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ORIGINAL ARTICLE

Monoterpene emissions from three *Nothofagus* species in Patagonia, Argentina

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Isoprenoid emissions have key roles in plant biology and plant interactions with the environment. Global emission inventories of isoprenoid emissions still lack information from a large number species, especially from South American vegetation other than the rainforest ecosystem. A study was conducted to identify the basal emission of isoprenoid under field conditions from three *Nothofagus* species. The three *Nothofagus* species were characterized as strong monoterpene emitters while the emission of isoprene was undetectable. The two deciduous species, *N. pumilio* and *N. antarctica*, had similar photosynthetic parameters, but monoterpene emission rate and, consequently, the fraction of photosynthetic carbon re-emitted in the atmosphere as monoterpenes, were more than three-fold higher in *N. pumilio* than in *N. Antarctica*. The evergreen species *N. dombeyi* showed intermediate values of both monoterpene emission rate and fraction of photosynthetic carbon re-emitted. The monoterpene emission spectrum was very similar among the three *Nothofagus* species screened, but clearly different from the spectrum reported in other monoterpene-emitting species of the Fagaceae family. The importance of these findings for atmospheric chemistry and phylogenic evolution are discussed.

Keywords: emission inventory; gas exchange; isoprenoids; limonene; photosynthesis

Introduction

All plants emit a wide range of volatile compounds among which biogenic volatile organic compounds (BVOCs), often referred also as non-methane organic compounds, have received particular attention in the last two decades (Guenther et al. 1993; Centritto et al. 2004; Brilli et al. 2007; Grote and Niinemets in press). Isoprenoids (isoprene, monoterpenes and sesquiterpenes) make the largest fraction of BVOC emissions. They were discovered to enhance and modulate plant tolerance to heat, pollutants, oxidative stress and abiotic stresses (Sharkey and Yeh 2001; Niinemets et al. 2004), and to affect plant-plant and plant-insect interactions (Gershenzon and Dudareva 2007). The global carbon emitted as BVOCs is about 1.1 Pg per year, half of which is emitted as isoprene, and is believed to be of the same order of magnitude than methane emissions (Guenther et al. 2000). The importance of isoprenoids also lies in their reactivity and potential for profoundly influencing the chemical and physical properties of the atmosphere (Kavouras et al. 1998; Di Carlo et al. 2004). In the atmosphere, isoprenoids rapidly react with hydroxyl radical (OH), the primary oxidizing agent of the atmosphere, affecting its tropospheric concentration (Atkinson and Arey 2003; Di Carlo et al. 2004). In non-polluted areas, isoprenoids cause the depletion of OH radicals in the troposphere and increase the lifetimes of other greenhouse gases (including methane) (Poisson et al. 2000). In polluted areas, in the presence of high NO_X concentrations, isoprenoids react in the atmosphere with anthropogenic compounds leading to a net production of tropospheric ozone and other photo-oxidants (Chameides et al. 1987; Fehsenfeld et al. 1992).

Furthermore, monoterpene and sesquiterpenes are significant precursors of secondary organic aerosols (Andreae and Crutzen 1997; Kavouras et al. 1998; Kanakidou et al. 2004; Vizuete et al. 2004). These less-volatile BVOC species condense onto particles in the atmosphere, resulting in the formation of secondary organic aerosols (SOA) which accounts for 20–50% of the total fine particulate matter in the atmosphere at continental mid-latitudes and up to 90% in tropical forested areas (Andreae and Crutzen 1997; Kanakidou et al. 2004). Moreover, although isoprenoid emission accounts for approximately 2% of the total C-exchange of 69 Pg between the biota and the atmosphere (Lal 1999), isoprenoids have not been considered in global C-cycling so far. This emphasizes the importance of biogenic emissions, and inventories of BVOC emissions are, consequently, a key issue in atmospheric sciences.

The emission of isoprenoids by plants was first discovered in the Amazons (Rasmussen and Jones 1973). Afterwards, inventories of the emission of

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isoprenoids have been made systematically for a large number of species in Europe (Simpson et al. 1995; Niinemets et al. 2002), North America (Guenther et al. 1996a, 2000), in Africa (Guenther et al. 1996b), Asia (Loreto et al. 2002; Geron et al. 2006), Australia (He et al. 2000), and South America (Kahl et al. 1999; Rinne et al. 2002; Greenberg et al. 2004). However, inventories about South American plant species are mostly limited to the rainforest vegetation over the Amazon, while information for other ecosystems is missing. More generally, the emission potential databases still lack information especially for monoterpene emitting species, which complicates the use of the emission inventories for predicting the emissions in globally changing environmental conditions (Grote and Niinemets in press). In the past, studies concerning the occurrence of isoprenoid production within the plant kingdom showed that many broad-leaved species were 'non-emitters' or low monoterpene emitters, in particular the species of the *Fagaceae* family (i.e. *Fagus*, *Nothofagus*, *Chrysolepis*, *Castanea* and *Lithocarpus*) (Kesselmeier and Staudt 1999). However, recent studies showed that *Fagus sylvatica* (European beech) is a moderately strong monoterpene emitter (Dindorf et al. 2006; Holzke et al. 2006).

The current series of experiments was designed to study emissions from temperate forests species of Argentina. We focused on three *Nothofagus* species (*N. antarctica*, *N. pumilio* and *N. dombeyi*) growing in natural forests in Patagonia, for the following reasons: (a) the *Nothofagus* genus (southern beech) is important and widespread being formed by 40 species of woody native plants of the southern hemisphere; (b) to our knowledge these three *Nothofagus* species have not been previously screened for BVOC emission; and (c) other species of the *Fagaceae* family (i.e. oaks) were reported to be strong emitters of isoprene or monoterpenes worldwide in the northern hemisphere (Loreto 2002). However, *Fagus sylvatica*, the closest plant species to *Nothofagus* among those vegetating in the northern hemisphere (Cronquist 1981), is controversial with respect to the emission of isoprenoids (Hewitt and Street 1992; Kesselmeier and Staudt 1999; Dindorf et al. 2006).

Materials and methods

Fully sunlit plants of *N. antarctica*, *N. pumilio* and *N. dombeyi* growing in natural forests in San Carlos de Bariloche (Argentina, Lat. 41.07°S, Long. 71.19°W), were studied during late summer 2005. *N. antarctica* and *N. pumilio* are deciduous species, whereas *N. dombeyi* is an evergreen species.

All gas exchange measurements were made between 11:00 and 15:00 h on the central section of a newly-expanded leaf from sunny branches collected early in the morning from 12–15 trees per species and placed in individual 0.5 dm^3 containers. Leaves within the same species were at similar phenological stage, without interference from water stress (i.e. relative water content values ranging between 90 and 95%, data not shown). Each branch was cut again under water before measuring gas exchange. The branches were transported to a near laboratory and remained under water from the time of being cut until the measurements were completed. It should be noted that gas exchange parameters measured in these branches equaled rates measured *in situ* (i.e. in native atmospheric conditions), indicating that this procedure did not cause any loss in photosynthetic potential. These gas exchange measurements were made in ambient CO2 concentration with a portable infrared analyser (Licor 6400, Li-Cor, Lincoln, Nebraska, USA).

To enable measurements of photosynthetic basal isoprenoid emission rates, leaves were illuminated using a red-blue light source attached to the gas-exchange system which maintain a PPFD (photosynthetic photon flux density) of 1000 μmol m^{-2}s^{-1}. The leaf temperature was controlled with Peltier thermoresistances and was maintained at 30°C. These conditions were selected because they have been reported as the environmental conditions at which the basal emission of isoprenoids is measured (Guenther et al. 1993). The vapor pressure deficit was maintained below 30 mbar bar^{-1} and the relative humidity in the cuvette was about 45%. The leaf was exposed to a flux of 0.5 l min^{-1} of ambient air. When CO_2 uptake and H_2O release had become steady, photosynthesis (A), transpiration, stomatal conductance (g_s) were measured and the air exiting the cuvette was diverted from the gas-exchange system to a two-stage trap filled with Carbograph 1 (0.034 g) and Carbograph 2 (0.17 g; Lara, Rome, Italy). The air flowing through the cartridge was measured by a flow meter placed at the cartridge exit. Before each measurement, ambient air from an empty IRGA cuvette was flown through the cartridge to determine the blank. After sampling 2–3 l of air the cartridge was removed, tightly capped, and maintained at low temperature and in the dark until analytical measurement on its content was carried out in Italy. Isoprenoids were analyzed by gas chromatography mass spectrometry as previously described by Baraldi et al. (1999). The trapped compounds were thermodesorbed at 250°C and cryofocused at −150°C on a fused silica liner using a Thermal Desorption Cold Trap Injector (Chrompack, Middleburg, The Netherlands) connected to a gas chromatograph-mass spectrometer (Hewlett Packard 5890-5970, Palo Alto, CA, USA). The desorbed sample was injected into a 60 m × 0.25 mm I.D. 0.25 μm film thickness capillary column (HP1, Hewlett Packard). Isoprenoids were separated maintaining the oven temperature at 40°C for 10 min and programming to 220°C at 5°C min^{-1}. The identity of the compounds of interest was achieved by comparison of their retention time and mass spectra to that of authentic standards. Quantification of isoprenoids was performed after calculation of standard curves and response factors for each compound, and using d14-cymene as internal standards. Isoprenoid concentration was calculated by dividing the amount collected in the cartridge by the volume of air sampled. Then isoprenoid emissions were calculated by multiplying the difference between isoprenoid concentrations in the sampling and in the corresponding blank by the air flowing through the leaf cuvette. Isoprenoid emission was then referred to leaf area by dividing the emission for the area of the leaf enclosed in the cuvette.

Data were tested using a simple factorial ANOVA, and where appropriate, the treatment means of gas exchange parameters were compared using Tukey's Post-hoc test.

Results and discussion

There were inherently different gas-exchange characteristics between the two deciduous species and the evergreen species of *Nothofagus* measured (Table 1). Photosynthesis, stomatal conductance and respiration in darkness were significantly higher in *N. antarctica* and *N. pumilio* (the two deciduous species) than in *N. dombeyi* (the evergreen species). Photosynthesis was on average ~31% higher in the deciduous species than in the evergreen one. Whereas g_s was ~58% and R_D ~40% higher on average in *N. antarctica* and *N. pumilio* than in *N. dombeyi*. These results are in keeping with previous findings showing that potential carbon gain (photosynthesis) and carbon loss (respiration) increase in similar proportion with decreasing leaf life-span, increasing leaf nitrogen concentration, and increasing leaf surface area-to-mass ratio (Reich et al. 1997; Wright et al. 2004).

Basal emissions of isoprenoids were measured at photosynthetic photon flux density of 1000 μmol $m^{-2}s^{-1}$ and at a leaf temperature of 30°C to normalize the emission dependency on environmental factors (Guenther et al. 2000) in fully expanded leaves of adult trees. All *Nothofagus* species were monoterpene emitters (Table 2), whereas they did not emit a detectable amount of isoprene. The three *Nothofagus* species had also inherently different monoterpene emission rates, but that was not related to the characteristic of deciduousness of three species (Table 1). The two deciduous species *N. pumilio* and *N. antarctica* had similar photosynthetic parameters, but monoterpene emission rate was more than three-fold, and the fraction of photosynthetic carbon lost was two-fold higher in *N. pumilio* than in *N. Antarctica*. The evergreen species *N. dombeyi* showed intermediate values for total monoterpene emissions, but highest values for the fraction of photosynthetic carbon lost. The emission rates of monoterpenes in the three *Nothofagus* species were similar to those observed in other monoterpene emitting species of the *Fagaceae* family, all of which belong to the *Quercus* genus (Loreto et al. 1998; Loreto 2002).

There is a debate on whether the *Nothofagus* genus, the only genus of the *Fagaceae* family in the southern hemisphere, is closely linked to plants of the family living in the northern hemisphere (Manos and Steele 1997; Li et al. 2004). Previous studies considered the *Nothofagus* family as genetically close to the *Fagus* genus (Cronquist 1981). However, Manos and Steele (1997), using phylogenetic analyses based on chloroplast DNA sequences, suggested that *Nothofagus* is largely independent genus, constituting a clade different than that including other *Fagaceae* (Manos and Steele 1997). More recent studies confirmed that *Nothofagus* is monophyletic and sister to the rest of *Fagales* (Li et al. 2004; Cook and Crisp 2005).

Isoprenoids have been used as a trait for systematic studies (Loreto et al. 1998; Lerdau and Gray 2003). *Fagus sylvatica* has been considered as a 'non-emitting' or low monoterpene emitting species (Hewitt and Street 1992; König et al. 1995), but several recent experiments in field conditions have shown that the emission of monoterpenes may be more relevant than previously indicated (Kahl et al. 1999; Kesselmeier and Staudt 1999; Dindorf et al. 2006; Holzke et al. 2006), although probably still lower than that reported in strong emitters such as some Mediterranean oak species (Loreto 2002). The rates of monoterpene emission by leaves of the three *Nothofagus* species were quite high, similar to those of Mediterranean oaks. However, the blend emitted from *Nothofagus* plants was different than those emitted by *Fagaceae* (Figure 1). In fact, sabinene and α-thuyene are the predominant compounds released by *Fagus sylvatica* leaves (Dindorf et al. 2006; Holzke et al. 2006), while α-pinene is the main

Table 1. Photosynthesis (A), stomatal conductance (g_s), respiration in darkness (R_D), total monoterpene emission, and percentage of photosynthetic carbon lost as isoprenoids in *Nothofagus antarctica* (deciduous), *N. pumilio* (deciduous) and *N. dombeyi* (evergreen). Data are means of 12–15 trees ± 1 SEM. Letters (a, b, c) indicate significant differences at $p < 0.05$ in the same column.

	A (μmol $m^{-2}s^{-1}$)	g_s (mmol $m^{-2}s^{-1}$)	R_D (μmol $m^{-2}s^{-1}$)	Monoterpene (nmol $m^{-2}s^{-1}$)	% Carbon lost
N. antarctica	6.02 ± 0.76 b	76.00 ± 13.87 b	−2.93 ± 0.32 b	2.63 ± 0.31 a	0.141 a
N. pumilio	5.93 ± 0.82 b	90.00 ± 7.71 b	−2.90 ± 0.23 b	8.02 ± 1.30 c	0.342 b
N. dombeyi	4.14 ± 0.53 a	34.83 ± 3.97 a	−1.77 ± 0.06 a	4.38 ± 1.20 b	0.437 c

Table 2. Emission of the most abundant monoterpenes (nmol $m^{-2}s^{-1}$) in *Nothofagus antarctica* (deciduous), *N. pumilio* (deciduous) and *N. dombeyi* (evergreen). Data are means of 12–15 trees ± 1 SEM. Letters (a, b, c) indicate significant differences at $p < 0.05$ in the same line.

Monoterpene	*N. antarctica*	*N. pumilio*	*N. dombeyi*
α-thuyene	0.040 ± 0.011 a	0.233 ± 0.045 b	0.039 ± 0.006 a
α-pinene	0.241 ± 0.061 a	0.620 ± 0.080 b	0.278 ± 0.087 a
sabinene	0.077 ± 0.012 a	0.163 ± 0.050 b	0.149 ± 0.045 b
β-pinene	0.325 ± 0.050 a	0.540 ± 0.082 b	0.441 ± 0.072 ab
β-myrcene	0.124 ± 0.027 a	0.348 ± 0.073 b	0.137 ± 0.030 a
p-cymene	0.070 ± 0.011 a	0.362 ± 0.098 c	0.165 ± 0.042 b
limonene	1.607 ± 0.175 a	5.332 ± 1.069 c	2.920 ± 0.690 b

compound emitted by *Quercus ilex* leaves (Loreto et al. 1996). In all *Nothofagus* species limonene was found to be the most abundant monoterpene emitted (Table 2), accounting for about 61–67% of the total emission, followed by β-pinene and α-pinene (Figure 1). This is interpreted as a possible indication that *Nothofagus* is genetically different from both *Quercus* and *Fagus* plant species, thus confirming recent phylogenetic analysis (Manos and Steele 1997). It should be mentioned that limonene has been reported as the main component of the blend emitted by some provenances of *Quercus suber*, *Quercus ilex* and hybrids of these two species (Staudt et al. 2004). It may be possible that the emission of limonene is a trait under environmental control (Geron et al. 2000). This should be further investigated under controlled environmental conditions.

Only evergreen species of the *Quercus* family of the northern hemisphere emit monoterpenes, while deciduous species only emit isoprene (Loreto 2002). A remarkable exception appears to be *Q. semecarpifolia*, an Asian species that only emit isoprene (Loreto et al. 1998). It is therefore noteworthy that the spectrum of the main monoterpene emitted is very similar among the two deciduous and the evergreen *Nothofagus* species, indicating the absence of differentiation based on the persistence of the leaf. This is another observation that may be explained by the environmental conditions experienced by the plants, as they share the same habitat and might have evolved the same emission pattern, independent of deciduousness.

The similar emission pattern in the three *Nothofagus* species might also indicate a substantially low interspecific difference at a genetic level. Manos (1997) examined the phylogenetic relationships within the *Nothofagaceae* family by analyzing the nucleotide sequences and their morphological character evolution from 22 *Nothofagus* species representing the four currently recognized subgenera (i.e. *Brassospora*, *Nothofagus*, *Fuscospora* and *Lophozonia*) and related outgroups. He showed that *N. pumilio*, *N. antarctica* and *N. dombeyi* belonged to the subgenus *Nothofagus*. Furthermore, Ramírez et al. (1997), using a morphological criterion, divided 11 taxa of South American *Nothofagus* in five groups. They found that *N. antarctica* and *N. dombeyi* belong to the same group having small leaves and that developed under temperate humid conditions; whereas *N. pumilio*, with mid-sized deciduous leaves, adapted to the cold and dry zones of the southern Andes, belongs to a group of isolated species with different requirements. However, *N. pumilio* and the group including *N. antarctica* and *N. dombeyi* all derived directly from the most primitive group formed by the *Nothofagus* species with large deciduous leaves (i.e. *N. obliqua*, *N. obliqua* var. *macrocarpa*, *N. leoni* and *N. alessandrii*). Recently, Stecconi et al. (2004) compared *N. antarctica* and *N. dombeyi* with their putative hybrid individuals found in natural stands by using morphological and isoenzymatic traits, and pointed out that *N. antarctica* and *N. dombeyi* are probably more closely related than previously assumed. Thus, the similarity in the monoterpene emission spectrum among the three screened species may mirror this common origin. Because the *Nothofagus* genus (formed by 40 species) has a distributional range that comprises the southern end of South America, Australia, New Zealand, New Caledonia, New Guinea and other small Pacific islands, the monoterpene emission spectrum may be a useful 'tool' to ascertain the phytogeographic origin and the phytogenic evolution of the *Nothofagus* genus.

Guenther et al. (2006) and Geron et al. (2006) have recently produced regional isoprenoid emission inventories, and have shown that species-level isoprenoid emission data are useful for assessing the potential impacts on air quality at regional and global scale. Geron et al. (2006) pointed out that the dramatic landcover changes occurring in South Asia, such as increasing in plantation area established with high isoprene emitting species (e.g. *Bambusa* spp. and *Eucalyptus* spp.), can lead to increases in BVOC emissions in the near future, and this may potentially increase the formation of tropospheric ozone altering the air quality over this rapidly developing region. The *Nothofagus* species dominate the temperate forests present in southern Chile and Argentina, which consist of evergreen, deciduous, needle and broadleaf forests occurring at latitudes south of the 30° S parallel (Veblen et al. 1996). This favors monoterpene emission over isoprene, and

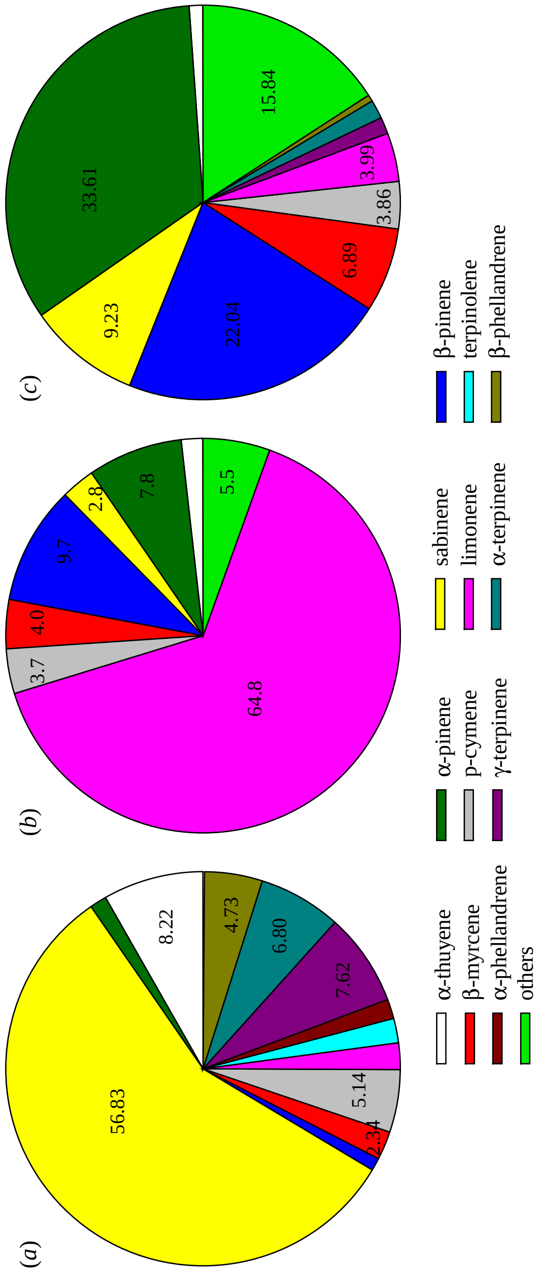

Figure 1. Basal monoterpene emission shown as percentage of total monoterpene emission (*a*) in *Fagus sylvatica* (redrawn from Dindorf et al. 2006), (*b*) in *N. antarctica*, *N. pumilio*, and *N. dombeyi* (combined mean), and (*c*) in *Quercus ilex* (redrawn from Loreto et al. 1996). A colour version of this figure is available online.

may influence the biogenic SOA produced in this region, despite the *Nothofagus* species are low emitters of sabinene (Table 2, Figure 1), which is the compound with higher new particle formation rate compared to other common monoterpenes (Koch et al. 2000). However, rapid industrial development and landcover changes may significantly affect future isoprenoid fluxes in southern Chile and Argentina. Thus, further inventory studies and advanced modeling system are needed to assess BVOC emissions and their impact on air quality and atmospheric chemistry in this region.

In conclusion, the experiments performed in the present study clearly indicate, for the first time to our knowledge, that *Nothofagus spp*. emits large quantities of monoterpenes, with limonene being the predominant compound released. We believe that this finding may be useful for a better parameterization of large scale emission models, because the current predictions on the impact of isoprenoid emissions on air quality at regional and global scale is currently limited by the available global emission inventories which still lack information from a large number of unmeasured species (Grote and Niinemets in press), especially from South American vegetation other than the rainforest ecosystem. Moreover, the three *Nothofagus* species tested had inherently different photosynthetic traits that were related to the characteristic of deciduousness of three species, whereas monoterpene emission rates were surprisingly independent from this character, an observation only rarely replicated worldwide. Finally, the monoterpene emission spectrum is very similar among the three *Nothofagus* species screened. This trait, that may have an important phytogeographic and phytogenic relevance, may spring from the same common origin.

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