogenetic and statistical analysis

The program Phylomatic [64] was used to build a phylogenetic tree of the species studied (Figure S1, supplementary information) as explained in Peñuelas *et al*. [62]. The statistical significance of the genetic differences between different species in explaining the variability of the studied variables was calculated employing Matlab 7.6.0 with the PHYSIG module developed by Blomberg *et al*. [65].

To analyze the relationships of foliage terpene concentrations with the other leaf studied characteristics (nutrient concentrations, leaf morphological traits and the level of herbivore attack), we conducted a general linear model (GLM) analysis both taking and not taking into account phylogenetic signal using Matlab 7.6.0 with REGRESSIONV2 module [66]. Thereafter, the model with a lower Akaike information criterion (AIC) was selected. When dealing with multiple correlations we used Bonferroni correction. (See supplementary material for detailed explanation of phylogenetic and statistical analyses).

3. Results and discussion

Foliar terpene presence was detected in 73 out of the 75 species analysed (Table 1). Table 1 and S1 (supplementary material) show the mono- and sesqui- that were clearly determined by GC-MS.

Only *Popowia pisocarpa* and *Xanthophyllum affine* leaves did not present mono- and sesquiterpenes (Tables 1 and S1, supplementary material). Eighty different terpene compounds were detected in the leaves of the analyzed plants, 15 monoterpenes and 65 sesquiterpenes. All the monoterpenes and 62 out of the 65 sesquiterpenes (Table 1) could be determined. Thus, only 3 peaks that corresponded to a sesquiterpene structure could not be identified. Only one leaf monoterpene (Linalool oxide) and one sesquiterpene ((*E*)-δ-Bisabolone) had phylogenetic signal ($k = 0.524$ and $P = 0.020$, and $k = 0.482$ and $P = 0.022$, respectively). Total leaf monoterpene and sesquiterpene concentrations were positively correlated ($R = 0.31$ and $P < 0.01$) across species. The total number of monoterpene, sesquiterpene and total terpene chemical species per each plant species did not have phylogenetic signal ($k = 0.072$ and $P = 0.831$, $k = 0.094$ and $P = 0.649$, and $k = 0.079$ and $P = 0.832$, respectively). Total leaf terpene concentrations (mg g^{-1}) were not different among the species of different successional stages ($P = 0.84$) and ranged on average between 2-3 mg g^{-1} in all categories of successional stages.

Leaf total monoterpenes were not correlated with the studied chemical and physical leaf traits (Table S2, supplementary material) and neither with the species succesional stage (data not shown).

This study provides novel information about terpene concentrations in Borneo plant species. Of the 75 species studied, 97% (73) contained terpenes in a detectable amount. This percentage was higher than previously observed in other parts of the world (apart from traditional phytotherapy studies which focus on plants with high secondary metabolite concentrations) such as Hawaii or the Mediterranean region but not compared to others such as the French Guaiana [67]. For instance, Sardans et al. (2010) [26] found detectable concentration of foliar terpenes in 25 out of 73 species (34%) sampled in Hawaii, and Llusia & Peñuelas (1998, 2000) [13, 68] found detectable foliar terpene concentration in 4 out of 7 species studied (57%) in the North Western Mediterranean basin. Courtois *et al*. (2009) [67] found terpene in all 55 species studied in French Guaiane.

As far as we know, within the 73 species that contained at least one mono- or sesquiterpene compound in detectable amounts, only 2 species (*Cinnamomum zeylanicum* and *Dipterocarpus gracilis*) had been previously reported as monoterpene and/or sesquiterpene-containing species [69, 70]. Therefore this study reports 71 species for the first time as mono- and/or sesquiterpene-containing species (Table 2, supplementary material). Furthermore, we have determined mono- and sesquiterpene compounds not previously reported in the two species previously reported as terpene-containing: the monoterpenes limonene, α-pinene and β-myrcene and the sesquiterpene γ-elemene in *Cinnamomum zelynicum*, and the monoterpenes limonene and α-pinene and the sesquiterpenes α-cubebene, bicyclogermacrene, γ-cadinene, germacrene D and selina-3,7(11)-diene in *Dipterocarpus gracilis* (Table 2, supplementary material). The studied species represent 39 genera, from a total of 64 genera studied, with terpene concentration reported for the first time (*Agelaea*, *Ardisia*, *Artocarpus*, *Baccaurea*, *Barringtonia*, *Caesalpinia*, *Chaetocarpus*, *Cleistanthus*, *Clidemia*, *Combretum*, *Dimorphocalyx*, *Diospyros*, *Durio*, *Endospermum*, *Etlinglera*, *Euphoria=Dimocarpus*, *Eusideroxylon*, *Fordia*, *Fagraea*, *Glochidion*, *Gluta*, *Hopea*, *Luvunga*, *Macaranga*, *Madhuca*, *Mallotus*, *Melastoma*, *Memecylon*, *Neonauclea*, *Palanquium*, *Parashorea*, *Payena*, *Pleurocarpidia*, *Poikilospermum*, *Pterospermum*, *Reinwarditiodendron*, *Swintonia*, *Symplocos*, *Uncaria*) (Table 2, supplementary material). In the case of *Ardisia elliptica*, plants of this species growing in Oahu (Hawaii) were analysed with the same protocol used in this study and no mono- and seaquiterpene compounds were detected [26]. On the other hand, 23 genera (*Callicarpa*, *Canarium*, *Cinnamomum*, *Chisocheton*, *Clausena*, *Dacryodes*, *Dipterocarpus*, *Dryobalanops*, *Ficus*, *Lansium*, *Myristica*, *Nauclea*, *Podocarpus*, *Polyalthia*, *Pouteria*, *Senna*, *Shorea*, *Sindorea*, *Syzygium*, *Tabernaemontana*, *Tarenna*, *Uvaria*, *Zingiber*) had been previously reported as mono- and sesquiterpene-containing genera, but

Table 1. Foliar concentrations of monoterpene and sesquiterpene compounds determined in the 75 Borneo rainforest species studied.

Species	**This study**		**Previous reports in the literature**
	Monoterpenes	**Sesquiterpenes**	**Mono- and Sesquiterpenes reported in the same species (labeled with *) or in the other species of the same Genus**
Agelaea borneensis	Limonene (56.0), α-Pinene (8.5), Total (64.5)	β-Caryophyllene (11.4), Germacrene D (2.5), Total (53.4)	
Ardisia elliptica	Limonene (4.4 ± 1.9), Total (4.4 ± 1.9)	α-Copaene (45.3 ± 32.0), β-Caryophyllene (485 ± 285), α-Cubebene (13.6 ± 11.1), α-Ylangene (0.58 ± 0.47), α-Farnesene (2.13 ± 1.74), α-Caryophyllene (99.0 ± 45.9), γ-Cadinene (11.4 ± 4.7), β-Selinenen (11.5 ± 5.4), α-Selinene (693 ± 493), Total (1331 ± 872)	
Arctocarpus odoratissimus	Limonene (13.7), α-Pinene (60.4), Total (74.3)	α-Copaene (33.5), β-Caryophyllene (84.5), Aromadendrene (99.8), Bicyclogermacrene (15.4), α-Mururolene (15.5 + 12.7), Total (260)	
Baccaurea macrocarpa	Limonene (1.99 ± 1.15), α-Pinene (1.70 ± 0.98) , Total (2.46 ± 1.01)	Bicyclogermacrene (0.64 ± 0.37), Bicycloelemene (14.3 ± 8.3), α-Caryophyllene (4.78 ± 2.76), α-Muurolene (15.5 + 12.7), Germacrene D (3.4 ± 2.8), Total (32.1 ± 26.2)	
Barringtonia sarctostachys	Limonene (3.1), α-Terpinene (15.4), Total (18.5)	α-Copaene (13.3), α-Amorphene (5.55), Calarene (7.3), E-Caryophyllene (578), Bicyclogermacrene (11.2), α-Caryophyllene (223), Germacrene D (181), Total (1020)	
Caesalpinia mezzoneuron	Limonene (7.3 ± 2.0), β-Ocimene (56.3 + 48.7), γ-Terpinene (9.6 ± 8.3), E-Sabinene (2.66 ± 2.31), Linalool (9.1 ± 7.9), α-Pinene (3.8 ± 2.5), Sabinene (16.0 ± 13.9),	Bicycloelemene (10.0 + 8.6), α-Copaene (33.3 + 26.5), β-Caryophyllene (97.7 ± 50.9), γ-Elemene (564 ± 488), α-Cubebene (10.4 ± 9.0), (-)-β-Elemene (547 ± 474), β-Cubebene (452 ± 391), β-Gurjunene (5.1 ± 4.4), α-Amorphene (0.96 ± 0.83), Δ-Elemene (180 ± 156), E-Caryophyllene (61.5 ± 53.3), Bicyclogermacrene (145 ± 126), α-Caryophyllene (375 + 175) γ-Cadinene (3.7 ± 3.2), β-Selinene (129 ± 111), Germacrene D (4.4 ± 2.2), Selina-3,7(11)-diene (2.1 ± 1.8), Total (2619 ± 1404)	

	Total (108 ± 50.6)		
Callicarpa longifolia	β-Pinene (332 ± 271), Limonene (302 ± 172), γ-Terpinene (54.9 ± 44.8), Linalool oxide (2.94 ± 1.70), α-Terpinene (34.6 ± 20.0), α-Pinene (846 ± 488), Sabinene (147 ± 85), Total (1275 ± 1040)	α-Copaene (21.7 ± 11.5), α-Santalene (18.6 ± 10.8), β-Caryophyllene (166 ± 96), E-α-Bisabolene (3.2 ± 1.9), E-γ-Bisabolene (2.2 ± 1.3), γ-Elemene (2.6 ± 2.2), β-Gurjunene (11.7 ± 6.8), α-Amorphene (2.75 ± 1.6), Calerene (3.1 ± 2.5), 1,5,5-thrimethyl cyclohexane (146 ± 64), α-Caryophyllene (141 ± 69), Germacrene D (47.7 ± 38.9), Total (410 ± 287)	*C. americana* and *C. japonica* (Cantrell *et al*. 2005) [86], *C. microphylla* (Chung et al. 2005) [87]
Canarium decumanum	Limonene (3.4)	β-Caryophyllene (1454), α-Caryophyllene (429), Total (1883)	*C .album* (Giang *et al*. 2006) [88], *C. boivbinii* (Billet *et al*. 1971) [89], *C. Zeylanicum* (Bandaranayake 1980) [90]
Canarium denticulatum	Limonene (37.0 ± 13.4), β-Ocimene (14.0 ± 11.4), α-Pinene (39.1 ± 23.1), Total (90.0 ± 46.3)	α-Copaene (153 ± 101), β-Caryophyllene (329 ± 155), γ-Elemene (32.3 ± 19.1), α-Cubebene (38.1 ± 31.1), (-)-β-Elemene (107 ± 37), Δ-Elemene (94.3 ± 39.5), 1,5,5-trimethyl-6-methylene-cyclohexene (319 + 90), α-Guaiene (9.9 ± 6.8), Allomadendrene (4.2 ± 3.4), α-Caryophyllene (22.0 ± 12.6), γ-Cadinene (14.4 + 0.8), Germacrene D (255 ± 154), Selina-3,7(11)-diene (14.4 ± 4.1), β-Bisabolene (81.8 ± 28.6), Total (1474 ± 380)	
Cassia (Senna) alata	Limonene (141), α-Pinene (9.3), Total (150)	α-Copaene (64), (-)-β-Elemene (146), Δ-Elemene (651), E-Caryophyllene (1139), β-Selinene (4233), Germacrene D (750), Selina-3,7(11)-diene (646), Total (6683)	*C. fistula* (Tzakou *et al*. 2007) [91], *C. javanica* (Chaudhuri & Chawla 1987) [92]
Chaetocarpus castanocarpus	Limonene (3.9), α-Pinene (1.31), Total (5.3)	α-Caryophyllene (84.1), Total (84.1)	
Chisocheton sarawakensis	Camphene (33.2), β-Pinene (25.5), Limonene (230), α-Pinene (1592), Sabinene (193), Total (2073)	β-Caryophyllene (6.2), α-Ionone (5.6), α-Caryophyllene (12.0), β-Selinene (4.4), Germacrene D (11.7), (+)-Spathulenol (9.7), Total (49.5)	*C. penduliflorus* (Phongmaykyn *et al*. 2008) [93]
Cinnamomum zeylanicum	Limonene (48.8 ± 26.0), α-Pinene (170 ± 96), β-Myrcene (15.9 ± 9.2), Total (156 ± 125)	β-Caryophyllene (83.0 ± 38.4), γ-Elemene (6.9 ± 5.6), α-Caryophyllene (40.4 ± 12.9), Germacrene D (10.2 ± 8.3), Total (99.4 ± 55.5)	*C.burmanii* (Sardans *et al*. 2010) [26], *C. malabatrum* (Leela *et al*. 2009) [94], (Jayaprakasha *et al*. 2003; Yang *et al*. 2005;Tira-Picos

			et al. 2009; Wang *et al*. 2009) [95-98], *C. zeylanicum* (Chen *et al.* 2010)[70]*
Clausena excavata	Limonene (56.9 ± 46.5), α-Pinene (30.2 ± 24.7), β-Myrcene (49.4 ± 33.5), Total (134 ± 104)	α-Copaene (22.8 ± 11.8), β-Copaene (3.6 ± 3.0), β-Caryophyllene (2.92 ± 2.40), γ-Elemene (8.5 ± 7.0), (-)-β-Elemene (24.5 ± 20.0), α-Amorphene (634 ± 511), Δ-Elemene (115 ± 94), E-Caryophyllene (358 ± 289), Bicyclo[3,1,1]hept-2-ene-2,6-dimethyl-3-penthyl) (16.7 ± 13.6), β-Selinene (1005 ± 414), Δ-Cadinene (3.6 ±2.9), β-Panasinsene (9.2 ± 7.5), Selina-3,7(11)-diene (7206 ± 160), Nerolidol (65.3 ± 53.3), Caryophyllene oxide (34.4 ± 8.8), Germacrene D (219 ± 154), Total (2537 ± 1284)	*C. harmandiana* (Thongthoom *et al*. 2010) [99], C. heptaphylla (Sohrab *et al*. 1999) [100], *C. lansium* (Chokeprasert *et al*. 2007) [101]
Cleistanthus bridelifolius	Limonene (81), α-Pinene (21.1) , Total (27.2)	α-Copaene (6.4),β-Copaene (4.7), Aromadendrene (2.61), α-Pharnesene (54.1), Total (67.8)	
Clidemia hirta	Limonene (18.2), Total (18.2)	β-Cubebene (5.7), Total (5.7)	
Combretum nigrescens	Limonene (3.64), α-Pinene (1.87), Total (5.5)	α-Copaene (5.2), E-α-Bergamolene (3.6), Germacrene D (7.4), Total (16.1)	
Dacryodes rugosa	Limonene (495), α-Pinene (2402), Total (2897)	α-Copaene (14.3), β-Caryophyllene (10.8), γ-Elemene (10.5), (-)-β-Elemene (13.9), α-Amorphene (19.0), Allomadendrene (58.5), α-Caryophyllene (13.3), Germacrene D (4.5), Total (133)	*D. edulis* (Ekong & Okogun 1969) [102]
Dimocarpus longan subsp. *malesianus* = *Euphoria malaiensis*	Limonene (15.3), α-Pinene (1.44), Total (16.7)	α-Copaene (397 ± 62), β-Caryophyllene (1392 ± 25), γ-Elemene (270 ± 143), (+)-Aromadendrene (1.72), α-Cubebene (2.7), Calerene (103 + 44), 1,5,5-trimethyl-6-methylene-cyclohexene (32.6 ± 9.2), Bicyclo[3,1,1]hept-2-ene-2,6-dimethyl-3-penthyl) (76.9 ± 35.5), β-Sesquiphenentrene (14.0 ± 8.1), Allomadendrene (147 + 40), α-Caryophyllene (1352 ± 59), Germacrene D (415 + 278), Selina-3,7(11)-diene (62.6 + 9.8), Total (3104 ± 1270)	
Dimorphocalyx murinus	Limonene (5.3), α-Pinene (4.8), Total (10.1)	γ-Elemene (28.6), α-Cubenene (9.5), α-Ylangene (8.8), (-)-β-Elemene (68.5), α-Cadinol (32.9), α-Selinene (143), α-Amorphene (19.0), Bicycloelemene (6.5), α-Gurjunene (6.9), E-Caryophyllene (68.3), Δ-Cadinene (50.9), E-α-Bergamotene (51.8), α-Caryophyllene (68.3), β-Selinene (112), β-Panasinsene (5.2), Selina-3,7 (11)-diene (113), Germacrene D (443), Δ-Cadinene (50.9), Total (1316)	
Diospyros durinoides	Limonene (6.3 ± 0.3),	β-Caryophyllene (1.7 ± 1.0), γ-Elemene (0.43 ± 0.35), α-Caryophyllene (3.0 ±	

	α-Pinene (33.6 ± 14.6), Total (26.6 ± 15.9)	0.9), Globulol (21.1 ± 6.2), Germacrene D (1.5 ± 0.9), Total (19.1 ± 10.4)	
Dipterocarpus sarawakensis	Limonene (5.9), Total (5.9)	β-Caryophyllene (31.8), 1,5,5-trimethyl-6-methylene-cyclohexene (43.5), Bicyclo[4,4,0]dec-1-ene-2-isopropyl-5-methyl-9-methylene (178), Germacrene B (6.6), α-Guaiene (6.2), α-Caryophyllene (11.), Germacrene D (6.8), Total (284)	*D.* species (Messer *et al*. 1990) [69]*, *D. kerrii* (Richardson *et al*. 1989 and 1991) [103, 104]
Dipterocarpus applanatus	Limonene (29.6 ± 81.2), α-Pinene (27.9 ± 16.1), Total (38.3 ± 21.1)	α-Copaene (653 ± 377), β-Caryophyllene (1097 ± 633), β-Cubebene (416 ± 240), Bicyclogermacrene (3543 ± 1934), Bicyclo[4,4,0]dec-1-ene-2-isopropyl-5-methyl-9-methylene (158 + 92), α-Caryophyllene (1217 ± 635), Germacrene D (52.9 + 43.2), γ-Cadinene (1425 ± 823), Total (5818 ± 560)	
Dipterocarpus gracilis	Limonene (6.3 ± 3.6), α-Terpinene (14.8 ± 8.5), α-Pinene (0.26 ± 0.15), Total (14.2 ± 11.6)	β-Caryophyllene (698 ± 401), α-Cubebene (55.7 ± 32.2), β-Cubebene (14.8 ± 8.5), E-Caryophyllene (283 ± 164), Aromadendrene (139 ± 80), Bicyclogermacrene (155 + 90), Germacrene D (78.2 ± 63.8), Selina-3,7(11)-diene (16.9 ± 9.8), α-Caryophyllene (674 ± 153), β-Selinene (56.6 ± 46.2), Total (1400 ± 633)	
Dryobalanops lanceolata	Camphene (286 ± 165), Limonene (11.4 ± 5.1), α-Pinene (0.40 ± 0.23), Total (199 ± 161)	α-Copaene (122 ± 71), β-Caryophyllene (5.9 ± 3.4), α-Amorphene (25.2 ± 14.5), Aromadendrene (5.8 ± 3.3), α-Caryophyllene (2.9 ± 1.7), γ-Cadinene (21.1 ± 12.2), β-Selinene (1.2 ± 1.0), Germacrene D (8.8 ± 7.2), Selina-3,7(11)-diene (13.2 ± 7.6), Total (142 ± 91.2)	*D. aromatica* (Park *et al.* 2003) [105]
Durio kutejensis	Limonene (14.3), α-Pinene (265), Total (280)		
Endospermum diadenum	Limonene (19.5), β-Ocimene (124), γ-Terpinene (81.0), E-Sabinene (44.9), Z-Sabinene hydrate (54.4), Linalool (183), γ-Terpinene (5.2), α-Pinene (20.7), Sabinene (442), Myrcene (19.5) , Total (994)	Bicycloelemene (29.1), α-Copaene (375), α-Cubebene (45.9), E-Caryophyllene (109), Bicyclogemacrene (496), α-Caryophyllene (293), Total (1484)	
Etlingera brevilabrum	Limonene (24.1), α-Pinene (656), Total	α-Copaene, (176) (-)-β-Elemene (15.6), β-Cubebene (921), 1,4,7-Cycloundecatriene-1,5,9,9-tetramethyl-Z,Z,Z- (14.0), Total (1126)	

	(680)		
Eusideroxylon zwangeri	β-Pinene (63.4 ± 27.3), Limonene (16.5 ± 2.3), α-Pinene (362 ± 11), Total (316 ± 30)	α-Copaene (1049 ± 108), β-Caryophyllene (2972 ± 460), γ-Elemene (448 ± 184), α-Cubebene (533 ± 57), α-Ylangene (103 ± 28), β-Cubebene (1046 ± 47), Calarene (138 ± 72), 1,5,5-trimethyl-6-methylene-cyclohexene (12.5 ± 7.5), E-Caryophyllene (1777 ± 377), Bicyclogermacrene (2290 ± 614), α-Guaiene (681 ± 556), E-β-Phanesene (48.1 ± 14.6), α-Caryophyllene (31.4 ± 1.3), γ-Cadinene (163 ± 40), α-Muurolene (28.7 ± 12.5), α-Cadinol (119 ± 48), Germacrene D (611 ± 499), Selina-3,7(11)-diene (61.8 ± 2.5), Total (8886 ± 3628)	
Ficus aurata	Limonene (7.7), α-Pinene (8.5), Total (16.2)		*F. carica* (Gibernau *et al*. 1997) [106], *F. exasperate* (Sonibare *et al*. 2006) [107]
Fordia splendidissima	Limonene (20.3) , Total (20.3)	β-Caryophyllene (6.6), α-Caryophyllene (21.1), Total (27.7)	
Fagraea cuspidata	Limonene (5.8), α-Pinene (0.66) , Total (6.4)		
Glochidion rubrum	Limonene (168), γ-Terpinene (106), α-Pinene (1402), Phellandrene (453), Total (2128)	α-Caryophyllene (15.6), Total (15.6)	
Gluta macrocarpa	Limonene (32.1), β-Ocimene (3229), α-Pinene (33.7), B-Myrcene (94.0), Total (3389)	β-Caryophyllene (914), (+)-Aromadendrene (36.1), 8-Isopropanyl-1,5-dimethyl-cyclodeca 1,5-diene (86.4), Δ-Elemene (725), Aromadendrene (67.3), E-α-Bergamotene (48.7), α-Caryophyllene (378), γ-Cadinene (82.7), β-Selinene (1383), Germacrene D (1711), Selina-3,7(11)-diene (62.7), Total (5515)	
Zingiber odoriferum	Limonene (35.0), α-Pinene (492), Total (527)	α-Copaene (260),β-Copaene (14.4), Bicyclogermacrene (715), Germacrene D (23.6) Aromadendrene (9.0), Total (1022)	*Z. aromaticum* (Kirara *et al*. 2003) [108], *Z. nimmonii* (Baby *et al*. 2006) [109], *Z. ottensii* (Akiyama *et al*. 2006) [110], *Z. officinalis* (Rani 1999; Bartley & Jacobs 2000; Ma *et al*. 2004; Picaud *et al*. 2006; Ma & Gang 2006; Menon *et*

			al. 2007) [111-116], *Z. zerumbet* (Damodaran & Dev 1967; Jang & Seo 2005; Sadhu *et al*. 2007; Yu *et al*. 2008a and 2008b) [117-121]
Hopea griffithii	β-Pinene (331), Limonene (40.9), α-Pinene (2812), Sabinene (52.2), β-Myrcene (93.0), Total (3329)	α-Copaene (62.5), Calarene (50.5), E-Caryophyllene (38.9), β-Cubebene (2), α-Caryophyllene (30.7), Germacrene D (19.1), Total (219)	
Hopea nervosa	Camphene (0.64 ± 0.58), β-Pinene (0.6662 ± 0.57), Limonene (80.9 ± 69.2), β-Ocimene (21.6 ± 19.7), Linalool (14.8 ± 13.5), α-Terpinene (9.5 ± 8.7), α-Pinene (387 ± 352), D-Calerene (0.69 ± 0.63), Total (1134 ± 1027)	Bicycloelemene (5.8 ± 5.3), α-Copaene (22.9 ± 14.3), α-Satalene (9.4 ± 6.6), β-Caryophyllene (117 ± 75), γ-Elemene (14.2 ± 12.9), α-Cubebene (2.14 ± 1.62), β-Elemene (0.87 ± 0.79), (-)-β-Elemene (4.9 ± 4.4),□β-Cubebene (3.0 ± 2.7), Bicyclogermecrene (55.2 ± 50.1), Aromadendrene (1.2 ± 1.1), α-Farnesene (1.3 ± 1.2), α-Caryophyllene (39.2 ± 17.2), γ-Cadinene (5.7 ± 3.6), β-Selinene (10.8 ± 9.4), Δ-Elemene (7.0 ± 6.4), 1,5,5-trimethyl-6-methylene-cyclohexene (0.44 ± 0.41), E-Caryophyllene (7.8 ± 6.9), Bicyclo[3,1,1]hept-2-ene-2,6-dimethyl-3-penthyl) (4.8 ± 4.4), E-α-Bergamolene (33.1 ± 20.7), β-Bisabolene (57.2 ± 52.3), Germacrene D (140 ± 65), Selina-3,7(11)-diene (6.1 ± 5.4), (+)-β-Gurjunene (0.41 ± 0.38), Δ-Cadinene (8.2 ± 7.5), Total (557 ± 225)	
Hopea nutans	Limonene (5.0 ± 2.9), β-Ocimene (34.6 ± 20.0), Total (26.4 ± 1.6)	α-Copaene (34.2 ± 19.7), β-Caryophyllene (97.5 ± 24.8), γ-Elemene (331 ± 270), (-)-β-Elemene (254 ± 208), β-Cubebene (259 ± 150), Δ-Elemene (91.7 ± 74.9), α-Caryophyllene (30.0 + 7.4), γ-Cadinene (7.8 ± 4.5), Selina-3,7(11)-diene (3.8 ± 2.2), Total (995 ± 714)	
Hopea sangal		(-)-β-Elemene (372), α-Lonone (1439), Bicyclogermacrene (21.0), γ-Cadinene (56.0), Aromadendrene (8.1), Total (1893)	
Lansium domesticum	Limonene (6.31), α-Pinene (32.9 + 23.7), Total (39.3 ± 24.8)	α-Copaene (1.3 + 1.0), β-Caryophyllene (30.6 + 20.2), γ-Elemene (105 + 84), α-Cubebene (48.5 ± 34.7), β-Cubebene (188 ± 63), Calarene (5.5 ± 4.5), 1,4,7-Cycloundecatriene-1,5,9,9-tetramethyl-Z,Z,Z- (4.0 ± 3.3), α-Caryophyllene (24.0 ± 16.2), γ-Cadinene (24.5 + 11.2), Total (432 ± 142)	*L. anamalayanum* (Krishnappa & Dev 1973) [122]
Luvunga heterophylla	Limonene (10.7), α-Pinene (5.8), Total	α-Copaene (1384), β-Caryophyllene (15.9), α-Cubebene (74.2), α-Ylangene (116), (-)-β-Elemene (800), α-Amorphene (168), Δ-Elemene (1448), α-	

	(16.5)	Gurjunene (59.8), E-Caryophyllene (254), Bicyclogermecrene (2201), Germacrene B (397), α-Guaiene (349), α-Caryophyllene (1790), β-Selinene (2079), γ-Selinene (1379), 5-Azulenemethanol (193), Germacrene D (70.9), Total (12778)
Macaranga conifera	β-Pinene (241), γ-Terpinene (80.3), α-Pinene (273), Phellandrene (132), Total (706)	α-Caryophyllene (11.0), Total (11.0)
Macaranga gigantea	Limonene (8.2 ± 6.7), α-Pinene (4.2 ± 3.4), Total (12.3 ± 5.8)	α-Copaene (35.2 ± 28.7), β-Caryophyllene (564 ± 240), (-)-β-Elemene (26.0 ± 21.2), 8-Isopropanyl-1,5-dimethyl-cyclodeca 1,5-diene (13.8 ± 11.2), β-Cubebene (9.5 ± 7.8), Δ-Elemene (27.5 ± 16.2), Bicyclo[3,1,1]hept-2-ene-2,6-dimethyl-6-(4-methyl-3-pentenyl)- (56.9 ± 39.0), E-α-Bergamolene (9.8 ± 8.0), β-Bisabolene (84.2 ± 68.7), E-β-Pharnesene (5.2 ± 4.3), α-Caryophyllene (913 ± 570), γ-Cadinene (18.9 ± 15.4), β-Selinene (16.7 ± 13.6), Veridiflorol (32.8 ± 28.8), Total (1780 ± 810)
Madhuca korthalsii	Limonene (6.3), α-Pinene (33.6), Total (40.0)	Bicycloelemene (12.4), α-Copaene (14.6), (-)-β-Elemene (13.3), α-Amorphene (4.3), Calarene (3.0), E-Caryophyllene (34.5), Aromadendrene (2.6), Bicyclogermacrene (181), Germacrene D (288), Selina-3,7(11)-diene (3.5), α-Caryophyllene (19.1), Total (580)
Mallotus mollissimus	β-Pinene (823 ± 373), Limonene (49.5 ± 19.5), γ-Terpinene (12.6 ± 5.2), α-Pinene (2197 ± 900), Total (3082 ± 1254)	α-Copaene (83.5 ± 35.8), Caryophyllene (252 ± 179), (-)-α-Selinene (341 ± 160), α-Cubebene (4.7 ± 3.8), β-Elemene (4.5 ± 3.7), Aromadendrene (31.2 ± 19.8), Bicyclogermacrene (330 ± 156), Germacrene B (109 ± 59), α-Caryophyllene (265 ± 132), β-Panasinsene (77.2 ± 63.1), Selina-3,7(11)-diene (60.7 ± 49.6), Germacrene D (62.5 ± 41.8), Total (1622 ± 763)
Mallotus wrayi	Limonene (4.6 ± 2.2), α-Pinene (3.69 ± 0.41), Total (8.3 ± 2.5)	α-Copaene (28.4 ± 14.5), α-Cubebene (71.1 ± 58.0), β-Elemene (3.8 ± 3.1), α-Amorphene (32.5 ± 26.5), E-Caryophyllene (153 ± 113), Bicyclogermacrene (8.1 ± 5.2), Germacrene B (1.9 ± 1.6), α-Farnesene (47.1 ± 38.4), α-Caryophyllene (120 ± 79), α-Muurolene (8.3 ± 6.6), β-Bisabolene (12.1 + 9.9), Δ-Cadinene (44.3 + 33.8), Globulol (11.1 ± 9.0), Viridiflorol (32.8 ± 26.8), Germacrene D (155 ± 65), Selina-3,7(11)-diene (87.1 ± 71.1), (+)-β-Gurjunene (5.4 ± 4.4), Total (801 ± 321)
Melastoma	Limonene (11.9 ± 1.0),	α-Caryophyllene (43.0 ± 24.8), Total (43.0 + 24.8)

malabathricum	γ-Terpinene (12.5 ± 10.2), α-Pinene (41.1 ± 3.1), Total (75.7 ± 23.0)		
Memecylon laevigatum	Limonene (3.3), α-Pinene (19.5), Total (22.8)	α-Copaene (5.5), E-α-Bergamolene (4.7), α-Caryophyllene (567), γ-Cadinene (11.0), β-Selinene (59.3), (+)-Spathulenol (16.0), Aromadendrene (70.0), Total (736)	
Myristica maxima		α-Copaene (22.1), Calarene (30.4), Aromadendrene (478), Bicyclogermacrene (105), α-Caryophyllene (392), Δ-Cadinene (7.4), Germacrene D (750), Selina-3,7(11)-diene (750), Total (1784)	*M. malabarica* (Baby *et al*. 2007) [123]
Nauclea subdita	Limonene (3.8), α-Pinene (1.90), Total (5.7)	α-Copaene (8.0), β-Caryophyllene (115),γ-Elemene (776), (-)-β-Elemene (7.9), E-Caryophyllene (33.1), Bicyclogermacrene (36.0), α-Caryophyllene (75.2), Germacrene D (129), Total (404)	*N. latifolia* (Maikal & Kobo 2008; Okwu & Uchenna 2009) [124, 125]
Neonauclea artocarpoides	Limonene (5.0), α-Pinene (47.7), Total (52.7)	α-Copaene (427), γ-Elemene (776), α-Cubebene (155), β-Elemene (457), (-)-β-Elemene (23.5), E-Caryophyllene (200), Aromadendrene (118), Bicyclogermacrene (751), Germacrene B (1332), α-Guaiene (918), α-Caryophyllene (459), β-Selinene (228), Azulene (2321), Δ-Cadinene (215), Viridiflorol (85.3), Total (8455)	
Palaquium microphyllum	Limonene (11.1), α-Pinene (25.3), Total (36.3)	Bicycloelemene (35.1), α-Cubebene (52.0), β-Elemene (57.7 + 49.9), (-)-β-Elemene (24.7), Bicyclogermacrene (449), α-Caryophyllene (224) , Total (784)	
Parashorea malaanonan	β-Pinene (28.2 ± 24.4), Limonene (26.8 ± 12.9), γ-Terpinene (19.9 ± 10.9), Linalool (778 ± 674), α-Pinene (185 ± 141), Sabinene (14.3 ± 12.4), Phellandrene (61.8 ± 53.6), β-Myrcene (17.0 ± 14.8), Total (1130 ± 934)	α-Copaene (25.3 ± 20.1), β-Caryophyllene (63.0 ± 45.5), γ-Elemene (6.8 ± 5.9), (-)-β-Elemene (232 ± 201), Δ-Elemene (11.4 ± 9.9), 1,5,5-trimethyl-6-methylene-cyclohexene (23.0 ± 19.9), Bicyclo[3,1,1]hept-2-ene-2,6-dimethyl-3-penthyl) (47.5 ± 41.2), β-Cubebene (6.0 ± 5.2), Bicyclogermacrene (61.3 ± 49.7), Bicyclo[4,4,0]dec-1-ene-2-isopropyl-5-methyl-9-methylene (30.7 ± 26.6), α-Loone (6.9 ± 6.0), α-Guaiene (5.2 ± 4.8), E-β-Farnesene (3.3 ± 2.9), α-Caryophyllene (113 + 90), γ-Cadinene (46.7 ± 40.4), E-α-Bergamotene (111 ± 10), β-Bisabolene (17.8 ± 15.4), (+)-Spathulenol (4.4 ± 3.8), Germacrene D (20.3 ± 13.6), β-Selinene (96.2 ± 67.4), Caryophyllene oxide (33.3 ± 28.8), Total (941 ± 100)	
Parashorea tomentella	Camphene (3.9 + 3.4),	Bicycloelemene (18.2 ± 16.3), α-Copaene (95.6 ± 69.3), β-Copaene (7.0 ± 4.4),	

	β-Pinene (10.5 + 9.4), Limonene (17.7 + 9.1), α-Pinene (203 + 167), Total (235 ± 179)	β-Bourbonene (15.6 ± 14.1), γ-Elemene (75.2 ± 67.3), Isospathulenol (4.5 ± 3.0), α-Ylangene (59.7 ± 53.4), α-Cubebene (64.6 ± 34.3), (-)-β-Elemene (9.0 ± 5.9), Δ-Elemene (40.5 ± 31.9), E-Caryophyllene (546 ± 488), Bicyclogermacrene (362 ± 147), α-Guaiene (3.8 ± 3.2), α-Farnesene (2.6 ± 2.3), α-Caryophyllene (474 ± 298), Δ-Cadinene (9.6 ± 4.2), (+) Spathulenol (40.8 ± 36.1), Germacrene D (384 ± 155), Total (2213 ± 990)	
Payena acuminata	Limonene (11.1), α-Pinene (107), Total (118)	β-Caryophyllene (94.3), α-Caryophyllene (36.7), Total (131)	
Pleiocarpidia sandahanica	Limonene (5.1 ± 0.5), α-Pinene (5.1 ± 1.8), Total (6.8 ± 3.4)	Bicycloelemene (15.0 ± 8.7), α-Copaene (2.78 ± 1.60), (+)-Aromadendrene (10.4 ± 6.0), (-)-β-Elemene (3.4 ± 2.8), α-Amorphene (131 ± 76), E-Caryophyllene (9.0 ± 5.2), Bicyclogermacrene (61.4 ± 35.5), Viridiflorol (5.4 ± 3.1), Germacrene D (3.3 ± 2.7), Selina-3,7(11)-diene (4.9 ± 2.8), Total (163 ± 133)	
Podocarpus neriifolius	Limonene (1.6 ± 0.9), α-Pinene (1.45 ± 0.84), Total (2.04 ± 1.67)	Bicycloelemene (4.0 ± 2.3), α-Copaene (2.4 ± 1.4), α-Cubebene (11.4 ± 6.6), α-Amorphene (3.0 ± 1.8), Calerene (1.8 ± 1.5), Bicycloelemene (3.56 ± 2.05), E-Caryophyllene (93.6 ± 2.4), Bicyclogermacrene (88.5 ± 7.4), α-Caryophyllene (53.4 ± 1.9), Germacrene D (36.2 ± 28.7), (+)-β-Gurjunene (3.0 ± 1.8) , Total (212 ± 9.7)	*P. andina* (Kubo *et al*. 1992) [126], *P. halli* (Perry *et al*. 2007) [127], *P. sensu latissimo* (Abdillahi *et al*. 2010) [128], *P. spicatus* (Lorimer & Weavers 1987) [129]
Poikilospermum cordifolium	Limonene (8.8 ± 1.3), α-Pinene (1.05 ± 0.61), Total (6.5 ± 3.1)	α-Copaene (544 ± 314), α-Cubebene (28.8 ± 16.6), γ-Elemene (79.3 ± 64.7),□ α-Ylangene (45.2 + 26.1), β-Elemene (191 + 110), □Δ-Elemene (423 + 345), E-Caryophyllene (98.0 ± 48.0), Aromadendrene (24.8 + 14.3), α-Guaiene (134 ± 78), α-Caryophyllene (340 ± 196), Δ-Cadinene (48.3 ± 27.0), α-Selinene (507 ± 292), 5-Azulenemethanol (62.9 ± 36.3), Germacrene D (596 ± 482), (+)-β-Gurjunene (746 ± 431), Total (2946 ± 2392)	
Polyalthia sumatrana	Limonene (3.3 ± 0.6), α-Pinene (32.8 ± 17.3), Total (24.1 ± 18.8)	α-Copaene (2.8 ± 1.6), β-Caryophyllene (6.9 ± 2.9), γ-Elemene (4.8 ± 4.0), α-Cubebene (1.7 ± 1.0), α-Ylangene (19.4 ± 11.2), (-)-β-Elemene (1.85 ± 1.51), 1,4,7-Cycloundecatriene-1,5,9,9-tetramethyl-Z,Z,Z- (3.7 ± 2.2), Allomadendrene (2.8 ± 1.6), γ-Cadinene (7.5 ± 4.4), β-Selinene (4.0 ± 3.3), Globulol (1.6 ± 0.9), α-Selinene (2.3 ± 1.3), Total (43.2 ± 33.2)	*P. cerasoide* (Kanokmedhakul *et al*. 2007) [130], *P. longifolia* (Ogunbinu *et al*. 2007) [131], *P. suaveolens* (Nyegue *et al*. 2008) [132]
Popowia pisocarpa			
Pouteria malaccensis	Limonene (3.9), Total (87.1)	β-Burbonene (5.6), β-Caryophyllene (270), (+)-Aromadendrene (36.9), E-α-Bisabolene (36.9), (-)-α-Selinene (161), α-Cubebene (62.1), 8-Isopropanyl-1,5-	*P. caimito* (Adron *et al*. 1972) [133], *P. splendens* (Sotes *et al*. 2006) [134]

		dimethyl-cyclodeca-1,5-diene (14.9), Bicyclo[4,4,0]dec-1-ene-2-isopropyl-5-methyl-9-methylene (6.5), E-α-Bergamotene (49.7), α-Caryophyllene (93.6), γ-Cadinene (81.2), β-Selinene (178), β-Bisabolene (6.8), (+)-Spathulenol (7.5), Germacrene D (37.2), Selina-3,7(11)-diene (77.2), Total (929)	
Pterospermum stapfianum	Camphene (41.2), Limonene (17.1), α-Pinene (94.5), Total (152.8)	α-Copaene (6.1), β-Caryophyllene (6.0), α-Cubebene (3.2), α-Caryophyllene (11.5), γ-Cadinene (14.6), β-Selinene (201), Selina-3,7(11)-diene (77.2), Veridiflorol (24.1), α-Selinene (190), Total (457)	
Reinwardtiodendron humile		α-Copaene (518 ± 226), β-Caryophyllene (396 ± 228), (+)-Aromadendrene (65.2 ± 37.6), α-Cubebene (30.9 ±17.8), α-Caryophyllene (12670 ± 285), β-Elemene (13.9 ± 8.0), (-)-β-Elemene (192 ± 157), α-Amorphene (58.7 ± 33.9), Calarene (299 ± 244), 1,5,5-trimethyl-6-methylene-cyclohexene (23.0 ± 13.3), Azulene (363 ± 221), α-Muurolene (32.7 ± 26.7), Viridiflorol (30.5 ± 17.7), α-Gurjunene (147 ± 85), E-Caryophyllene (1187 ± 684), Germacrene D (100 ± 82), Selina-3,7(11)-diene (150 ± 87), α-Guaiene (158 ± 78), Bicyclogermacrene (626 ± 361), α-Caryophyllene (12670 ± 285), (+)-Spathulenol (7.1 ± 4.1), Total (3899 + 2510)	
Shorea acuta	Limonene (49.1), β-Ocimene (560), Linalool (154), α-Terpinene (2990), β-Myrcene (36.3), Δ-3-Carene (32.8), Total (3822)	γ-Elemene (565), α-Cubebene (163), β-Elemene (10435), Germacrene B (4469), Germacrene D (5024), Total (20657)	*S*. species (Bisset *et al*. 1971) [135], *S negrosensis* (Ishi & Kadoya 2003) [136]
Shorea fallax	Limonene (1.14 ± 0.93), α-Pinene (0.71 ± 0.58), Total (1.85 + 1.51)	β-Caryophyllene (1.5 ± 1.2), □α-Cubebene (14.2 ± 11.1), (-)-β-Elemene (13.6 ± 11.1), 1,5,5-trimethyl-6-methylene-cyclohexene (27.9 + 16.2), Bicyclogermacrene (202 ± 165), β-Sesquiphellandrene (16.6 ± 13.5), E-Caryophyllene (38.8 ± 25.0), Allomadendrene (3.1 ± 2.6), α-Caryophyllene (22.0 ± 13.5), β-Selinene (118 ± 96), Germacrene D (224 ± 187) , Total (692 ± 2278)	
Shorea johorensis	Limonene (6.8 ± 5.6), α-Terpinene (37.8 ± 30.9), α-Pinene (14.8 ± 8.3), Total (59.3 ± 31.9)	β-Caryophyllene (25.3 ± 20.7), α-Cubebene (5.2 ± 3.4), β-Elemene (31.5 ± 27.5), α-Amorphene (6.4 ± 3.7), Bicycloelemene (3.2 + 2.6), E-Caryophyllene (324 ± 205), Bicyclogermacrene (132 ± 83), Germacrene B (39.1 ± 31.9), α-Caryophyllene (201 ± 125), Germacrene D (294 ± 64), Total (1062 ± 436)	

Sindorea irpicina		α-Copaene (33.1 ± 15.3), β-Caryophyllene (4.3 ± 2.5), γ-Elemene (133 ± 108), β-Elemene (803 ± 563), β-Cubebene (29.5 ± 17.1), Calarene (51.3 ± 41.9), Δ-Elemene (29.4 ± 24.0), E-Caryophyllene (91.5 ± 52.9), Bicyclogermacrene (298 ± 172), Germacrene B (2.9 ± 2.3), α-Caryophyllene (15.5 ± 3.3), β-Selinene (239 ± 195), Germacrene A (55.6 ± 32.1), Δ-Cadinene (3.8 ± 2.2), Germacrene D (60 ± 33), Total (1404 ± 851)	*S. sumatrana* (Heymann *et al*. 1994; Jang *et al*. 2004) [137, 138]
Swintonia acuta	Limonene (1.75), α-Pinene (1.84), Total (3.6)	β-Caryophyllene (132), α-Cubebene (3.7), α-Ylangene (14.3), Bicycloelemene (3.3), Bicyclogermacrene (35.2), α-Caryophyllene (95.1), Total (284)	
Symplocos fasciculata		β-Caryophyllene (288), γ-Elemene (5358), α-Cubebene (88.7), 8-Isopropanyl-1,5-dimethyl-cyclodeca-1,5-diene (4045), Bicycloelemene (1327), Bicyclogermacrene (2383), α-Caryophyllene (86.6), Total (13577)	
Syzygium campanulatum	β-Pinene (30.0 ± 24.5), Limonene (22.5 ± 1.9), β-Ocimene (212 + 122), γ-Terpinene (0.96 ± 0.78), Linalool oxide (1.53 ± 0.88), Linalool (21.6 ± 12.4), α-Terpinene (2.52 ± 1.46), α-Pinene (26.7 ± 15.4), Sabinene (5.5 ± 3.2), Total (226 ± 68.5)	α-Copaene (6.8 ± 3.9), α-Santalene (70.4 ± 40.6), β-Caryophyllene (107 ± 62), E-α-Bisabolene (4.9 ± 2.8), E-γ-Bisabolene (3.2 ± 1.8), γ-Elemene (2.8 ± 2.3), α-Cubebene (38.4 ± 22.1), (-)-β-Elemene (7.8 ± 6.4), α-Amorphene (4.5 ± 2.6), Δ-Elemene (26.2 ± 21.4,), 1,5,5-trimethyl-6-methylene-cyclohexene (2.9 ± 1.9),E-α-Bergamolene (2.4 ± 2.0), α-Caryophyllene (82.6 ± 3.0), α-Muurolene (1.8 ± 1.1), Selina-3,7(11)-diene (6.2 ± 3.6), Total (273 ± 121)	*S. aromaticum* (Gopalakrishnan 1994; López *et al*. 2006) [139, 140], *S. formosanum* (Chang *et al*. 1999) [141]
Tarbernaemontana macrocarpa	Limonene (22.3), α-Pinene (10.1), Total (32.4)	Bicyclogermacrene (10.8), α-Caryophyllene (20.9), Germacrene D (4.7), Total (36.1)	*T. markgrafiana* (Nielsen *et al*. 1994) [142]
Tarenna cumingiana	β-Pinene (528), Limonene (22.8), α-Pinene (1082), β-Myrcene (54.9), Total (1687)	α-Copaene (1879), β-Caryophyllene (71.2), E-α-Bisabolene (5010), α-Cubebene (202), (-)-β-Elemene (2079), 8-Isopropanyl-1,5-dimethyl-cyclodeca-1,5-diene (201), Δ-Elemene (158), Bicyclo[3,1,1]hept-2-ene-2,6-dimethyl-6-(4-methyyl-3-pentenyl)- (442), E-α-Bergamolene (4815), β-Sesquiterpene (399), α-Caryophyllene (1746), γ-Cadinene (282), β-Selinene (757), Allomadendrene (162), β- Bisabolene (4518), Selina-3,7(11)-diene (3869), (+)-Spathulenol (161), Germacrene D (356), Total (27109)	*T. madagascariensis* (Salmoun *et al*. 2007) [143]
Uncaria cordata	Limonene (5.7), α-Pinene (2.57), Total		

	(8.3)		
Uvaria sorzogonensis	Camphene (93.8), Limonene (8.6), Total (102)	β-Caryophyllene (12.5), α-Guaiene (3.4), Germacrene B (7.5), α-Caryophyllene (13.8), (+)-Spathulenol (62.1), Total (99.0)	*U*. species (Parmar *et al*. 1994) [144], *U. lucida* (Weenen & Nkunya 1990) [145], *U. scheffleri* (Nkunya 2005) [146], *U. tanzaniae* (Weenen *et al*. 1991) [147]
Xanthophyllum affine			

We show only the chemical species that were determined with more than 95% of certainty according with literature spectra. Values between brackets are mean ± S.E. (μg g^{-1}). The existence of previous studies on mono- and sesquiterpenes for the same species and genus are reported in the last column.

species of these genera studied here had not been previously reported as mono- and/or sesquiterpene containing species (Table 2, supplementary material). We did not detect terpenes in the species studied of the genera *Popowia* and *Xanthophyllum*. As far as we know, no previous studies have described terpene content in species of these genera. We report for the first time that two of the three *Dipterocarpus* studied species (*D. sarawakensis* and *D. applanatus)*, are terpene containing species. The third studied species, *D. gracilis*, had already been reported as containing different caryophyllene isomers [69], but we have determined for the first time α-Cubebene, β-Cubebene, Bicyclogermacrene, γ-Cadinene, Germacrene D and Selina-3,7,(11)-diene for this species. Finally, *Cinnamonum zeylanicum* had already been reported as terpene containing species [70].

This high proportion of terpene containing taxa in this old tropical forest suggests that terpene content can be a favourable selective trait in these environmental conditions. These results also suggest that terpene accumulation can be widespread in tropical rainforest plants. Further research is necessary to corroborate whether this higher frequency of species terpene accumulators in tropical rainforest than in other forest ecosystems is a general trend or not, and to gain knowledge on the ecological significance of this higher frequency of accumulator species in these tropical ecosystems. Moreover, Courtois *et al*. (2009) [67] have also observed in a set of 55 tree species of a rainforest in the French Guiana that all studied species emitted VOCS, most of them mono- and sesquiterpenes, further suggesting the widespread terpene production of rainforest trees.

There were poor relationships between leaf terpene concentrations and phylogeny among the 75 studied species. This agrees with results observed in similar studies in other floras such as those for 73 Oahu forest species [26]. Moreover, the number of different mono- and sesquiterpene chemical species per each plant species did not present phylogenetic signal. As far as we know, there is a lack of comparable studies on the phylogenetic signal of leaf terpene concentrations in a broad set of plant species but the results are in accordance with terpenes being found in most plant Families [71], and also with studies finding genes linked to terpene biosynthesis pathways in several plant groups [72].

Higher nutrient availability may be expected to translate into higher carbon fixation and activity of the enzymes involved in isoprenoid production [38, 40]. But it might also be expected the other way around, that a higher nutrient availability translates into more growth than allocation to carbon based secondary compounds such as terpenes, following the “carbon excess” hypotheses [42, 44]. The available literature does not show clear general relationships between leaf N and P concentrations and/or availability with leaf terpene concentrations [34, 73]. This study confirms most of the available literature: Leaf terpene concentration had no relationship with nutrient concentrations. The lack of relationships between leaf terpene concentration and leaf nutrient concentrations does not thus support the “nutrient driving synthesis hypothesis” [39, 40], nor the “carbon excess hypotheses”. In general, previous studies have not detected relationships between N and P concentrations or availability and leaf terpene concentrations. For example, although NPK fertilization increased terpene concentrations in *Chrysanthemum boreale* [33], and increased some monoterpene compounds and decreased others in *Larix lariciana* [74], no relationships have been observed between P concentration and terpene concentration in the leaves of *Eucalyptus polybractea* [75], or in the leaves of *Pinus halepensis* and *Quercus ilex* [34]. Studies on the relationships between leaf N and terpene concentrations, although scarce, are more abundant than those of P concentrations and terpene concentrations relationships. While some studies have observed an increase [76-78] or decrease [79] in leaf terpene concentrations with increasing N availability and/or concentration, other studies have not either detected a clear relationship [34, 44, 75, 80], or have shown a different direction of the relationship depending on the species [32] or depending on the leaf age [81]. Thus, the results of the study observing no relationships between leaf N concentration with terpene concentration largely agree with previous literature, suggesting multiple factors affecting the nutrient-terpene relationship including the strength of the nutrient limitation and the ecological benefits of terpene production in each environmental circumstance.

The observed negative relationships between leaf terpene concentration and leaf length corroborates previous studies that have shown that leaf morphological traits exert some effect on terpene concentration storage capacity through regulation of gland dimensions [75] or in the accumulation of enzymes responsible for terpene synthesis per unit of leaf area [82]. However, we did not find any significant relationship between leaf mono- and sesquiterpene concentration and the other leaf morphological traits nor with leaf photosynthetic capacity.

Thus, there were not general relationships between leaf terpene concentrations and leaf trais related to defence and to production capacity. This can be due to the highly diverse functions of terpenes and not related to a single compound or structure. The relationships between herbivores and plants in tropical rainforest are very diverse [30, 61]. Previous studies have also observed poor relationships between leaf anatomical traits and leaf terpene concentrations in tropical rainforest [83]. Certainly, as commented previously, terpenes can act as herbivore deterrents [18, 19] mainly against generalist herbivores [20-22], but they also have other properties, such as defence against fungi and pathogens [25] and against abiotic stresses such as high temperature, ozone or excess of radiation [4, 5, 84] and signaling and communication [11, 85]. These roles for terpenes can be advantageous in tropical ecosystems where the radiation intensity and temperatures are high and where there are multiple and diverse biotic interactions due to the high species diversity and organisms density.

Summarizing, the high proportion of species that accumulate terpenes and the general lack of phylogenetic conservatism suggest that terpene accumulation is a widespread trait in this tropical forest that confers adaptative advantage in all plant taxon spectrum across a wide range of angiosperm phylogeny. The negative correlation between monoterpene concentration and leaf length might suggest a link between leaf anatomy and the capacity to store terpenes. Functions such as temperature protection, radiation protection or signaling and communication could underlie the high frequency of terpene-containing species of this tropical ecosystem which has multiple and very diverse interactions among multiple species.

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Supporting Information

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