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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 (C_5H_8) 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 $5.9 \times 10^6\,km^2$, 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

(Guenther *et al*., 1999). Isoprene emissions are estimated as follows:

$$\text{emission rate } (\text{mg C m}^{-2}\text{h}^{-1}) = \varepsilon D \gamma_P \gamma_T, \qquad (1)$$

where ε is a landscape average isoprene emission capacity [μg C g(DW)$^{-1}$ h^{-1}], D is foliar density [g(DW) m^{-2}(ground)], and γ_P and γ_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. ε 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 μmol m^{-2} s^{-1}. Effects of varying light and temperature are incorporated via γ_P and γ_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

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 Biologica do Cuieiras, Manaus, AM	M	2°35′S/60°07′W	Upland terra firme forest	Jan 2000	44% ($n = 16$)
Floresta Nacional da Caxiuanã, 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, April 2001	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 ($\mu g C g^{-1} h^{-1}$)
Anacardiaceae	*Anacardium occidentalis*	B	Y	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	–
	Duquetia 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
	Lacmellea aculeata	T	N	c	d	0.1
	Tabernaemontana sp.	C	N	b	c	0.2
Araliaceae	*Schefflera morototoni*	B	Y	a	a	–
Arecaceae	*Astrocaryum ratacanthus*	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 bataua	B	Y	a	a	–
Asteraceae	*Vernonia* sp.	R	N	b	a	–
Bignoniaceae	*Jacaranda copaia*	B	N	a	a	–
	Tabebuia sp.	R	N	b	a	–
	Tabebuia impetiginosa	T	N	c	e	BDL
Bixaceae	*Bixa orelana*	M	N	b	c	0.5
Bombacaceae	*Cavanillesia 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 subserratum	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	Y/N	c	b	26
	Bauhinia forficate	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 amazonicum	A	N	b	a	–
	Sclerolobium melanocarpum	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	–

Table 2 (Contd.)

Plant family	Species	Site	Isoprene emitter?	Collection technique	Analytical technique	Normalized emission rate ($\mu g\,C\,g^{-1}\,h^{-1}$)
	V. guianensis	T	Y	c	d	48
	Vismia japurensis	B	Y	a	a	–
	Vismia sp.	C	Y	b	a	–
	Vismia sp.	T	Y	c	d	6
Combretaceae	*Buchenavia* sp.	B	N	a	a	–
Connaraceae	*Rourea* sp.	C	Y	b	c	12
Dilleniaceae	*Davilla rugosa*	R	Y	b, c	a, b	44
	Doliocarpus sp.	B	Y	a	a	–
Euphorbiaceae	*Croton lanjouwensis*	B	N	a	a	–
	Croton matourensis	M	N	b	c	0.2
	Hevea guianensis	B	N	a	a	–
	Mabea sp.	B	Y	a	a	–
Flacourtiaceae	*Casearia decandra*	T	Y	c	d	16
	Casearia rusbiana	M	Y	b	c	84
Humiriaceae	*Humiria* sp.	B	Y	a	a	–
	Endopleura uchi	T	Y	b	c	57
Icacinaceae	*Emmotum nitens*	B	N	a	a	–
Lauraceae	*Aniba canelilla*	B	N	a	a	–
	Ocotea rubra	T	N	c	e	BDL
	Ocotea sp.	B	N	a	a	–
	Ocotea sp.	J	N	b	d	0.3
Lecythidaceae	*Couratari stellata*	M	N	b	c	0.3
	Eschweilera sp.	B	Y	a	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	a	–
Malvaceae	*Urena* sp.	A	N	b	a	–
Melastomataceae	*Bellucia grossularioides*	B	N	a	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	a	–
	Guarea grandifolia	M	N	b	c	0.3
	Guarea sp.	B	N	a	a	–
Mimosaceae	*Inga capitata*	C	Y	b	c	67
	Inga caynendensis	M	Y	b	c	195
	Inga heterophylla	B	Y	a	a	–
	Inga sp.	B	N/Y	a	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	a	–
	Stryphnodendron sp.	A	N	b	a	–
Monimiaceae	*Siparuna amazonica*	B	N	a	a	–
Moraceae	*Bagassa guianensis*	A	N	b	a	0.6
	Brosimum sp.	C	N	b	c	0.3
	Ficus sp.	B	Y	a	a	–

(*continued*)

Table 2 (Contd.)

Plant family	Species	Site	Isoprene emitter?	Collection technique	Analytical technique	Normalized emission rate ($\mu g\,C\,g^{-1}\,h^{-1}$)
	Ficus sp.	A	Y	b, c	a, b	89, 111
	Helicostylis	T	Y	c	d	0.4
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 jambolana	A	Y	b, c	a, b	55
Ochnaceae	*Ouratea* sp.	B	Y	a	a	–
Papilionaceae	*Alexa* sp.	B	Y	a	a	–
	Amburana sp.	A	Y	b, c	a, b	70, 113
	Clitoria racemosa	R	Y	b	c	41
	Dipteryx sp.	B	Y	a	a	–
	Machaerium sp.	M	N	b	c	1.1
	Poecilanthe effusa	C	Y	b	c	0.5
	P. effusa	T	N	c	d	0.3
	Swartzia sp.	C	Y	b	c	34
	Swartzia sp.	R	Y	b	a, d	51
Passifloraceae	*Passiflora coccinea*	M	N	b	c	BDL
Phytolaccaceae	*Gallesia integrifolia*	A	N	b	a	–
Piperaceae	*Piper hostmandianum*	M	N	b	c	0.5
Rhamnaceae	*Ampelozizyphus amazonicus*	B	N	a	a	–
Rubiaceae	*Chimarrhis turbinata*	T	N	c	d	BDL
	Pagamea duckei	B	N	a	a	–
	Pagamea sp.	B	N	a	a	–
	Palicourea 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	*Pseudimia* 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
Simaroubaceae	*Simarouba armara*	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	*Apeiba* sp.	C	N	b	c	0.2
Ulmaceae	*Trema micrantha*	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
	R. guianensis	M	N	b	c	0.1
Vochysiaceae	*Erisma uncinatum*	C	N	b	c	BDL

Sites: A, Abracos site; B, Balbina; C, FLONA Caxiuanã; J, Reserva Biológica do Jaru; M, Manaus; T, FLONA Tapajós.
Collection: [a]Static branch enclosure; [b]Dynamic, uncontrolled leaf enclosure; [c]Dynamic, controlled leaf enclosure.
Analysis: [a]Photoionization detector *in situ*; [b]reduction gas detector *in situ*; [c]cartridge + gas chromatography with flame ionization detector (GC-FID) (HP3390); [d]cartridge + gas chromatography with mass spectrometry; [e]*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 ($\mu g\,C\,g^{-1}\,h^{-1}$) is also provided, normalized to photon flux density of $1000\,\mu mol\,m^{-2}\,s^{-1}$ 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 monoterpenes 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 $\mu mol\, m^{-2}\, s^{-1}$ 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 Carbotrap 200, 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 $\mu g\, C\, g^{-1}\, h^{-1}$.

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 Amazônia). 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 $500\,\mu mol\,m^{-2}\,s^{-1}$) and leaf temperatures (28–36 °C). Values in Table 2 were corrected to standard conditions (PFD of $1000\,\mu mol\,m^{-2}\,s^{-1}$ 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 $\mu g\,C\,g^{-1}\,h^{-1}$ 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 $190\,\mu g\,C\,g^{-1}\,h^{-1}$ (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 $1500\,\mu mol\,m^{-2}\,s^{-1}$; emissions increased by about 15% as light was raised from 1000 to $1500\,\mu mol\,m^{-2}\,s^{-1}$. The light response was modeled using the light algorithm of Guenther *et al.* (1999),

$$\text{emission rate} = \varepsilon_0 \frac{\alpha C_L\,\text{PFD}}{\sqrt{1+\alpha^2\,\text{PFD}^2}}, \qquad (2)$$

where ε_0 is the emission rate under standard conditions of 30 °C and PFD equal to $1000\,\mu mol\,m^{-2}\,s^{-1}$, and α 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 $66.5\,\mu g\,C\,g^{-1}\,h^{-1}$ at PFD of $1000\,\mu mol\,m^{-2}\,s^{-1}$): the original light algorithm of Guenther *et al.* (1993) using their default parameterization; 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.

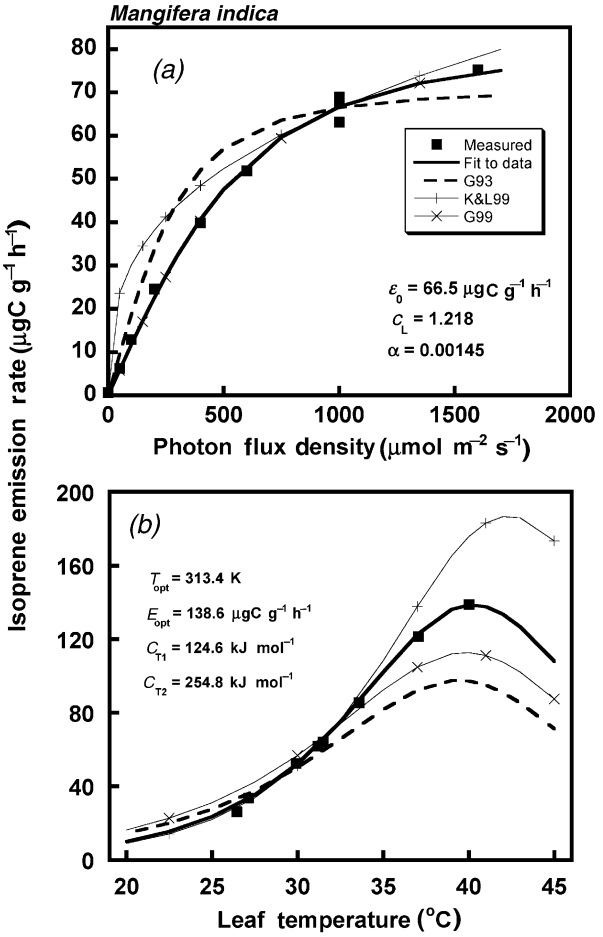

Fig. 1 Response of isoprene emissions from a single leaf of mango (*Mangifera indica* L.) to variations in PFD (a) and leaf temperature (b). Measurements were made on a sun-adapted leaf at Reserva Biológica do Jaru, RO, Brazil. Parameters shown on each figure are based on nonlinear least-squares fits to the data (solid lines) to Eqn (2) (PFD) and Eqn (3) (temperature).

The temperature response of isoprene emission (PFD constant at $1000\,\mu mol\,m^{-2}\,s^{-1}$) is shown in Fig. 1b. Rates of isoprene emission increase exponentially up to about 35 °C (Q_{10} 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),

$$\text{emission rate} = \frac{E_{\text{opt}} C_{T2}\,\exp(C_{T1}x)}{C_{T2} - C_{T1}(1-\exp(C_{T2}x))}, \qquad (3)$$

where

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

and T_L is leaf temperature (K), R is the gas constant (0.008314 kJ K^{-1} mol^{-1}), T_{opt} is the temperature optimum (K), E_{opt} is the emission rate (μg C g^{-1} h^{-1}) at T_{opt}, and C_{T1} and C_{T2} are empirical coefficients representing the energies of activation and deactivation, respectively (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.

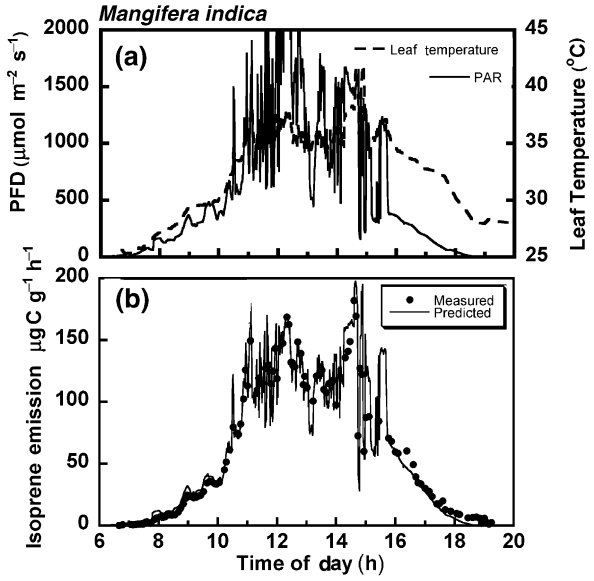

Fig. 2 (a) Values of PFD and leaf temperature measured at 1 min intervals over the daylight hours of February 15, 1998 at Reserva Biológica do Jaru, RO, Brazil. Measurements were made using a LI-6400 photosynthesis system. (b) Diurnal pattern of measured isoprene emissions from a single leaf of mango (*Mangifera indica* L.; same leaf as in Fig. 1). Model predictions (solid line) are based on the PFD and temperature dependencies depicted in Fig. 1, using as inputs the PFD values and leaf temperatures shown in panel (a).

If one integrates the area under the isoprene emission data in Fig. 2b, and compares the total amount of carbon lost with the integrated 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 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 μg C g^{-1} h^{-1}). A significant fraction of tree species, however, is capable of producing much larger amounts of isoprene (up to 200 μg C g^{-1} h^{-1} at 30 °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 μg C g^{-1} 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 ($\mu g\,C\,g^{-1}\,h^{-1}$) 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).

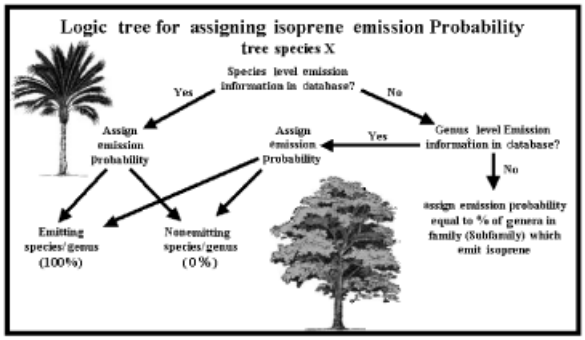

Fig. 3 Logic tree for assigning isoprene emission probabilities to taxa for which no data exist.

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

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
Arecaceae	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	Papilionaceae*	58	74
(Caesalpineae)	(12)	(8)	Rubiaceae	26	2
(Detarieae)	(21)	(52)	Rutaceae	7	21
Celastraceae	4	0	Sapindaceae	17	15
Chrysobalanaceae	2	25	Sapotaceae	7	0
Clusiaceae	9	94	Sterculiaceae	11	5
Combretaceae	6	0	Tiliaceae	8	25
Euphorbiaceae	34	32	Ulmaceae	4	0
Flacourtiaceae	9	67	Vochysiaceae	2	0

*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 $\mu mol\, m^{-2}\, s^{-1}$. 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 $\mu mol\, m^{-2}\, s^{-1}$.

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 Amazonica de Inventarios Forestales/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 crown area, and basal area of each measured tree was calculated, assuming a bole circular in cross-section, as $\pi(\mathrm{dbh}/2)^2$, using the reported values of dbh. All species in the same genus were combined, and the relative importance of each genus and plant family within each study area was estimated as the proportion of total site basal area contributed by each taxa (Table 5). Although using changes in plot-scale basal area over time to estimate changes in forest biomass has been criticized for a variety of methodological reasons (Clark, 2002; Phillips *et al.*, 2002) we regard our technique as providing a good approximation of the relative importance of different genera in the composition of the forest stands examined.

The contribution of each genus of tree to the percentage of isoprene-emitting biomass is simply the isoprene emission probability assigned to that genus, weighted by the percent contribution of that genus to the total composition of the site, as determined by its relative basal area. Summing these values for all genera yields the percentage of isoprene-emitting biomass for a given site. A greatly simplified example of this procedure is presented in Table 4, which depicts the results of a hypothetical site survey consisting of only 12 trees (eight genera in four plant families). Applying the protocol outlined above, the percentage of isoprene-emitting biomass is estimated to be 28.7%.

We applied this procedure to data from 14 tree censuses in four locales (Table 5). Across all sites, the percentage of isoprene-emitting biomass ranged from 20% to 42% (mean = 31%; SD = 8%). The observed variation is not explained by any obvious correlations with forest type or geographic location, nor does it scale with stand basal area. The values from two floodplain sites are within the range from terra firme sites. Because the ability to produce and emit isoprene is scattered throughout the families of angiosperms, the percentage of isoprene-emitting biomass for a given site is fundamentally a function of species composition. Table 6 lists 18 important plant families encountered across the four sampling sites, and lists for each of the 14 surveys the percent contribution of each family to total stand basal area and the percent of total plot biomass comprised of isoprene-emitting members of each family. For example, the first census at FLONA Caxiuanã indicates that trees in the Caesalpinaceae comprise 6.8% of the total plot basal area, and that 2.7% of the total plot biomass is comprised of isoprene-emitting members of the Caesalpinaceae. Sites dominated by members of families that emit little isoprene, such as Apocynaceae, Bombacaceae, Cecropiaceae, Combretaceae, Lauraceae, Melastomataceae, Meliaceae, Rubiaceae, Sapotaceae or Vochysiaceae, will have relatively low emission potentials. If such isoprene-emitting families as Anacardiaceae, Arecaceae, Burseraceae, Euphorbiaceae, Flacourtiaceae, Lecythidaceae, Moraceae, Myristicaceae, or any of the three legume families (Caesalpinaceae, Mimosaceae, Papilionaceae) represent a high fraction of stand biomass, high emission potentials will result. 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 Caxiuanã with those at the westernmost site, Jatun Sacha in Ecuador, significant differences are apparent. At Caxiuanã, the palms (Arecaceae) 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 ($\mathrm{m^2\,m^{-2}}$) multiplied by the average SLM ($\mathrm{g\,m^{-2}}$) for a given site. Estimates of LAI in FLONA Tapajós range from about 5 to 7 $\mathrm{m^2\,m^{-2}}$, averaging about 6.5 (Nepstad *et al.*, 2002) and a value of 5.7 $\mathrm{m^2\,m^{-2}}$ has been reported for the Ducke Reserve (McWilliam *et al.*, 1993). We have adopted a reasonable LAI value of 6.0 $\mathrm{m^2\,m^{-2}}$ 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
				Basal area (m^2)	Emits isoprene?	% of genera in family (subfamily) which emit	Probability that genus emits isoprene	% of total basal area	Percentage of isoprene-emitting biomass in stand
Plant family	Plant subfamily	Plant species	dbh (m)	$\pi(\text{dbh}/2)^2$	Yes/no unknown	From Table 3	Unitless	(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 fimbriatum*	0.148	0.0172	Y	71	1.0	3.8	3.8
Burseraceae		*P. fimbriatum*	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	Caesalpinieae	*Apuleia molaris*	0.159	0.0199	N	8	0	4.4	0
Caesalpinaceae	Caesalpinieae	*Apuleia* sp.	0.113	0.0100	N	8	0	2.2	0
Caesalpinaceae	Detarieae	*Brownea 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		*Cecropia sciadophylla*	0.202	0.0320	N	0	0	7.1	0
Cecropiaceae		*C. sciadophylla*	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	28.7

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.

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Table 5 Estimates of the percentage of isoprene-emitting biomass for sites within Amazônia

Site ID#	Site	Location	Ecosystem	Basal area ($m^2\,ha^{-1}$)	Percent biomass emitting isoprene	Midday isoprene flux estimate		% Biomass from unscreened taxa
						Literature ($mg\,C\,m^{-2}\,h^{-1}$)	This study* ($mg\,C\,m^{-2}\,h^{-1}$)	
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) 4.6¶ (REA)	6.3	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)	3.2	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 $1200\,\mu mol\,m^{-2}\,s^{-1}$ and 29 °C air temperature.
†RAINFOR data base (Malhi *et al.*, 2002).
‡Jacob & Wofsy (1988).
§Greenberg *et al.* (2004).
¶Stefani *et al.* (2000).
‖ Helmig *et al.* (1998).
**Rice *et al.* (2004).
††Nepstad *et al.* (2002).
‡‡Rinne *et al.* (2002).
§§Keller *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 ($m^2\,ha^{-1}$) is given for each site, and estimates of above-canopy isoprene flux ($mg\,C\,m^{-2}\,h^{-1}$) 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.

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Table 6 List of 18 plant families which comprised a significant fraction of total tree basal area for the tree census sites analyzed

Plant family		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	2.2	2.0	0.4
	% biomass emitting isoprene	0	0.3	0.2	0.3	0.4	0.5	0	0	0	0.7	0.7	2.1	1.6	0.4
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
	% biomass emitting isoprene	0	0	0	0.5	0.1	0.1	0	0.1	0	0	0	0.1	0	0.1
Arecaceae	% of total basal area	0	0	0	0.1	2.0	2.3	9.6	3.4	5.5	3.2	0	0	0	2.0
	% biomass emitting isoprene	0	0	0	0.1	2.0	2.3	7.2	2.4	4.3	2.4	0	0	0	2.0
Burseraceae	% of total basal area	6.0	6.0	3.5	8.6	5.3	5.3	3.8	3.7	2.2	0.9	3.8	3.9	4.6	5.3
	% biomass emitting isoprene	5.9	5.3	3.5	8.5	5.3	5.2	3.7	3.3	2.1	0.9	3.9	4.0	4.5	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
	% biomass emitting isoprene	2.7	0.5	0.8	0.7	0.8	1.1	0	0.4	0.1	0	2.3	0.4	0.1	0.8
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
	% biomass emitting isoprene	0.7	0.1	0.3	0.1	0.7	0.5	0.9	2.5	0.5	0.3	0.3	0.3	0.3	0.7
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
	% biomass emitting isoprene	0.3	0.8	0	0	0.1	0.3	1.3	1.6	0.5	0.3	0.3	1.2	0.4	0.1
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
	% biomass emitting isoprene	0.5	0.4	0.1	0	0	0	2.7	1.5	0.4	2.9	0.5	0.1	0.7	0
Lauraceae	% of total basal area	2.2	4.6	2.7	1.7	3.2	3.7	2.0	2.1	2.2	1.0	3.7	2.7	7.3	3.2
	% biomass emitting isoprene	0.1	0.1	0.2	0.1	0.4	0.4	0.1	0.1	0.3	0	0.3	0.3	0.4	0.4
Lecythidaceae	% of total basal area	19.9	12.5	5.0	7.1	17.0	15.2	0.6	1.7	0.8	0.8	14.0	11.2	14.1	17.0
	% biomass emitting isoprene	9.2	8.9	2.8	3.5	13.3	12.4	0.3	1.2	0.5	0.1	1.5	1.3	1.9	13.3
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
	% biomass emitting isoprene	5.3	3.2	3.0	3.1	2.4	2.7	5.5	5.7	2.8	5.2	2.3	1.1	1.7	2.4
Moraceae	% 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
	% biomass emitting isoprene	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
Myristicaceae	% of total basal area	0.7	5.3	3.2	1.0	2.9	1.9	21.3	18.3	17.0	11.9	2.5	5.2	3.7	2.9
	% biomass emitting isoprene	0.1	3.3	2.2	0.7	1.1	0.4	8.9	5.6	6.9	3.6	1.7	2.9	2.4	1.1
Myrtaceae	% 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
	% biomass emitting isoprene	0.1	0.1	0.3	0.1	0.4	0.4	0.8	0.5	0.4	0.1	0.9	0.3	0.9	0.4
Papilionaceae	% of total basal area	13.2	15.6	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	12.7	11.7	11.6	6.1	4.5	5.7	0.7	1.9	0.1	0.1	2.9	1.1	1.5	4.5
Rubiaceae	% of total basal area	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	0.1	0.1	0.1	0.1	0
Sapotaceae	% of total basal area	16.1	16.1	22.6	20.6	14.3	15.3	5.4	2.3	1.3	2.0	10.0	5.1	3.8	14.3
	% biomass emitting isoprene	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vochysiaceae	% of total basal area	0.3	0.1	3.0	2.2	1.1	1.2	2.2	5.8	11.6	0	14.5	25.4	12.8	1.1
	% 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.

forests vary quite widely, from an average of 61 $g\,m^{-2}$ (D. Nepstad, personal communication.) at Tapajós to 110 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 $\mu mol\,m^{-2}\,s^{-1}$. 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 $\mu mol\,m^{-2}\,s^{-1}$. 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

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 $\mu g\,C\,g^{-1}\,h^{-1}$ (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 ($\pm$ 9.5) $nmol\,m^{-2}\,s^{-1}$; assuming an average SLM of 85 $g\,m^{-2}$, this is equivalent to 67 $\mu g\,C\,g^{-1}\,h^{-1}$. Working in a dry tropical forest in Puerto Rico, Lerdau & Keller (1997) calculated a mean isoprene emission rate of 35.3 ($\pm$ 16.4) $nmol\,m^{-2}\,s^{-1}$, which corresponds to a rate of 90 $\mu g\,C\,g^{-1}\,h^{-1}$ (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 $\mu g\,C\,g^{-1}\,h^{-1}$; 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 $\mu g\,C\,g^{-1}\,h^{-1}$. 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 $\mu g\,C\,g^{-1}\,h^{-1}$. 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 $\mu g\,C\,g^{-1}\,h^{-1}$, the area-averaged emission capacity for the site (εD 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 $\mu mol\,m^{-2}\,s^{-1}$ 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 $\mu mol\,m^{-2}\,s^{-1}$) 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 Ducke Reserve) using the relaxed eddy accumulation technique, and reported average midday values of approximately 4.6 $mg\,C\,m^{-2}\,h^{-1}$ (PFD = 1200 $\mu mol\,m^{-2}\,s^{-1}$ 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 Ducke 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 Caxiuanã, 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 $0\,\mu g\,C\,g^{-1}\,h^{-1}$ 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 $75\,\mu g\,C\,g^{-1}\,h^{-1}$, 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

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
Arecaceae	Iriartea	Bombacaceae	Matisia
	Jessenia		Phragmotheca
Caesalpinaceae	Chamaechrista	Caryocaraceae	Caryocar
	Vouacapoua	Cecropiaceae	Coussapoa
Clusiaceae	Chrysochlamys	Chrysobalanaceae	Couepia
Euphorbiaceae	Glycydendron	Elaeocarpaceae	Sloanea
	Margaritaria	Lauraceae	Licaria
Flacourtiaceae	Pleuranthodendron		Mezilaurus
	Tetrathylacium	Melastomataceae	Mouriri
Lecythidaceae	Bertholettia	Olacaceae	Minquartia
	Holopixydium	Rubiaceae	Alseis
Mimosaceae	Newtonia		Chimarrhis
	Pseudopiptadenia		Coussarea
Moraceae	Batocarpus		Pentagonia
	Clarisia	Sapotaceae	Diploon
	Pseudolmedia		Ecclinusa
Myristicaceae	Iryanthera		Micropholis
	Osteophloeum		Neoxytheca
	Otoba		Pradosia
Ochnaceae	Cespedesia		Prieurella
Papilionaceae	Hymenolobium		Syzygiopsis
		Ulmaceae	Ampelocera
		Vochysiaceae	Qualea

Genera were assigned an isoprene emission capacity based on the percentage of isoprene-emitting genera in the plant family.

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 $50\,\mu g\,C\,g^{-1}\,h^{-1}$, were obtained, and we are confident that our choice of $75\,\mu g\,C\,g^{-1}\,h^{-1}$ 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 CO_2 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

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 Amazônia 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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