Variation in potential for isoprene emissions among Neotropical forest sites

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Abstract

As part of the Large Scale Biosphere–Atmosphere Experiment in Amazônia (LBA), we have developed a bottom-up approach for estimating canopy-scale fluxes of isoprene. Estimating isoprene fluxes for a given forest ecosystem requires knowledge of foliar biomass, segregated by species, and the isoprene emission characteristics of the individual tree species comprising the forest. In this study, approximately 38% of 125 tree species examined at six sites in the Brazilian Amazon emitted isoprene. Given logistical difficulties and extremely high species diversity, it was possible to screen only a small percentage of tree species, and we propose a protocol for estimating the emission capacity of unmeasured taxa using a taxonomic approach, in which we assign to an unmeasured genus a value based on the percentage of genera within its plant family which have been shown to emit isoprene.

Combining this information with data obtained from 14 tree censuses at four Neotropical forest sites, we have estimated the percentage of isoprene-emitting biomass at each site. The relative contribution of each genus of tree is estimated as the basal area of all trees of that genus divided by the total basal area of the plot. Using this technique, the percentage of isoprene-emitting biomass varied from 20% to 42% (mean = 31%; SD = 8%).

Responses of isoprene emission to varying light and temperature, measured on a sun-adapted leaf of mango (Mangifera indica L.), suggest that existing algorithms developed for temperate species are adequate for tropical species as well. Incorporating these algorithms, estimates of isoprene-emitting biomass, isoprene emission capacity, and site foliar biomass into a canopy flux model, canopy-scale fluxes of isoprene were predicted and compared with the above-canopy fluxes measured at two sites. Our bottom-up approach overestimates fluxes by about 50%, but variations in measured fluxes between the two sites are largely explained by observed variation in the amount of isoprene-emitting biomass.

Keywords: atmospheric chemistry, forest inventory, isoprene, Neotropical forests, VOC

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Introduction

Isoprene (C₅H₈) is a reactive hydrocarbon emitted by leaves of many tree species (Kesselmeier & Staudt, 1999), and is the most important volatile organic
compound (VOC) in most rural atmospheres. Guenther et al. (1995) estimated that the terrestrial biosphere is the source of over 90% of all nonmethane hydrocarbons emitted into the global atmosphere, with isoprene alone comprising approximately 44%. It is an extremely reactive gas and plays a dominant role in photochemistry and regulation of the oxidant balance of the troposphere, including ozone production (Poisson et al., 2000; Monson & Holland, 2001). Through its effects on the oxidant balance, it also affects the atmospheric lifetimes of many radiatively active species affecting climate (Collins et al., 2002).

The ability to produce isoprene is widespread in the plant kingdom. Among the angiosperms it is confined largely to woody taxa, and of more than 1500 woody spp., screened for isoprene emission, approximately 30% appear to emit. Isoprene is not stored within the plant and although its function remains open to debate, experiments have clearly demonstrated that high levels of isoprene within leaves confer protection against both high temperatures (Singsaas et al., 1997) and ozone (Loreto & Velikova, 2001). Carbon losses in the form of isoprene are highly temperature dependent, but at temperatures of 30°C, 1–2% of carbon fixed in net photosynthesis is immediately re-emitted in the form of isoprene. In warm environments with a high percentage of isoprene-emitting species, this may represent a significant fraction of the carbon budget (Guenther 2002; Kesselmeier et al., 2002a). Crutzen et al. (1999) suggest that VOC emissions from tropical forests represent approximately 3% of net primary productivity, and argue that ecosystem C budgets should include VOC.

Growing recognition of the importance of biogenic VOC to tropospheric chemistry and the oxidant balance of the atmosphere has stimulated considerable research on VOC emissions from a variety of ecosystem types, with an emphasis on temperate deciduous forests, where the relatively low tree species diversity has allowed researchers to develop detailed species-level biogenic emission databases and regional emission models (Guenther et al., 1996; Geron et al., 1997). By contrast, inaccessibility of many tropical forests, coupled with extremely high species diversity and a general lack of tree canopy access has impeded development of VOC emission databases for tropical species, although some information has been published for Costa Rica (Geron et al., 2002), Panama (Keller & Lerdau, 1999; Lerdau & Throop, 1999), Puerto Rico (Lerdau & Keller, 1997), China (Klinger et al., 2002), and central (Klinger et al., 1998; Guenther et al., 1999) and southern Africa (Guenther et al., 1996; Harley et al., 2003).

Tropical forests comprise roughly 7% of global terrestrial land area, but because of large amounts of biomass, high insolation, warm temperatures, and high rates of biological productivity, tropical forest ecosystems are estimated to emit a disproportionately high 30% of global VOC (Guenther et al., 1995) and represent the single largest source for biogenic exchange of reactive gases with the atmosphere. With high VOC loading, warm temperatures, high radiation and high humidity, the tropics also dominate global photochemistry. Accurate estimates of VOC emissions are critical for improving regional and global models of tropospheric chemistry.

Covering approximately 5.9 × 106 km2, the Amazon Basin contains about one-half of the world’s tropical forest. The role of biogenic trace gas fluxes on tropospheric chemistry in the Amazon basin has been a focus of two major field campaigns, the Atmospheric Boundary Layer Experiment (ABLE) (Jacob & Wofsy 1988; Rasmussen & Khalil 1988; Zimmerman et al., 1988) and the Large Scale Biosphere–Atmosphere Experiment in Amazônia (LBA) (Kesselmeier et al., 2000, 2002b; Andreae et al., 2002), an international effort led by Brazil. Soils and precipitation vary widely across Amazônia and the Amazon Basin comprises a number of distinct phytogeographical regions. The recent World Wildlife Fund/National Geographic classification system describes 12 ecoregions (Olson et al., 2001; http://www.nationalgeographic.com/wildworld/terrestrial.html), each of which contains a variety of ecosystem types, the most prevalent being upland evergreen forest (‘terra firme’) and several forest types which are inundated for a significant fraction of the year. Despite this heterogeneity, current global isoprene emission models distinguish only two forest types, tropical rain forest and tropical seasonal forest (Guenther et al., 1995).

There have been a number of recent estimates of isoprene flux at different sites in Amazônia (Helmig et al., 1998; Stefani et al., 2000; Rinne et al., 2002; Greenberg et al., 2004), with fluxes, determined under high light and warm temperatures, varying from about 2.2 to over 9 mg C m⁻² h⁻¹. These studies suggest that emissions vary by at least a factor of 3 across the Amazon basin.

This paper uses a bottom-up approach to estimate the potential for isoprene emission for different sites within Amazônia, with the goal of better understanding observed differences in above-canopy isoprene fluxes. We have developed a strategy for improving isoprene emission estimates, based on available forest inventories and a growing database of isoprene emission rates from tropical trees.

The Global Biosphere Emissions and Interactions System (GLOBEIS) is a modeling framework established to estimate VOC emissions at the landscape scale.
Isoprene emissions are estimated as follows:

\[
\text{emission rate} \ (\text{mg} \text{C m}^{-2} \text{h}^{-1}) = \varepsilon D \gamma_P \gamma_T.
\]

where \(\varepsilon\) is a landscape average isoprene emission capacity [\(\mu g \text{C g(DW)}^{-1} \text{h}^{-1}\)], \(D\) is foliar density [g(DW) m\(^{-2}\) (ground)], and \(\gamma_P\) and \(\gamma_T\) are emission activity factors which account for both the instantaneous effects on isoprene emissions of photon flux density (PFD) and leaf temperature, respectively, and the effects of acclimation to previous PFD and temperature conditions. \(\varepsilon\) represents the average leaf-level emission capacity of sun-adapted leaves of all species represented in the region of interest, measured at standard conditions of 30°C and PFD of 1000 \(\mu\text{mol m}^{-2} \text{s}^{-1}\). Effects of varying light and temperature are incorporated via \(\gamma_P\) and \(\gamma_T\) using a multilayer canopy model to estimate light and temperature profiles with canopy depth.

Modeling stand or regional-scale isoprene emissions from the bottom up, therefore, requires a minimum of three things: (1) a detailed census of tree foliar biomass, segregated by species, (2) an indication of which species emit isoprene, and at what rates, and (3) an understanding of how isoprene emissions respond to instantaneous changes in light and temperature. Foliar biomass (g m\(^{-2}\) ground) is equivalent to the product of leaf area index (LAI, m\(^2\) leaf m\(^{-2}\) ground) and specific leaf mass (SLM, g m\(^{-2}\) leaf), while characterizing species as either isoprene emitters or nonemitters may be accomplished by a screening survey using one of several approaches. Effects of light and temperature are determined via experiments in which isoprene emission measurements are made as environmental parameters are varied. In this paper, we develop a strategy for estimating isoprene fluxes for high diversity and relatively inaccessible tropical forest sites by employing a limited number of isoprene screening measurements, a technique for estimating emission rates of unmeasured species using taxonomic relationships, and analysis of detailed tree inventories. Using a variety of different techniques, we screened approximately 125 tree species for their ability to emit isoprene during five field campaigns between January 1999 and June 2002. Armed with these data and isoprene emission estimates made on related tree species or genera from elsewhere in the tropics, we made initial estimates of the isoprene emission potential of a variety of forest sites to assess the range of variation in this important variable for estimating regional photochemistry.

## Methods

**Isoprene screening techniques**

Leaf-level emissions of isoprene were measured on 160 plants at six sites during five field campaigns (Table 1), conducted as part of LBA. Isoprene emissions were determined by passing air through an activated charcoal filter to remove hydrocarbons, then through a leaf enclosure at a known flow rate. Samples of air exiting the enclosure were analyzed for isoprene by a variety of techniques. Details of leaf enclosures and analytical systems varied from site to site, as outlined below and in Table 2.

Four different enclosure systems, with varying levels of control over flow rate and leaf environment, were employed. A few qualitative measurements were made using a static enclosure that provided no light or temperature control. Branches were enclosed in a polyethylene bag (0.7 L) for 1 min, after which an air sample was withdrawn for analysis. Additional qualitative screening was accomplished by enclosing approximately 25 cm\(^2\) of leaf material in an in-house produced clear Lucite cuvette for 5 min, then sampling

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**Table 1** Location, brief description and dates of field studies in Brazil at which isoprene screening exercises were carried out

| Site location                     | ID | Latitude/longitude | Ecosystem                        | Dates          | % of screened taxa which emit isoprene |
|-----------------------------------|----|--------------------|----------------------------------|----------------|---------------------------------------|
| Balbina, AM                        | B  | 1°57’S/59°17’W     | Upland terra firme forest         | Feb 1998       | 44% (n = 45)                          |
| ABRACOS site, RO                   | A  | 10°46’S/62°21’W    | Pasture and forest remnants       | Feb 1999       | 50% (n = 10)                          |
| Reserva Biológica do Jaru, RO      | J  | 10°05’S/61°56’W    | Upland terra firme forest         | Feb 1999       | 57% (n = 7)                           |
| Reserva Biológica do Cuieiras,     | M  | 2°35’S/60°07’W     | Upland terra firme forest         | Jan 2000       | 44% (n = 16)                          |
| Manaus, AM                         |    |                    |                                   |                |                                       |
| Floresta Nacional da Caxiuana, PA  | C  | 1°43’S/51°28’W     | Upland terra firme forest         | Jan 2000       | 25% (n = 24)                          |
| Floresta Nacional do Tapajós, PA   | T  | 2°51’S/54°58’W     | Upland terra firme forest         | June 2000,     | 42% (n = 26)                          |

Final column lists the percentage of screened species which emitted isoprene.
Table 2  List of species screened for isoprene emission from six different sites, using a variety of different techniques

| Plant family   | Species               | Site | Isoprene emitter? | Collection technique | Analytical technique | Normalized emission rate (µg C g⁻¹ h⁻¹) |
|---------------|-----------------------|------|-------------------|----------------------|---------------------|--------------------------------------|
| Anacardiaceae | Anacardium occidentalis | B    | A                 | a                    | a                   | –                                    |
|               | Mangifera indica       | A    | Y                 | c                    | b                   | 42                                   |
|               | M. indica              | J    | Y                 | c                    | b                   | 46                                   |
|               | Spondias mombin        | R    | Y                 | b                    | a                   | –                                    |
| Annonaceae    | Annona sp.             | A    | N                 | b                    | a                   | –                                    |
|               | Duquebia sp.           | J    | N                 | b                    | d                   | BDL                                  |
|               | Guatteria sp.          | R    | N                 | b                    | c                   | 0.2                                  |
|               | Guatteria sp.          | T    | N                 | c                    | e                   | BDL                                  |
|               | Rollinia sp.           | C    | N                 | b                    | c                   | 0.1                                  |
| Apocynaceae   | Anartia sp.            | M    | N                 | b                    | c                   | 0.4                                  |
|               | Geissospermum sp.      | R    | N                 | b                    | c                   | BDL                                  |
|               | Lamellia aculeata      | T    | N                 | c                    | d                   | 0.1                                  |
|               | Tabernaemontana sp.    | C    | N                 | b                    | c                   | 0.2                                  |
| Araliaceae    | Schefflera morototoni  | B    | Y                 | a                    | a                   | –                                    |
| Areceae       | Astrocaryum ratanatexis | C    | N                 | b                    | c                   | 0.7                                  |
|               | Astrocaryum sociale    | B    | Y                 | a                    | a                   | –                                    |
|               | Astrocaryum aculeatissimum | A    | Y                | b, c               | a, b               | 36, 53                               |
|               | Astrocaryum sp.        | T    | N                 | c                    | d                   | 0.4                                  |
|               | Attalea phalerata      | A    | Y                 | b, c               | a, b               | 39                                   |
|               | Geonoma sp.            | C    | N                 | b                    | c                   | BDL                                  |
|               | Mauritia sp.           | A    | Y                 | b, c               | a, b               | 69                                   |
|               | Oenocarpus hataua      | B    | Y                 | a                    | a                   | –                                    |
| Asteraceae    | Vernonia sp.           | R    | N                 | b                    | a                   | –                                    |
| Bignoniaceae  | Jacaranda copia        | B    | N                 | a                    | a                   | –                                    |
|               | Tabebuia sp.           | R    | N                 | b                    | a                   | –                                    |
|               | Tabebuia impetiginosa  | T    | N                 | c                    | e                   | BDL                                  |
| Bixaceae      | Bixa orellana          | M    | N                 | b                    | c                   | 0.5                                  |
| Bombacaceae   | Canavillesia arborea   | A    | N                 | b                    | a                   | –                                    |
|               | Scleronema micranthum  | B    | N                 | a                    | a                   | –                                    |
| Boraginaceae  | Cordia sp.             | C    | N                 | b                    | c                   | 0.6                                  |
| Burseraceae   | Protium sp.            | B    | Y                 | a                    | a                   | –                                    |
|               | Protium heterophyllum  | A    | Y                 | b, c               | a, b               | 86, 167                              |
|               | Protium sp.            | T    | Y                 | c                    | e                   | 47                                   |
|               | Protium opacum         | M    | Y                 | b                    | c                   | 33                                   |
|               | Protium polybotrym     | M    | Y                 | b                    | c                   | 45                                   |
|               | Protium suberratum     | C    | N                 | b                    | c                   | 3                                    |
|               | Tetragastris altissima | T    | Y                 | c                    | e                   | 143                                  |
| Caesalpinaceae| Bauhinia sp.           | A    | Y                 | b, c               | a, b               | 139                                  |
|               | Bauhinia sp.           | A    | N/N               | c                    | b                   | 26                                   |
|               | Bauhinia forficata     | J    | Y/N               | b                    | d                   | 18.3                                 |
|               | Cassia sp.             | R    | N                 | b                    | a                   | –                                    |
|               | Copaifera sp.          | J    | Y                 | b                    | d                   | 8                                    |
|               | Copaifera multijuga    | T    | Y                 | c                    | d                   | 32                                   |
|               | Dialium guianense      | B    | N                 | a                    | a                   | –                                    |
|               | D. guianense           | T    | N                 | c                    | d                   | 0.2                                  |
|               | Macrolobium arenarium  | B    | N                 | a                    | a                   | –                                    |
|               | Schizolobium amazonicu | A    | N                 | b                    | a                   | –                                    |
|               | Sclerolobium melanosarpum | T    | N                 | c                    | d                   | 0.2                                  |
| Cecropiaceae  | Cecropia sciadophylla  | B    | N                 | a                    | a                   | –                                    |
|               | Cecropia sp.           | A    | N                 | b                    | a                   | –                                    |
|               | Cecropia sp.           | T    | N                 | c                    | e                   | BDL, 0.5                             |
|               | Tachigali sp.          | R    | N                 | b                    | c                   | 0.3                                  |
| Celastraceae  | Goupia sp.             | C    | N                 | b                    | c                   | BDL                                  |
| Chrysobalanaceae | Licania sp.          | C    | N                 | b                    | c                   | 0.1                                  |
| Clusiaceae    | Clusia sp.             | B    | Y                 | a                    | a                   | –                                    |
|               | Vismia guianensis      | B    | Y                 | a                    | a                   | –                                    |

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| Plant family | Species | Site | Isoprene emitter? | Collection technique | Analytical technique | Normalized emission rate (µg C g⁻¹ h⁻¹) |
|--------------|---------|------|-------------------|----------------------|---------------------|-----------------------------------------|
|              | V. guianensis | T Y c d | 48                |                      |                     |                                         |
|              | Visnia japurensis | B Y a | –                 |                      |                     |                                         |
|              | Visnia sp. | C B Y N b a | – |                      |                     |                                         |
| Combretaceae | Rourea sp. | C Y b c | 12                |                      |                     |                                         |
|              | Datoila rugosa | R Y b | –                 |                      |                     |                                         |
|              | Croton lanjouensis | B N a | –                 |                      |                     |                                         |
|              | Croton matsuorensis | M N b c | 0.2               |                      |                     |                                         |
|              | Hevea guianensis | B N a | –                 |                      |                     |                                         |
|              | Mabea sp. | B Y a | –                 |                      |                     |                                         |
| Flacourtia | Casearia decandra | T Y c d | 16               |                      |                     |                                         |
|              | Casearia rubiana | M Y b c | 84               |                      |                     |                                         |
| Humiriaceae | Humiria sp. | B Y a | –                 |                      |                     |                                         |
|              | Endopleura uchi | T Y b c | 57               |                      |                     |                                         |
| Icacinaceae | Emmnotum nitens | B N a | –                 |                      |                     |                                         |
| Lauraceae   | Aniba canelilla | B N a | –                 |                      |                     |                                         |
|              | Ocotea rubra | T N c e | BDL       |                      |                     |                                         |
|              | Ocotea sp. | B N a | –                 |                      |                     |                                         |
|              | Ocotea sp. | J N b d | 0.3               |                      |                     |                                         |
| Lecythidaceae | Couratari stellata | M N b c | 0.3               |                      |                     |                                         |
|              | Eschweilera sp. | B Y a | –                 |                      |                     |                                         |
|              | Eschweilera sp. | J Y b d | 82               |                      |                     |                                         |
|              | Eschweilera odorata | T Y c e | 57               |                      |                     |                                         |
|              | Lecythis idatimon | C N b c | 0.8               |                      |                     |                                         |
|              | Lecythis lurida | T N c e | BDL       |                      |                     |                                         |
| Linaceae    | Hebepetalum sp. | C N b c | BDL       |                      |                     |                                         |
| Loganiaceae | Strychnos sp. | C N b c | 0.8               |                      |                     |                                         |
| Malpighiaceae | Byrsonima duckeana | M Y b c | 56               |                      |                     |                                         |
|              | Byrsonima crispa | B Y a | –                 |                      |                     |                                         |
| Malvaceae   | Ureni sp. | A N b a | –                 |                      |                     |                                         |
| Melastomataceae | Bellucia grossularioides | B N a | –                 |                      |                     |                                         |
|              | B. grossularioides | M N b c | 0.5               |                      |                     |                                         |
|              | Bellucia sp. | C N b c | BDL       |                      |                     |                                         |
|              | Miconia pyrifolia | M N b c | 0.1               |                      |                     |                                         |
|              | Miconia sp. | T N b c | 0.2               |                      |                     |                                         |
| Meliaceae   | Carapa guianensis | B N a | –                 |                      |                     |                                         |
|              | Guarea grandifolia | M N b c | 0.3               |                      |                     |                                         |
|              | Guarea sp. | B N a | –                 |                      |                     |                                         |
| Mimosaceae  | Inga capitata | C Y b c | 67               |                      |                     |                                         |
|              | Inga cayenensis | M Y b c | 195              |                      |                     |                                         |
|              | Inga heterophylla | B Y a | –                 |                      |                     |                                         |
|              | Inga sp. | B N/Y a | –                 |                      |                     |                                         |
|              | Inga sp. | C Y b c | 24               |                      |                     |                                         |
|              | Inga sp. | M Y b c | 57               |                      |                     |                                         |
|              | Inga sp. | R Y b c | 6                |                      |                     |                                         |
|              | Marmaroxylon racemosum | C N b c | 0.6               |                      |                     |                                         |
|              | Parkia sp. | B N a | –                 |                      |                     |                                         |
|              | Stryphnodendron sp. | A N b a | –                 |                      |                     |                                         |
| Monimiaceae | Siparuna amazonica | B N a | –                 |                      |                     |                                         |
| Moraceae    | Bagassa guianensis | A N b a | 0.6               |                      |                     |                                         |
|              | Brosimum sp. | C N b c | 0.3               |                      |                     |                                         |
|              | Ficus sp. | B Y a | –                 |                      |                     |                                         |
|              | Ficus sp. | A Y b c a, b | 89, 111 |                      |                     |                                         |

(continued)
| Plant family | Species | Site | Isoprene emitter? | Collection technique | Analytical technique | Normalized emission rate (μg C g⁻¹ h⁻¹) |
|--------------|---------|------|-------------------|----------------------|----------------------|------------------------------------------|
| Myristicaceae | Virola pavonis | B     | N                 | a                    | a                    | –                                        |
| Myrtaceae    | Eugenia sp.   | B     | N                 | a                    | a                    | –                                        |
|              | Myrcia sp.    | B     | Y                 | a                    | a                    | –                                        |
|              | Psidium sp.   | J     | N                 | b                    | d                    | 0.5                                      |
|              | Psidium sp.   | A     | Y                 | b, c                 | a, b                 | 38                                       |
|              | Syzygium jambosana | A   | Y                | b, c                 | a, b                 | 55                                       |
| Ochnaceae    | Ouratea sp.   | B     | Y                 | a                    | –                    | –                                        |
| Papilionaceae| Alexia sp.    | B     | Y                 | a                    | –                    | –                                        |
|              | Amburana sp.  | A     | Y                 | b, c                 | a, b                 | 70, 113                                  |
|              | Cithoraria racemosa | R   | Y                | a                    | –                    | –                                        |
|              | Dypteryx sp.  | B     | Y                 | a                    | –                    | –                                        |
|              | Machaerium sp. | M    | N                 | b                    | c                    | 1.1                                      |
|              | Poecilanthus effusa | C   | Y                | b                    | c                    | 0.5                                      |
|              | P. effusa     | T     | N                 | c                    | d                    | 0.3                                      |
|              | Saurea sp.    | C     | Y                 | b                    | c                    | 34                                       |
|              | Saurea sp.    | R     | Y                 | b                    | a, d                 | 51                                       |
| Passifloraceae| Passiflora coccinea | M  | N                 | b                    | c                    | BDL                                      |
| Phytolaccaceae| Gallesia integrifolia | A | N                | a                    | –                    | –                                        |
| Piperaceae   | Piper hostmandianum | M   | N                 | b                    | c                    | 0.5                                      |
| Rhamnaceae   | Ampelozizyphus amazonicus | B  | N                 | a                    | a                    | –                                        |
| Rubiaceae    | Chinarrhis turbinata | T  | N                 | c                    | d                    | BDL                                      |
|              | Paguna duckei | B     | N                 | a                    | a                    | –                                        |
|              | Paguna sp.    | B     | N                 | a                    | a                    | –                                        |
|              | Pulicaria sp. | C     | N                 | b                    | c                    | 0.7                                      |
|              | Psychotria sp. | A     | N                 | b                    | a                    | –                                        |
|              | Uncaria       | R     | N                 | b                    | c                    | BDL                                      |
| Rutaceae     | Citrus sp.    | R     | N                 | b                    | c                    | 0.3                                      |
| Sapindaceae  | Pseudinum sp. | R     | Y                 | b                    | c                    | 16                                       |
|              | Talisia retusa | T    | N                 | c                    | d                    | 0.2                                      |
| Sapotaceae   | Manilkara amazonica | B  | N                 | a                    | a                    | –                                        |
|              | Pouteria sp.  | B     | N                 | a                    | a                    | –                                        |
|              | Pouteria sp.  | C     | N                 | b                    | c                    | BDL                                      |
|              | Pouteria sp.  | T     | N                 | c                    | e                    | 0.3                                      |
| Simarouboaceae| Simarouba arnara | T  | N                 | c                    | e                    | BDL                                      |
| Siparunaceae | Siparuna amazonica | B  | N                 | a                    | a                    | –                                        |
| Solanaceae   | Solanum paniculatum | R  | N                 | c                    | a                    | –                                        |
| Sterculiaceae| Theobroma cacao | A    | N                 | b                    | a                    | –                                        |
|              | Theobroma grandiflorum | M  | Y                | b                    | c                    | 7                                        |
|              | T. grandiflorum | T   | Y                | c                    | d                    | 16                                       |
| Tiliaceae    | Acetospora    | C     | N                 | b                    | c                    | 0.2                                      |
|              | Ulmaceae      | B     | N                 | a                    | a                    | –                                        |
| Verbenaceae  | Aegiphila filipes | R  | N                | b                    | a, d                 | BDL                                      |
| Violaceae    | Rinorea sp.   | C     | N                 | b                    | c                    | 0.1                                      |
|              | Rinorea guianensis | T   | N                | c                    | e                    | BDL                                      |
| Vochysiaceae | Erismia uncinata | C   | N                | b                    | c                    | BDL                                      |

Sites: A, Abracos site; B, Balbina; C, FLONA Caxiuana; J, Reserva Biológica do Jaru; M, Manaus; T, FLONA Tapajós.
Collection: *Static branch enclosure; †Dynamic, uncontrolled leaf enclosure; ‡Dynamic, controlled leaf enclosure.
Analysis: *Photoionization detector in situ; †reduction gas detector in situ; ‡cartridge + gas chromatography with flame ionization detector (GC-FID); •cartridge + gas chromatography with mass spectrometry; ‣in situ GC-FID (SRI).
Enclosure techniques and analytical techniques are indicated for each measurement. All species are designated as either emitters or nonemitters of isoprene; when obtained, a quantitative measurement of isoprene emission (μg C g⁻¹ h⁻¹) is also provided, normalized to photon flux density of 1000 μmol m⁻² s⁻¹ and leaf temperature of 30 °C. BDL = below detection limit.
enclosure air using a hand-held photoionization detector (PID) (see below) with an internal pump. Measurements were made in both full sunlight and darkness to distinguish light-dependent emissions, assumed to be isoprene, from emissions independent of light (e.g. most monoterpnes or compounds released in response to wounding) (Klinger et al., 1998). Although this protocol would fail to distinguish between isoprene and light-dependent monoterpene emissions, only one Amazonian tree has been identified as a light-dependent monoterpene emitter (Kuhn et al., 2002). Quantitative screening measurements were made using an enclosure system constructed of Delrin (Dupont, Wilmington, DE, USA), and a glass top, measuring 12 by 9 by 3 cm. Airflow was supplied by a small, variable speed pump and flow rate through the enclosure was measured (AWM3000 Microbridge Mass Airflow Sensor, Honeywell, Freeport, IL, USA). PFD and leaf temperature were not controlled, but were measured and recorded. Additional quantitative measurements were made using an LI-6400 photosynthesis system (Li-Cor, Lincoln, NE, USA), utilizing the standard leaf cuvette enclosing 6 cm$^2$ of leaf area, with illumination controlled by an array of red light-emitting diodes (LEDs) (670 nm). Leaf temperature was controlled using thermoelectric cooling elements. Incident PFD during measurements was maintained at 1000 μmol m$^{-2}$ s$^{-1}$ and leaf temperature was kept as close as possible to 30°C.

Samples of air exiting the enclosure systems were analyzed immediately in the field or collected onto adsorbent cartridges for subsequent analysis in the laboratory. For initial screening of VOC emissions, a hand-held PID (Thermo Environmental Instruments, Inc., Woburn, MA, USA, Model 580B) was used, following the procedure of Klinger et al. (1998). In most cases, VOC emission inferred by PID screening was confirmed using other techniques. Branches sampled using the PID were cut under water to maintain physiological activity and leaves inserted into a leaf cuvette for reanalysis. Air samples were withdrawn through a 2 mL sample loop using a 20 mL syringe and injected directly onto a chromatographic column; isoprene was quantified using a reduction gas detector (RGD2, Trace Analytical, Menlo Park, CA, USA) (details in Greenberg et al., 1993). For cartridge sampling, 500 mL samples of enclosure air were pulled through multistage adsorbent cartridges (Supelco, 350 mg Carbopak C18, 150 mg Carbosieve SIII, 70 mg glass beads) using a 500 mL syringe.

Cartridges were analyzed at National Center for Atmospheric Research (NCAR) (Boulder, CO, USA) using gas chromatography with flame ionization detector (GC-FID) (Model HP 5890 Series II gas chromatograph) and a DB-1 fused silica capillary column. The instrument was calibrated daily against a 201 ppbv NIST neohexane standard. Additional cartridge samples were analyzed at NCAR using gas chromatography (Model HP 5890 Series II) equipped with a mass selective detector (HP 5972). An analytical column identical to that described above was used, and measurements were made in selected ion mode. Isoprene was quantified by comparison with a laboratory-prepared isoprene standard. Analytical details are described elsewhere (Greenberg et al., 1999).

In some cases, samples of air exiting the LI-6400 leaf cuvette were collected into 3 L Teflon bags (5-mil, SKC Inc., Eighty Four, PA, USA) and analyzed within 30 min of collection using a commercially available GC-FID (Model 310, SRI Instruments, Inc., Las Vegas, NV, USA) equipped with a home-made inlet preconcentration system.

After sampling, leaves were dried for 24 h at 70°C and weighed, and isoprene emission rates were expressed as μg C g$^{-1}$ h$^{-1}$.

Light and temperature response curves

In order to establish light and temperature dependencies of isoprene, emission data were collected from a sun-adapted leaf of mango (Mangifera indica L.) on a large tree at Reserva Biológica do Jaru, Rondônia (although not native to the New World, mango is the most commonly planted street tree throughout Amazonia). Leaf gas exchange measurements were made using the LI-6400 photosynthesis system. A T-fitting was placed in the line exiting the cuvette and samples were withdrawn using a 20 mL glass syringe. Isoprene was quantified using the gas chromatograph with reduction gas detector discussed above. Calibrations were performed throughout the day, using a 41 ppbv isoprene standard prepared at NCAR. On the day following the establishment of light and temperature dependencies of isoprene emission, the LED light source was replaced with a transparent cuvette lid, and measurements of leaf gas exchange and cuvette environment were logged continuously at 1 min intervals. Air samples were withdrawn for isoprene analysis as frequently as possible (approximately every 5 min). Leaf gas exchange measurements were made continuously for a 24 h period; isoprene data were collected only during daylight hours.

Results

Isoprene screening

Results from isoprene screening exercises conducted during five field campaigns are shown in Table 2.
Species that yielded a large hydrocarbon response in the light using the PID instrument, but a much reduced response in the dark, are shown simply as isoprene emitters. Quantitative data are given for those measurements in which air flowed through the cuvette at a known rate and for which isoprene was determined using gas chromatography. Quantitative results were obtained over a range of PFD values (all above 500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) and leaf temperatures (28–36 °C). Values in Table 2 were corrected to standard conditions (PFD of 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 30 °C) using light and temperature algorithms for isoprene emission developed by Guenther et al. (1993). Species that emitted isoprene at rates greater than 5 \( \mu \text{g C g}^{-1} \text{h}^{-1} \) were considered to be confirmed isoprene emitters. Of 125 species examined, 47 were found to emit isoprene (37 of 108 genera); in six cases, multiple measurements gave ambiguous results within a single genus or species. Emission rates of isoprene-producing species (corrected to standard conditions) varied widely, from 6 to over 190 \( \mu \text{g C g}^{-1} \text{h}^{-1} \) (mean = 51; SD = 39). Possible reasons for this large amount of variation are discussed below.

**Light and temperature responses**

The responses of isoprene emission to varying light and temperature for a leaf of mango are shown in Fig. 1. During measurement of the PFD response, leaf temperature varied from 29.6 to 32.2 °C. Data shown (Fig. 1a) are corrected to 30 °C using the temperature algorithm obtained from the data in Fig. 1b. On this sun-exposed leaf, the light response of isoprene failed to reach light saturation at PFD greater than 1500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \); emissions increased by about 15% as light was raised from 1000 to 1500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). The light response was modeled using the light algorithm of Guenther et al. (1999),

\[
\text{emission rate} = \varepsilon_0 \frac{aC_L \text{PFD}}{\sqrt{1 + x^2 \text{PFD}^2}},
\]

(2)

where \( \varepsilon_0 \) is the emission rate under standard conditions of 30 °C and PFD equal to 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), and \( a \) and \( C_L \) are empirical coefficients. The fit to the data is shown in Fig. 1a as the solid line, using best-fit parameters shown, obtained using a nonlinear least-squares regression routine (KaleidaGraph, Synergy Software). For comparison, predictions of three other models are shown (normalized to an emission of 66.5 \( \mu \text{g C g}^{-1} \text{h}^{-1} \) at PFD of 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)):

- the original light algorithm of Guenther et al. (1993)
- the modified algorithm of Guenther et al. (1999), parameterized for leaves near the top of the canopy (LAI = 0.5); and
- the light function proposed by Keller & Lerdau (1999) for tropical tree species in Panama.

The temperature response of isoprene emission (PFD constant at 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) is shown in Fig. 1b. Rates of isoprene emission increase exponentially up to about 35 °C (Q10 between 25 °C and 35 °C of 4.3) and the temperature optimum appears to be at or above 40 °C (although at temperatures above about 38 °C, the system becomes unstable and emission rates decline over time). The response of isoprene emission to leaf temperature was modeled using the temperature algorithm of Guenther et al. (1999),

\[
\text{emission rate} = \frac{E_{\text{opt}}C_{T2} \exp(C_{T1}x)}{C_{T2} - C_{T1}(1 - \exp(C_{T2}x))},
\]

(3)
where

\[ x = \frac{(1/T_{opt}) - (1/T_L)}{R} \]

and \( T_L \) is leaf temperature (K), \( R \) is the gas constant \((0.008314 \text{ kJ K}^{-1} \text{ mol}^{-1})\), \( T_{opt} \) is the temperature optimum (K), \( E_{opt} \) is the emission rate \((\mu\text{g C g}^{-1} \text{ h}^{-1})\) at \( T_{opt} \) and \( C_{T1} \) and \( C_{T2} \) are empirical coefficients representing the energies of activation and deactivation, respectively \((\text{kJ mol}^{-1})\). Parameters were again obtained using nonlinear least-squares regression. The resulting fit to the data (solid line) and parameter values are shown in Fig. 1b. Again, results of the three other models are shown for comparison.

After PFD and temperature responses of isoprene emission were determined, the opaque cuvette lid was replaced with clear plastic and the leaf reinserted. Gas-exchange parameters and environmental variables were logged automatically at 1 min intervals over a 24 h period, while isoprene measurements were made as rapidly as possible during daylight hours only (Fig. 2). Using measured values of PFD and leaf temperature (Fig. 2a), isoprene emission rates were predicted (Fig. 2b, solid line) using the light and temperature functions shown in Fig. 1.

If one integrates the area under the isoprene emission data in Fig. 2b, and compares the total amount of carbon lost with the integrated \( \text{CO}_2 \) uptake (data not shown), the calculated loss of carbon in the form of isoprene between 07:00 and 19:00 hours was approximately 3.3% of that fixed. Because the leaf continued to respire carbon through the night, the calculated percentage of daily (24 h) net \( \text{C} \) uptake that was lost as isoprene was approximately 4.4%.

**Discussion**

Emissions of isoprene from different species vary over several orders of magnitude (Harley et al., 1999; Kesselmeier & Staudt, 1999). All leaves produce the isoprene precursor, dimethylallyl pyrophosphate, in the light, and it is likely that leaves of most or all tree species can produce very small amounts of isoprene (i.e. less than \( 1\mu\text{g C g}^{-1} \text{ h}^{-1} \)). A significant fraction of tree species, however, is capable of producing much larger amounts of isoprene (up to \( 200\mu\text{g C g}^{-1} \text{ h}^{-1} \) at \( 30^\circ \text{C} \) under high light) in a reaction catalyzed by isoprene synthase (Silver & Fall, 1991). These enzyme-catalyzed rates vary widely between and within species, depending on light and temperature during measurement, leaf age, canopy position, etc. (Harley et al., 1997, 1999; Kesselmeier & Staudt, 1999), and light and temperature conditions experienced by the leaves in the days prior to measurement (Sharkey et al., 1999; Petron et al., 2001).

**Assigning isoprene emission probabilities to screened and unscreened taxa**

Of the 125 species screened during this study, 47 were identified as emitters of isoprene (Table 2), with isoprene emission capacities ranging from 6 to nearly \( 200\mu\text{g C g}^{-1} \text{ h}^{-1} \). However, using these data to assign species-specific isoprene emission capacities is problematic. In some cases, trees were characterized as emitters or nonemitters without a quantitative determination, and even quantitative results were, in many cases, based on a single measurement. Although isoprene emission capacity is generally defined on the basis of sun-adapted leaves, measurements were frequently made on leaves growing in relatively low-light environments near the ground, where emission capacity is likely depressed (Geron et al., 2002). This accounts for at least some of the wide variation in values reported in Table 2. We chose, therefore, not to assign specific emission capacities to individual tree species. Initially, we simply segregate species into isoprene-emitting or nonemitting categories. We then estimate the percent of isoprene-emitting biomass for a
given site. Below we attempt to use these data to predict isoprene fluxes for specific sites, at which point an average isoprene emission capacity (μg C g⁻¹ h⁻¹) must be assigned.

Initially, tree species for which unambiguous data exist are assigned either a zero or 100% probability of emitting isoprene. These assignments are based on our data (Table 2) combined with the much more extensive community database (Wiedinmyer et al., 2004) established as part of Global Emissions Inventory Activity of the International Global Atmospheric Chemistry Project (IGAC-GEIA). This database currently contains information on over 1500 taxa, and is accessible online [http://bvoc.acd.ucar.edu; researchers are strongly encouraged to submit VOC emission data for incorporation into this database.] In those cases where emission data are ambiguous, a probability is assigned reflecting that uncertainty (i.e. if two of three studies indicate that a species emits isoprene, it is assigned a 0.67 probability of emitting isoprene).

In the tree censuses discussed below, over 450 genera in 75 plant families were encountered. In the course of our screening exercise, we characterized a total of only 108 genera in 55 plant families. Clearly, a protocol is required for predicting the probability that unsampled taxa emit isoprene. In common with other efforts (Benjamin et al., 1996; Karlik & Winer, 2001) we have chosen to take a taxonomic approach, in which the likelihood of emission from an unsampled species is based on the characteristics of the most closely related taxa for which information is available (Fig. 3).

If members of a given genus have been shown to emit isoprene, other unmeasured species in the same genus are assumed to emit. Lacking information for a genus, it is assigned a probability proportional to the percentage of emitting genera in the plant family. To facilitate this procedure, we compiled data on isoprene emission characteristics of all the plant families encountered in the study. The percentage of isoprene-emitting genera in 32 important woody Neotropical plant families is given in Table 3. In the course of this study, it became

![Logic tree for assigning isoprene emission probabilities to taxa for which no data exist.](image)

**Table 3** Number of genera in important tropical tree families which have been screened for isoprene emission and the percentage shown to emit

| Plant family       | # genera sampled | % of genera emitting isoprene | Plant family       | # genera sampled | % of genera emitting isoprene |
|--------------------|------------------|-------------------------------|--------------------|------------------|-------------------------------|
| Anacardiaceae      | 15               | 27                            | Lauraceae          | 12               | 13                            |
| Annonaceae         | 14               | 7                             | Lecythidaceae      | 5                | 20                            |
| Apocynaceae        | 19               | 8                             | Melastomataceae    | 2                | 0                             |
| Arecaaceae         | 36               | 74                            | Meliaceae          | 10               | 0                             |
| Bignoniaceae       | 17               | 0                             | Mimosaceae         | 20               | 23                            |
| Bombacaceae        | 8                | 13                            | Moraceae           | 20               | 38                            |
| Boraginaceae       | 4                | 0                             | Myristicaceae      | 7                | 21                            |
| Burseraceae        | 7                | 71                            | Myrtaceae          | 20               | 83                            |
| Caesalpinaceae     | 40               | 33                            | Rubiaceae          | 26               | 2                             |
| (Caesalpineae)     | (12)             | (8)                           | Rutaceae           | 7                | 21                            |
| (Detarieae)        | (21)             | (52)                          | Sapindaceae        | 17               | 15                            |
| Celastraceae       | 4                | 0                             | Sapotaceae         | 7                | 0                             |
| Chrysobalanaceae   | 2                | 25                            | Sterculiaceae      | 11               | 5                             |
| Clusiaceae         | 9                | 94                            | Tiliaceae          | 8                | 25                            |
| Combretaceae       | 6                | 0                             | Ulmaceae           | 4                | 0                             |
| Euphorbiaceae      | 34               | 32                            | Vochysiaceae       | 2                | 0                             |
| Flacourtiaecae     | 9                | 67                            |                     |                  |                               |

*Only woody genera of the Papilionaceae are included.

Two important subfamilies of the Caesalpinaceae are included. Information was compiled using the data found in Table 2, in conjunction with data included in a community VOC emissions database (Wiedinmyer et al., 2004; http://bvoc.acd.ucar.edu).
apparent that additional information could also be found at the subfamily level. In the important legume family Caesalpinaceae for example, 33% of the 40 genera investigated have been shown to emit isoprene. Breaking the family down into its generally recognized subfamilies, however, provided greater resolution. An unknown tree in subfamily Caesalpinieae (8% emitters; Table 3) is less likely to emit isoprene than a tree in Detarieae (52% emitters). Given the preponderance of trees in subfamily Caesalpinieae in the tree censuses, this distinction results in a significantly lower estimate of isoprene-emitting biomass than would have been the case had all members of the Caesalpinaceae been treated identically. Thus, for each of the three families of legumes, emission probabilities were assigned to unmeasured taxa on the basis of their subfamilial classification. As mentioned above, all species in a given genus were assumed to be either emitters or nonemitters. This is not always a valid assumption, and it may be possible to extend this analysis to the subgeneric level, as has been done in the large genera Quercus (Loreto et al., 1998) and Acacia (Harley et al., 2003). In summary, based on Table 3, an unmeasured genus in the family Anacardiaceae is assigned an isoprene emission probability of 27%, while an unsampled member of Caesalpinaceae, subfamily Detarieae, is assigned a value of 52%.

Responses of isoprene emission to PFD and temperature in tropical trees

Most models of isoprene emissions, at all scales, use algorithms developed by Guenther et al. (1993, 1999) to describe effects of light and temperature. These were parameterized using data from temperate tree species, and it has been suggested (Lerdau & Keller, 1997; Lerdau & Throop, 1999) that these parameterizations fail to capture the behavior of tropical trees. In particular, they suggest that, in contrast to the Guenther algorithm, isoprene emission in upper canopy tropical leaves fails to show light saturation at values of PFD below 2000 μmol m⁻² s⁻¹. This observation is supported by data of Kuhn et al. (2002) who failed to observe light saturation in Hymenaea courbaril at PFD up to 1000, and by our data on mango (Fig. 1). Kuhn et al. (2002) nevertheless obtained good agreement between their measured isoprene fluxes and a model based on the Guenther algorithms. Consistent with the observations of Lerdau & Keller (1997), failure of isoprene emission to saturate at high light has been observed for upper canopy leaves of temperate species (Harley et al., 1997) and it now appears that whether or not a leaf reaches light saturation depends on the light environment to which it is adapted and is not a distinction between tropical and temperate species; sun leaves often fail to show light saturation whereas shade leaves generally saturate below 1000 μmol m⁻² s⁻¹.

It has also been demonstrated that the shape of the isoprene temperature response, including the temperature optimum, changes with growth temperature (Petron et al., 2001), but the temperature optimum shown for leaves of mango (40 °C) agrees well with that reported by Lerdau & Keller (1997). Modifications to the Guenther algorithm (Guenther et al., 1999) capture well the range of variation in light responses and incorporate the effects of light and temperature growth environment by varying algorithm parameters as a function of depth in the canopy and average temperatures over the preceding 15 days. The parameters obtained for the best fit to the data in Fig. 1 correspond to an LAI of 0.5 (leaves at the top of the canopy) and average temperature of 30 °C. The fits in Fig. 1 indicate that our attempts to model isoprene emission using the Guenther et al. (1999) algorithms were successful, and Fig. 2 indicates that these light and temperature algorithms are capable of providing excellent fits to emission data collected over a wide range of ambient PFD and temperature. The four models shown in Fig. 1b agree closely at temperatures below about 35 °C, and the algorithms of Guenther et al. (1999) were used in the canopy-scale simulations performed below.

Assessing variation in isoprene emission capacity at the landscape scale

Having established light and temperature dependencies of isoprene emission and developed a protocol for assigning isoprene emission probabilities to all species encountered, we sought to estimate the percentage of isoprene-emitting biomass for several Neotropical sites to better understand observed regional differences in landscape-scale isoprene emissions. We took advantage of a number of tree census activities which have been carried out in Amazônia, some in conjunction with LBA (Keller et al., 2001; Nepstad et al., 2002; Rice et al., 2004) and some through the Red Amazônica de Inventários Forestais/Rede Amazônica de Inventários Florestais (RAINFOR) project (Malhi et al., 2002), an international network to monitor forest dynamics across Amazônia. Although we are aware of over 60 suitable tree censuses within Amazônia, we have chosen to focus initially on 14 surveys conducted at four sites to assess the utility of our approach, and have included those few sites for which above-canopy isoprene flux data exists – either measurements using tower-based micrometeorological flux techniques, or estimates based on isoprene profiles measured through the mixed layer of the atmosphere. These sites are listed in Table 5. At each site at least 1 ha
of forest was sampled and all trees over 10 cm diameter at breast height (dbh; typically 1.3 m) were identified (to at least plant family, usually genus, and often species) and their dbh measured. (The two surveys conducted at the Ducke Reserve near Manaus currently report only colloquial names; we have attempted to assign them to the correct genus or family (Ribeiro et al., 1999) but considerable uncertainty in identification remains). The contribution of a given tree to canopy-scale processes such as isoprene emission is best estimated by the amount of illuminated foliage or by crown volume, but this information is rarely available at the stand scale. Tree basal area is here assumed to be proportional to amount of illuminated foliage or by crown volume, but such as isoprene emission is best estimated by the contribution of a given tree to canopy-scale processes (Ribeiro et al., 1999) but considerable uncertainty in identification remains. The protocol outlined above, the percentage of isoprene-emitting biomass while 5.8% of total plot biomass is comprised of isoprene emitters in Burseraceae, 6.1% in Lecythidaceae and 10.5% in Papilionaceae. Across the sites investigated here, even for sites with similar amounts of isoprene-emitting biomass, the tree families comprising that biomass may be very different. For instance, contrasting the easternmost censuses at Caxianã with those at the westernmost site, Jatun Sacha in Ecuador, significant differences are apparent. At Caxianã, the palms (Areaceae) and Myristicaceae contribute very little isoprene-emitting biomass while 5.8% of total plot biomass is comprised of isoprene emitters in Burseraceae, 6.1% in Lecythidaceae and 10.5% in Papilionaceae. Averaged over four censuses at Jatun Sacha, 4.1% of total biomass is comprised of emitting palms, and 6.3% by Myristicaceae, while Burseraceae, Lecythidaceae and Papilionaceae contribute only 2.5%, 0.5% and 0.7%, respectively.

Bottom-up modeling of canopy-scale isoprene fluxes

In order to estimate canopy-scale isoprene fluxes for different sites, site-specific estimates of the percentage of isoprene-emitting biomass are necessary but far from sufficient. Only when that information is incorporated into a model of canopy-scale emissions, which includes estimates of stand foliar biomass, the average emission capacity of isoprene-emitting leaves, and the effects of varying PFD and leaf temperature with canopy depth, can comparisons be made with above-canopy flux estimates. Foliar biomass can be estimated as LAI (m² m⁻²) multiplied by the average SLM (g m⁻²) for a given site. Estimates of LAI in FLONA Tapajós range from about 5 to 7 m² m⁻², averaging about 6.5 (Nepstad et al., 2002) and a value of 5.7 m² m⁻² has been reported for the Ducke Reserve (McWilliam et al., 1993). We have adopted a reasonable LAI value of 6.0 m² m⁻² for both sites. Surprisingly, estimates of SLM from Amazonian
Table 4: Results of a hypothetical tree survey, depicting the protocol for estimating the percentage of isoprene-emitting biomass at a given site

| Col. #1 | Col. #2 | Col. #3 | Col. #4 | Col. #5 | Col. #6 | Col. #7 | Col. #8 | Col. #9 | Col. #10 |
|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| Plant family | Plant subfamily | Plant species | dbh (m) | $\pi(dbh/2)^2$ | % of genera in family (subfamily) which emit isoprene | Probability that genus emits isoprene | % of total basal area | (basal area/total) × 100 | Col. #8 × Col. #9 |
| Apocynaceae | | Aspidosperma vargasii | 0.134 | 0.0141 | N | 8 | 0 | 3.1 | 0 |
| Apocynaceae | | Himatanthus succuba | 0.262 | 0.0539 | U | 8 | 0.08 | 12.0 | 1.0 |
| Burseraceae | | Protium fimbratum | 0.148 | 0.0172 | Y | 71 | 1.0 | 3.8 | 3.8 |
| Burseraceae | | P. fimbratum | 0.266 | 0.0556 | Y | 71 | 1.0 | 12.4 | 12.4 |
| Burseraceae | | Protium nodulosum | 0.212 | 0.0353 | Y | 71 | 1.0 | 7.9 | 7.9 |
| Caesalpinaceae | | Apuleia molaris | 0.159 | 0.0199 | N | 8 | 0 | 4.4 | 0 |
| Caesalpinaceae | | Caesalpinieae | | | | | | | |
| Caesalpinaceae | | Apuleia sp. | 0.113 | 0.0100 | N | 8 | 0 | 2.2 | 0 |
| Caesalpinaceae | | Detarieae | Brownia grandiceps | 0.127 | 0.0127 | U | 52 | 0.52 | 2.8 | 1.4 |
| Caesalpinaceae | | Detarieae | Hymenaea oblongifolia | 0.113 | 0.0100 | Y | 52 | 1.0 | 2.2 | 2.2 |
| Cecropiaceae | | Cercropia scidaphylla | 0.202 | 0.0320 | N | 0 | 0 | 7.1 | 0 |
| Cecropiaceae | | C. scidaphylla | 0.385 | 0.1164 | N | 0 | 0 | 25.9 | 0 |
| Cecropiaceae | | Pourouma bicolor | 0.302 | 0.0716 | N | 0 | 0 | 16.0 | 0 |
| Totals | | | 0.4488 | | | | | | 100.0 |

% of total basal area

Genera screened for isoprene emission are assigned a 0% or 100% probability of emitting isoprene; unscreened genera are assigned a probability equal to the percent of emitting genera in their plant family or subfamily.

$^	ext{r}$2004 Blackwell Publishing Ltd, Global Change Biology 10, 630–650
Table 5  Estimates of the percentage of isoprene-emitting biomass for sites within Amazônia

| Site ID# | Site                        | Location         | Ecosystem                     | Basal area \( (m^2 \text{ ha}^{-1}) \) | Percent biomass emitting isoprene | Midday isoprene flux estimate | % Biomass from unscreened taxa |
|---------|-----------------------------|------------------|-------------------------------|---------------------------------------|----------------------------------|-------------------------------|-------------------------------|
| C1      | FLONA Caxiuaná, PA, Brazil  | 01°43'S, 51°28'W | Upland terra firme             | 34.9\(^+\)                            | 39.3                             | —                             | 25 (11)                       |
| C2      |                             |                  |                               | 32.5\(^+\)                            | 39.1                             | —                             | 35 (15)                       |
| C3      |                             |                  |                               | 33.4\(^+\)                            | 29.0                             | —                             | 35 (15)                       |
| C4      |                             |                  |                               | 33.1\(^+\)                            | 27.9                             | —                             | 34 (16)                       |
| M1      | Ducke Forest AM, Brazil     | 02°56'S, 59°55'W | Upland terra firme             | 26.8\(^+\)                            | 41.2                             | 6.0 (MLG)                     | 29 (18)                       |
| M2      |                             |                  |                               | 27.7\(^+\)                            | 41.5                             | 5.3 (MLG)                     | 34 (21)                       |
| E1      | Jatun Sacha, Ecuador        | 01°05'S, 77°35'W | Upland terra firme, 450 m.a.s.l | 29.8\(^+\)                            | 37.3                             | 3–8 (MLG)                     | 44 (9)                        |
| E2      | Jatun Sacha, Ecuador        | 01°05'S, 77°35'W | Forest near river, 450 m.a.s.l. | 30.6\(^+\)                            | 29.8                             | —                             | 41 (8)                        |
| E3      | Jatun Sacha, Ecuador        | 01°05'S, 77°35'W | Ridgetop forest               | 33.9\(^+\)                            | 29.0                             | —                             | 29 (7)                        |
| E4      | Jatun Sacha, Ecuador        | 01°05'S, 77°35'W | Floodplain forest, 400 m.a.s.l. | 35.2\(^+\)                            | 24.2                             | —                             | 37 (10)                       |
| T1      | FLONA Tapajós, Km 67, PA, Brazil | 02°51'S, 54°58'W | Upland terra firme             | 25.7**                                | 21.5                             | —                             | 29 (7)                        |
| T2      |                             |                  |                               | 25.6††                               | 20.5                             | 2.0†† (EC)                    | 22 (7)                        |
| T3      |                             |                  |                               | 23.7††                               | 21.0                             | —                             | 23 (6)                        |
| T4      | FLONA Tapajós, Km 83, PA, Brazil | 03°01'S, 54°58'W | Upland terra firme             | 29.0††                                | 2.2†† (MLG)                     | —                             | 23 (15)                       |

*Flux estimates from this study assume above-canopy photon flux density of 1200 µmol m\(^{-2}\) s\(^{-1}\) and 29 °C air temperature.

1RAINFOR data base (Malhi et al., 2002).
2Jacob & Wofsy (1988).
3Greenberg et al. (2004).
4Stefani et al. (2000).
5Helming et al. (1998).
6Rice et al. (2004).
7Nepstad et al. (2002).
8Rinne et al. (2002).
9Keller et al. (2001).

Techniques employed for flux measurements: eddy covariance (EC), relaxed eddy accumulation (REA) and mixed layer gradient with box model (MLG). Tree basal area \( (m^2 \text{ ha}^{-1}) \) is given for each site, and estimates of above-canopy isoprene flux \( (\text{mg C m}^{-2} \text{ h}^{-1}) \) are shown where information is available. For each site, the percentage of tree biomass comprised of genera which have not been screened for isoprene emission is given; numbers in parentheses represent the percentage of tree biomass which would be comprised of unscreened genera if the 44 genera listed in Table 7 were investigated.
forests vary quite widely, from an average of 61 g m$^{-2}$ (D. Nepstad, personal communication.) at Tapajós near Manaus (McWilliam et al., 1993). Assuming LAI of 6 m$^2$ m$^{-2}$ and an average SLM of 85 g m$^{-2}$, site foliar biomass was estimated to be 510 g m$^{-2}$.

Assigning isoprene emission capacities to emitting species

Isoprene emission capacity, as defined in the canopy-scale model of Guenther et al. (1999), represents the isoprene emission rate of a healthy, sun-adapted leaf at the top of the canopy, measured at 30°C and PFD of 1000 µmol m$^{-2}$ s$^{-1}$. Isoprene emission rates reported in Table 2 are adjusted, using the PFD and temperature algorithms of Guenther et al. (1993), to reflect emissions at 30°C and 1000 µmol m$^{-2}$ s$^{-1}$. However, many of these determinations were made on leaves growing in shaded environments and are likely to underestimate the emission capacity of the species. Because many of the rates in Table 2 were obtained under nonoptimal conditions, and because we were reluctant to assign specific emission capacities on the basis of a single

| Plant family   | % of total basal area | C1  | C2  | C3  | C4  | M1 | M2 | E1 | E2 | E3 | E4 | T1 | T2 | T3 | T4 |
|---------------|----------------------|-----|-----|-----|-----|----|----|----|----|----|----|----|----|----|----|
| Anacardiaceae | % of total basal area | 0.3 | 0.5 | 0.2 | 0.2 | 0.4 | 0.6 | 0.3 | 0.3 | 0.4 | 1.1 | 1.3 | 1.0 | 0.4 | 2.0 |
| Annonaceae    | % of total basal area | 1.1 | 0.2 | 1.5 | 3.5 | 2.4 | 2.3 | 1.5 | 2.9 | 0.4 | 0.8 | 1.3 | 1.3 | 2.1 | 2.4 |
| Areceae       | % of total basal area | 0   | 0   | 0   | 0.5 | 0.1 | 0.1 | 0   | 0   | 0   | 0.7 | 0.7 | 2.1 | 1.6 | 0.4 |
| Burseraceae   | % of total basal area | 6.0 | 6.0 | 3.5 | 8.5 | 5.3 | 5.3 | 3.8 | 3.7 | 2.2 | 0.9 | 3.8 | 3.9 | 4.6 | 5.3 |
| Caesalpinaceae| % of total basal area | 6.8 | 4.5 | 7.0 | 4.0 | 1.9 | 2.0 | 0.8 | 7.4 | 1.0 | 0.5 | 12.3 | 6.6 | 11.8 | 1.9 |
| Clusiaceae    | % of total basal area | 0.7 | 0.2 | 0.3 | 0.1 | 0.8 | 0.5 | 1.0 | 2.6 | 1.4 | 0.3 | 0.3 | 0.2 | 0.2 | 0.8 |
| Euphorbiaceae | % of total basal area | 0.4 | 1.7 | 0   | 0   | 0.3 | 0.6 | 2.7 | 3.8 | 1.0 | 2.2 | 0.8 | 1.7 | 1.3 | 0.3 |
| Flacourtiaceae| % of total basal area | 0.8 | 0.6 | 0.1 | 0   | 0   | 0   | 3.5 | 1.9 | 0.6 | 4.2 | 0.8 | 0.1 | 0.8 | 0.0 |
| Lauraceae     | % of total basal area | 2.2 | 4.6 | 2.7 | 1.7 | 3.2 | 3.7 | 2.0 | 2.1 | 1.0 | 3.7 | 2.7 | 3.3 | 3.2 | 3.4 |
| Lecythidaceae | % of total basal area | 19.9| 12.5| 5.0 | 7.1 | 17.0| 15.2| 0.6 | 1.7 | 0.8 | 1.0 | 11.2| 14.1| 17.0| 3.4 |
| Mimosaceae    | % of total basal area | 6.4 | 8.0 | 7.7 | 5.5 | 3.5 | 4.3 | 7.7 | 7.6 | 9.1 | 7.6 | 6.2 | 3.1 | 3.0 | 3.5 |
| Moraceae      | % of total basal area | 5.3 | 3.2 | 3.0 | 3.1 | 2.4 | 2.7 | 5.5 | 5.7 | 5.2 | 2.3 | 1.1 | 1.7 | 2.4 | 3.8 |
| Myristicaceae | % of total basal area | 0.5 | 3.0 | 1.7 | 1.1 | 4.9 | 6.1 | 9.4 | 3.6 | 3.9 | 7.9 | 3.3 | 3.5 | 3.8 | 4.9 |
| Myrtaceae     | % of total basal area | 0.3 | 2.3 | 1.5 | 0.5 | 3.6 | 4.9 | 4.5 | 2.1 | 2.1 | 5.1 | 2.3 | 2.9 | 3.2 | 3.6 |
| Papilionaceae | % of total basal area | 0.7 | 5.3 | 3.2 | 1.0 | 2.9 | 1.9 | 2.1 | 3.2 | 1.7 | 2.9 | 2.4 | 1.1 | 1.7 | 2.4 |
| Rubiaceae     | % of total basal area | 0.1 | 3.3 | 2.2 | 0.7 | 1.1 | 0.4 | 0.9 | 5.6 | 6.9 | 3.6 | 1.7 | 2.9 | 2.4 | 1.1 |
| Sapotaceae    | % of total basal area | 0.1 | 0.1 | 0.3 | 0.2 | 0.4 | 0.4 | 0.9 | 0.7 | 0.4 | 0.1 | 1.1 | 0.4 | 1.2 | 0.4 |
| Vochysiaceae  | % of total basal area | 0.3 | 13.2| 11.9| 6.2 | 5.0 | 7.1 | 0.9 | 2.1 | 0.2 | 0.3 | 3.5 | 1.3 | 1.9 | 5.0 |
| % biomass emitting isoprene | 0.5 | 12.7| 11.6| 6.1 | 4.5 | 5.7 | 0.7 | 1.9 | 0.1 | 0.1 | 2.9 | 1.1 | 15.0| 4.5 |
| % biomass emitting isoprene | 0.5 | 1.0 | 0.7 | 1.7 | 0 | 0 | 2.1 | 4.2 | 1.8 | 7.0 | 7.6 | 6.8 | 3.6 | 0  |
| % biomass emitting isoprene | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  |
| % biomass emitting isoprene | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0  |

Sites for which tree survey data were analyzed, numbered as in Table 5. Shown are the percentage of total basal area contributed by each family in each of 14 tree censuses, and the percent of total plot biomass comprised of isoprene-emitting members of each family.
measurement, we chose to categorize species as either emitters or nonemitters. Nonemitters are assigned an emission capacity of zero. We now adopt the simplifying assumption that the emission capacity of all emitting trees is the same. We justify this somewhat arbitrary decision as follows, on the basis of isoprene emission data collected elsewhere.

Isoprene emission data for temperate forest species far exceeds that for tropical forests. Original reports of emission capacities for a number of temperate trees were quite variable, but included many low estimates (on the same order as low values reported in Table 2) as well as high ones. When investigators re-examined 24 such species, taking care to measure only sun-adapted foliage, the range of variation was greatly reduced and the emission capacity of all species increased substantially, falling in the range of 39–158 µg C g⁻¹ h⁻¹ (mean of 86; Geron et al., 2001). Based on measurements on 15 isoprene-emitting tree species in Panama, Keller & Lerdau (1999) reported a mean emission capacity of 26.3 (± 9.5) nmol m⁻² s⁻¹; assuming an average SLM of 85 g m⁻², this is equivalent to 67 µg C g⁻¹ h⁻¹. Working in a dry tropical forest in Puerto Rico, Lerdau & Keller (1997) calculated a mean isoprene emission rate of 35.3 (± 16.4) nmol m⁻² s⁻¹, which corresponds to a rate of 90 µg C g⁻¹ h⁻¹ (SLM = 85 g m⁻²). Geron et al. (2002) also determined emission capacities for 20 common tree species at La Selva, Costa Rica, 10 of which were shown to emit isoprene. Five of those determinations were made on sun-exposed foliage, and the mean emission capacity was 91 µg C g⁻¹ h⁻¹; five were made on leaves growing in low-light environments, and the mean emission capacity was 28. It is our expectation, therefore, that healthy, sun-lit upper canopy leaves of emitting taxa will have emission capacities in the range of 50–150 µg C g⁻¹ h⁻¹. For the purposes of this analysis, we assume that all emitting species have the same emission capacity, and assign to each a value of 75 µg C g⁻¹ h⁻¹. The protocol we have outlined can easily accommodate changes in this value if necessary as additional data accumulate.

Taking the average value of isoprene-emitting biomass (21%) for the three tree censuses at FLONA Tapajós (km 67) and assuming an emission capacity of 75 µg C g⁻¹ h⁻¹, the area-averaged emission capacity for the site (λD in Eqn (1)) is 8.0 mg C m⁻² h⁻¹. One can then use this value in the canopy light attenuation model employed by Guenther et al. (1999) to estimate regional isoprene fluxes. Given PFD above the canopy of 1200 µmol m⁻² s⁻¹ and leaf temperature of 29 °C, and using the light and temperature algorithms of Guenther et al. (1999) (Fig. 1) the model predicts a midday canopy-scale isoprene flux of 3.2 mg C m⁻² h⁻¹. This prediction scales linearly with isoprene-emitting biomass. Thus, for the same environmental conditions and using the same biomass estimate for the Ducke forest data, but with 41% emitting biomass, area-averaged emission capacity is 15.7 mg C m⁻² h⁻¹, and the predicted flux almost doubles to 6.3 mg C m⁻² h⁻¹.

Comparison with stand-scale isoprene flux measurements

Above-canopy isoprene fluxes have been measured at relatively few tropical sites (Guenther et al., 1999; Geron et al., 2002). Rinne et al. (2002), measuring isoprene flux using the eddy covariance technique, estimated maximum fluxes of approximately 2 mg C m⁻² h⁻¹ at FLONA Tapajós at high PFD (1200–1600 µmol m⁻² s⁻¹) and air temperature of 29 °C. Stefani et al. (2000) measured above-canopy isoprene fluxes from a tower north of Manaus (approx. 40 km NW of the Duke Reserve) using the relaxed eddy accumulation technique, and reported average midday values of approximately 4.6 mg C m⁻² h⁻¹ (PFD = 1200 µmol m⁻² s⁻¹ and air temperature of 30 °C). The relative fluxes measured at Tapajós and Manaus are consistent with the estimates of isoprene-emitting biomass at each site as estimated above. Fluxes at three sites within Amazônia have also been estimated by Greenberg et al. (2004) using isoprene concentration profiles measured using a tethered balloon and a chemical box model which determines the canopy isoprene flux required in order to best match the measured profiles, given a certain boundary layer height and assuming a certain chemical loss rate. Maximum midday isoprene flux estimated from a site in FLONA Tapajós was approximately 2.2 mg C m⁻² h⁻¹, while that near Balbina, 150 km north of Manaus, was 5.3. These results too are generally consistent with estimates of isoprene-emitting biomass from the two sites (using Duke Reserve data as a surrogate for Balbina). Comparing our bottom-up model estimates with the measured fluxes reported above for these two sites, it appears that our approach overestimates the isoprene flux by 20–60%. It should be noted that there are significant uncertainties associated with both our scaling-up exercise and the above-canopy flux determinations to which they are compared. Taken as a whole however, the comparisons are consistent in suggesting that there is significant site-to-site variation in the potential for isoprene emission within the Amazon basin, and that the variation may be explained in large part by differences in the amount of isoprene-emitting foliage. Greenberg et al. (2004) estimated a significantly higher midday flux at a third site (Reserva Biológica do Jaru in Rondônia) of approximately 9.8 mg C m⁻² h⁻¹. If our assumptions with respect to site biomass and isoprene emission capacity are reasonable for the Jaru site, this implies about 65%
isoprene-emitting biomass, which is quite high, but we have no forest inventory data for the region against which to compare. Geron et al. (2002) report high isoprene fluxes from La Selva (Costa Rica) and estimated isoprene-emitting biomass at about 50%.

Major sources of uncertainty in site-specific emission capacity assignments

We have presented a protocol for estimating the isoprene emission potential of high biomass, high biodiversity tropical forest sites, where making measurements on all species present is impractical. Although we believe this represents an advance in our ability to characterize tropical sites, we recognize a number of shortcomings in the technique. The site-specific capacities we have assigned depend on (1) the estimate of the biomass of each taxa in the stand under consideration, (2) the foliar biomass estimate for the entire stand, estimated as LAI multiplied by average SLM, and (3) the emission capacity assigned to each taxa.

Estimating the contribution of each taxa to the total isoprene emissions of the stand

We have estimated the relative biomass of each genus within a stand based on the total basal area of that genus relative to the basal area of the stand. Given the strong light dependency of isoprene emission (Fig. 1a), this may bias our estimate in favor of smaller diameter trees. If two isoprene-emitting genera have the same amount of basal area within a stand, but one genus consists of a single large, emergent tree while the other consists of a number of smaller, understory trees, they will receive equal weight in our analysis, although the contribution of the former to the total isoprene emission of the stand is likely to be greater. Using estimates of tree volume (basal area times tree height) rather than basal area might redress this bias, but tree height data is not available for many sites. Using data collected for the FLONA Tapajós, where tree height data were available, we recalculated the site-specific isoprene emission capacity using tree volume rather than basal area to weight each genus. The site-specific percentage of isoprene-emitting biomass changed only slightly, and was in fact less when computed on the basis of tree volume (19% vs. 21.5% when weighted using basal area). The same analysis was carried out for two censuses at Caxiuana, again resulting in only slight changes (29.0% and 27.9% when weighted by area vs. 30.3% and 26.8% when weighted by volume.) These results suggest that there exists no strong tendency for isoprene emitting trees to be either taller or shorter than the stand average.

Another difficulty in estimating both total foliar biomass and the percentage of isoprene-emitting taxa involves the role of lianas in tropical forests. Although not accurately sampled in forest inventories, lianas constitute a variable but potentially large fraction (up to 30%) of total foliage (Gerwing & Lopes Farias, 2000). In the course of our fieldwork, we measured significant isoprene emissions from several unidentified liana species and Keller & Lerdau (1999) found seven of 21 sampled genera of vines to emit isoprene in Panama. If roughly a third of liana species emit isoprene, ignoring liana biomass in our protocol will not have a dramatic effect on estimated percentages of isoprene-emitting biomass at our sites (mean of 31%), but only increased sampling will resolve this issue.

Assigning emission capacities to individual taxa

Species screened for isoprene emissions in this study were classified as either emitting or nonemitting, and then assigned an emission capacity of 75 or $0 \mu \text{g C g}^{-1} \text{h}^{-1}$ on that basis. These assignments were based on very few actual measurements, and measurements were frequently made on shade-adapted leaves. Furthermore, genera for which no emission data exist often comprised a large percentage of biomass at a given site (Table 5), averaging 31%. Although our taxonomic approach to assigning emission capacities to unsampled taxa seems reasonable, a reduction in the uncertainty of these values is obviously desirable, and can only be attained through continued compilation of isoprene emission data from tropical species. To that end, researchers are encouraged to contribute VOC emission data to the IGAC-GEIA community database (Wiedinmyer et al., 2004; http://bvoc.acd.ucar.edu). In the course of this study, we identified 44 genera, each of which comprises at least 1% of the stand basal area of one or more of our sites, for which no isoprene data exist (Table 7). If these 44 genera were targeted for screening, the average site biomass comprised of unscreened taxa would drop to 12%, and confidence in our estimates significantly improve.

The predicted canopy-scale fluxes scale linearly with the assigned emission capacity of $75 \mu \text{g C g}^{-1} \text{h}^{-1}$, and this represents a significant uncertainty in the estimates. Whether it is reasonable to assign a single value to represent the emission capacity of all emitting taxa remains an open question. In no case have measurements of isoprene emission capacity been made on a large number of leaves of tropical species in order to characterize the range of variation within an individual tree (with canopy position for example), between
individuals of the same species, or across taxa. Even if the simplifying decision to apply a single emission capacity to all isoprene emitters is demonstrated to be reasonable, more work will be required to establish whether tropical tree species have emission rates similar to temperate species, and to determine the value which best represents the average emission capacity of tropical plants. When care has been taken to assure that emission capacities are obtained on high-light adapted leaves however, in both temperate (Harley et al., 1997; Geron et al., 2001) and tropical tree species (Lerdau & Keller, 1997; Geron et al., 2002), high values, exceeding 50 μgC g⁻¹ h⁻¹, were obtained, and we are confident that our choice of 75 μgC g⁻¹ h⁻¹ is within 50% of the actual value.

### Conclusions

We have proposed a bottom-up modeling approach for predicting isoprene emissions from tropical forests. In common with bottom-up models of CO₂ uptake, it is critical to have good estimates of foliar biomass. Because both processes are strongly light dependent, it is also important to characterize the light dependencies and incorporate a canopy model that treats light extinction in a reasonable way. However, because only roughly a third of woody species emit isoprene in significant quantities, and in contrast to models of stand-level photosynthesis, isoprene emission models require detailed species composition data for each stand, as well as information about which of those species have the capacity to emit isoprene. We have presented isoprene screening data for 125 species collected during several field campaigns in Brazil, 38% of which were isoprene emitters. However, because screened species represent a small percentage of the total number of species encountered in Neotropical forests, we developed a taxonomic protocol for predicting whether an unscreened species emits isoprene, in which (a) species in a genus known to emit isoprene are assumed to emit, and (b) the probability that an unscreened genus emits isoprene is proportional to the percentage of emitting genera within the plant family.

Assessing the isoprene emission characteristics of tropical genera is useful in scaling up emission

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**Table 7** Genera comprising over 1% of the total basal area in one or more tree census plots for which no information exists regarding isoprene emissions

| Families with >20% of isoprene-emitting genera | Genera          | Families with <20% of isoprene-emitting genera | Genera          |
|------------------------------------------------|-----------------|-----------------------------------------------|-----------------|
| Areaceae                                       | Iriartea        | Bombacaceae                                   | Matisia         |
| Caesalpinaceae                                 | Jessenia        | Caryocaraceae                                 | Phragmotheca    |
| Clusiaceae                                     | Chamaechrista   | Cercropiaceae                                 | Caryocar        |
| Euphorbiaceae                                  | Chrysobalanaceae| Chrysobalanaceae                              | Coussapoa       |
| Flacoumiaceae                                  | Glycyndron      | Elaeocarpaceae                                | Couepia         |
| Lecithidae                                     | Margaritaria    | Lauraceae                                     | Sloanea         |
| Lecithidae                                     | Pleuranthodendron| Melastomataceae                               | Licaria         |
| Lecithidae                                     | Tetrathylacium  | Olacaceae                                     | Mezilaurus       |
| Mimosaceae                                     | Bertheletia     | Rubiaceae                                     | Minquartia      |
| Moraceae                                       | Holopixydium    | Sapotaceae                                    | Aiseis          |
| Myristicaceae                                  | Newtonia        | Pentagonia                                    | Chimarrhis      |
| Myristicaceae                                  | Pseudopiptadenia| Coussarea                                     | Coussapoa       |
| Ochnaceae                                      | Batocarpus      | Sapotaceae                                    | Diploon         |
| Ochnaceae                                      | Clarisia        | Sapotaceae                                    | Ecclinusa       |
| Ochnaceae                                      | Pseudolmedia    | Sapotaceae                                    | Ecclinusa       |
| Ochnaceae                                      | Iryanthera      | Micropholis                                   | Neoxytheca      |
| Ochnaceae                                      | Osteophloeum    | Micropholis                                   | Neoxytheca      |
| Ochnaceae                                      | Otoba           | Micropholis                                   | Pradosia        |
| Ochnaceae                                      | Cespedesia      | Micropholis                                   | Prieurella      |
| Papilionaceae                                  | Hymenolobium    | Syzygiopsis                                   | Prieurella      |
| Papilionaceae                                  | Ulmaceae        | Syzygiopsis                                   | Prieurella      |
| Papilionaceae                                  | Vochysiaceae    | Syzygiopsis                                   | Qualea          |

Genera were assigned an isoprene emission capacity based on the percentage of isoprene-emitting genera in the plant family.
estimates only if the species composition of the forest is known in considerable detail. Combining isoprene screening with tree survey data allows one to make a reasonable estimate of the percentage of isoprene-emitting biomass for a given site. These data can then be incorporated into a canopy-scale isoprene flux model. Utilizing this approach, predictions of midday isoprene fluxes from four sites across Amazonía range from about 3.2 to 6.3 mg C m\(^{-2}\) h\(^{-1}\) which is similar to the range observed in above-canopy flux measurements (2.2–6). Although when compared with flux measurements from nearby sites, our estimates are up to 60% higher, our predictions for sites in FLONA Tapajós and near Manaus are consistent with relative differences between sites in measured fluxes, suggesting that changes in species composition are a primary source of site-to-site variation in emissions.

Although large uncertainties remain in each step of the analysis, the protocol proposed here is sufficiently flexible that new information (LAI, SLM, species composition, isoprene emission capacities, etc.) can be easily incorporated. If we hope to reduce the level of uncertainty in predictions of isoprene and other VOC from highly diverse tropical forest, there is no substitute for continued screening of tropical species for VOC emissions. This process can be carried out more efficiently however, if attention is focused on those species that comprise a significant fraction of stand biomass, which information is available in the form of these tree censuses.

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