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Isoprene emission capacity for US tree species

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Abstract

Isoprene emission capacity measurements are presented from 18 North American oak (*Quercus*) species and species from six other genera previously found to emit significant quantities of isoprene. Sampling was conducted at physiographically diverse locations in North Carolina, Central California, and Northern Oregon. Emissions from several sun leaves of each species were measured at or near standard conditions (leaf temperature of 30°C and photosynthetically active radiation of 1000 $\mu mol\,m^{-2}\,s^{-1}$) using environmentally controlled cuvette systems and gas chromatography with reduction gas detectors. Species mean emission capacity ranged from 39 to 158 $\mu g\ C\,g^{-1}\,h^{-1}$ (mean of 86), or 22 to 79 $nmol\,m^{-2}\,s^{-1}$ (mean of 44). These rates are 2–28 times higher than those previously reported from the same species, which were summarized in a recent study where isoprene emission rates were assigned based on published data and taxonomy. These discrepancies were attributed to differences in leaf environment during development, measurement technique (branch or plant enclosure versus leaf enclosure), and lack of environmental measurements associated with some of the earlier branch enclosure measurements. Mass-based emission capacities for 15 of 18 oak species, sweetgum (*Liquidambar styraciflua*), and poplars (*Populus trichocarpa and P. deltoides*) were within ranges used in current biogenic volatile organic compound (BVOC) emission models, while measured rates for the remaining three oak species, *Nyssa sylvatica, Platanus occidentalis, Robinia pseudoacacia, Salix nigra, and Populus* hybrids (*Populus trichocarpa* × *P. deltoides*) were considerably higher. In addition, mean specific leaf mass of the oak species was 30% higher than assumed in current emission models. Emission rates reported here and in other recent studies support recent conclusions that isoprene emission capacities for sun leaves of high emitting species may be better represented by a value of 100 ± 50 $\mu g\ C\,g^{-1}\,h^{-1}$ during hot summer conditions. We also find that intermediate isoprene emission rates previously suggested for some tree species may not represent their true emission capacities, and that broadleaf plant species may have either low (<1.0 $\mu g\ C\,g^{-1}\,h^{-1}$) or very high (~ 100 $\mu g\ C\,g^{-1}\,h^{-1}$) genetic capacity to emit isoprene when mature foliage is exposed to a high ambient temperature and light environment. Published by Elsevier Science Ltd.

Keywords: *Liquidambar*; *Nyssa*; *Populus*; *Quercus*; *Robinia*; *Salix*; Oak; Emission factor; Isoprene capacity; Leaf temperature; Photosynthetically active radiation

1. Introduction

Global annual isoprene emissions are thought to equal or exceed the global methane flux on a carbon mass basis (Guenther et al., 1995). It is estimated that over 90% of global isoprene production is from vegetation (Guenther et al., 1995). In the contiguous United States, annual isoprene emissions are estimated to range from 15 to 20 million metric tons yr^{-1} (Pierce and Dudek, 1996), comparable to total annual non-methane volatile organic compound (VOC) emissions from US anthropogenic sources. Isoprene is very reactive with the hydroxyl (OH•) radical, much more so than most atmospheric hydrocarbons, such that even at relatively low concentrations it can control regional photochemistry. In regions with high tropospheric nitrogen oxide (NO_x) concentrations, it has been demonstrated that isoprene can react to form high levels of ozone (O_3) (Williams et al., 1997), and can affect oxidant control strategies in rural (Trainer

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et al., 1987) and even urban (Chameides et al., 1988) environments.

Regional to global isoprene emission estimates are typically based on an emission capacity [EC, in units of $\mu g\ C\ g^{-1}$ (leaf dry weight) h^{-1}] at standard conditions [in this paper, leaf temperature of 30°C and photosynthetically active radiation (PAR) of $1000\ \mu mol\ m^{-2}\ s^{-1}$]. These ECs are applied to forest inventory data and adjusted for canopy position, incident light, and leaf temperature effects (Geron et al., 1994; Guenther et al., 1995). To assign ECs to plant species for which no emission rate data exist, taxonomic relations with species for which rates have been determined are used (Guenther et al., 1994; Geron et al., 1994; Benjamin et al., 1996). Unfortunately, in the case of many plant species for which enclosure measurements of isoprene emission have been made, light and/or leaf temperature values during measurement were not recorded (Khalil and Rasmussen, 1992; Lamb et al., 1986, 1985, 1984) or are difficult to interpret. In addition, branch or whole plant enclosures were typically employed, leading to varying degrees of self-shading. Where static chambers were used, photosynthesis and isoprene emission could potentially be affected by carbon dioxide (CO_2) reduction, water vapor condensation, thermal stress, etc. (Csiky and Seufert, 1999). Measurements from foliage on cut branches or otherwise perturbed environments have also been reported (Klinger et al., 1998; Helmig et al., 1999), although the effects of such treatments have not been well characterized. Isoprene emission capacity increases with growth light intensity in both laboratory (Grinspoon et al., 1991; Harley et al. 1994; Litvak et al., 1996) and field (Harley et al., 1997; Sharkey et al., 1996) environments. EC data collected during greenhouse or laboratory experiments often feature developmental PAR regimes that are considerably lower than the ambient sunlight levels to which foliage is exposed at the top of forest canopies. Similarly, field settings where access to upper canopy levels is limited often necessitate sampling of at least partially shade-adapted foliage. Lerdau and Throop (1999) found that shaded foliage of three tree species in Panama emitted no detectable isoprene, even though sun leaves of the same species emitted at high rates. Similarly, Guenther et al. (1999) found that shaded foliage of two Central African species emitted almost no isoprene upon initial enclosure, but were induced to emit steadily increasing amounts of isoprene after exposure to PAR of $1000\ \mu mol\ m^{-2}\ s^{-1}$ and leaf temperature of 30°C for periods from 15 min to 2 h. Such sampling bias would be expected to lead to underestimation of actual leaf isoprene emission capacity.

Isoprene flux estimates using the canopy model of Guenther et al. (1995) incorporating the short-term light dependency of Guenther et al. (1993) indicate that greater than 80% of canopy emissions are from the top one-third of the canopy. It is therefore critical to accurately model isoprene emissions from the upper canopy. This cannot be accomplished unless the emission capacity of sunlit upper canopy leaves is appropriately measured and represented in isoprene emission models.

In recent studies, when species with previously reported low emission capacities (see summary of Benjamin et al., 1996) were re-examined in sunlit upper canopy positions during warm summer conditions, emission capacities were determined to be considerably greater (Harley et al., 1997; Sharkey et al., 1996). These higher rates have been found to be more accurately scaled to fluxes at mature tree, canopy, and landscape levels (Doskey and Gao, 1999; Fuentes et al., 1995, 1996, 1999; Fuentes and Wang, 1999; Guenther et al., 1996a–c; Geron et al., 1997; Goldstein et al., 1998; Lamb et al., 1996; Pier 1995; Pier and McDuffie, 1997; Pierce et al., 1998). The purpose of this study is to examine mid-to-late summer-isoprene emission capacities from fully exposed sun leaves of some common tree species, some of which have been previously reported to emit significant quantities of isoprene. Leaf gas exchange systems are used which allow more precise control over environmental conditions. These rates are compared with previously reported ranges applied in biogenic volatile organic compound (BVOC) emission models.

2. Methods

We studied isoprene emissions from 18 oak tree species (*Quercus spp.*) as well as *Liquidambar styraciflua, Nyssa sylvatica, Platanus occidentalis, Populus trichocarpa, P. deltoides*, (and *P. deltoides* × *P. trichocarpa hybrids*), *Robinia pseudoacacia*, and *Salix nigra*. Using the methods of Geron et al. (1994) with additional forest inventory data for the western US, we estimate that these species account for 23.3 and 5.4% of the total projected tree crown area in the contiguous 37 eastern and 11 western US, respectively (see Table 1 for percentages by individual species). Regionally, these species can account for a much greater percentage of crown area. For instance, the western oak species account for over 23% of the crown area in California (*Q. chrysolepis* and *Q. kelloggii* each account for 8.2%). These species represent genera that account for approximately 98% of the forest isoprene source in the contiguous United States. Individually *Quercus* accounts for 63.7%, *Populus* 12.6%, *Liquidambar* 11.2%, *Nyssa* 6.9%, *Robinia* 1.4%, *Salix* 1.2%, and *Platanus* 0.9%. Spruce (*Picea Spp*) accounts for most (1.9%) of the remainder. The oak species examined here account for 82.7% of oak crown area in the US, with *Quercus alba* (17.6%), *Q. rubra* (16.2%), *Q. nigra* (10.0%), *Q. falcata* (8.5%), *Q. velutina* (8.2%), *Q. stellata* (7.0%), and *Q. prinus* (6.0%) dominating. Oaks are relatively less abundant in the westernmost 11 United States, but can be locally or regionally important. Considering only

Table 1
Summary of emission capacity data at leaf temperature of 30°C and PAR of 1000 μmol $m^{-2} s^{-1}$ from this study

Species	N[a]	SLM[b]	*B96*[c]	DW[d]	SD[e]	Min[e]	Max[e]	LA[f]	%Crn[g]
California									
Quercus agrifolia	6	142	**31.1**	**77**	27	48	117	50	0.4
Q. berberidifolia	9	151	**NA**	**73**	7.4	62	81	51	< 0.1
Q. chrysolepis	10	179	**21.9**[h]	**48**	11	32	71	39	1.9
Q. douglasii	15	124	**7.7**	**71**	13	44	96	41	0.6
Q. engelmannii	6	152	**21.9**[h]	**39**	5.4	32	47	27	< 0.1
Q. lobata	14	97	**3.0**	**86**	14	52	103	39	< 0.1
Q. kelloggii	7	109	**21.9**[h]	**78**	23	48	116	39	1.9
Q. wislizenii	52	150	**11.0**	**74**	14	38	114	50	0.3
North Carolina									
Q. alba	8	119	**6.9**	**92**	19	51	114	50	4.3
Q. falcata	13	113	**21.9**[h]	**112**	40	35	159	57	1.6
Q. laevis	4	115	**21.4**	**151**	29	126	188	79	0.2
Q. nigra	12	124	**21.7**	**81**	27	39	118	46	1.7
Q. phellos	13	114	**28.4**	**93**	26	61	129	48	0.5
Q. prinus	11	112	**5.7**	**44**	14	28	77	23	1.8
Q. rubra	8	99	**13.1**	**67**	19	50	103	30	2.6
Q. stellata	12	147	**NA**	**73**	16	45	107	50	2.0
Q. velutina	5	97	**16.7**	**157**	25	126	181	72	2.2
Q. virginiana	9	186	**17.8**	**46**	11	34	71	40	0.2
Liquidambar styraciflua	11	115	**16.7**	**68**	26	36	113	37	4.1
Nyssa sylvatica	3	84	**NA**	**77**	9.7	66	84	30	1.4
Platanus occidentalis	14	66	**24.3**	**71**	26	28	111	22	0.3
Robinia pseudoacacia	8	64	**10.5**	**151**	23	118	192	45	0.5
Salix nigra	3	86	**22.2**	**93**	13	82	107	37	0.2
Oregon									
Populus deltoides	8	96	**37.0**	**97**	21	72	134	43	< 0.1
P. trichocarpa	8	97	**43.6**[h]	**97**	29	69	144	44	< 0.1

[a] *N* denotes the number of leaves sampled.
[b] SLM is specific leaf mass in g m^{-2}.
[c] *B96* is the mean emission capacity in μg C $g^{-1} h^{-1}$ assigned by Benjamin et al. (1996).
[d] DW is the emission factor in μg C $g^{-1} h^{-1}$.
[e] SD, min, and max are the standard deviation, minimum, and maximum of measured ECs, respectively, in μg C $g^{-1} h^{-1}$.
[f] LA is the emission factor in nmol $m^{-2} s^{-1}$.
[g] %Crn is estimated percentage of total forest crown cover that each species accounts for in the western (California species and *Populus trichocarpa*) and eastern (North Carolina species and *Populus deltoides*) contiguous United States.
[h] Indicates that EC is derived by phylogenetic classification instead of direct emission measurement.

western oak crown area, *Q. kelloggii* accounts for 32.7%, followed by *Q. chrysolepis* (24.8%), *Q. gambelii* (13.9%), *Q. garryana* (10.5%), *Q. douglasii* (5.0%), *Q. agrifolia* (4.5%), and *Q. wislizenii* (3.8%).

Sun leaves were randomly selected from the south-facing, upper portion of each tree crown, although in a few cases, leaves on north-facing portions of crowns or in partially shaded positions were measured as mentioned below. These measurements were excluded from the summary in Table 1. The leaves of large trees were accessed using fixed towers, articulating boom lift trucks, or elevated platforms. Isoprene emissions from eastern US species were measured at the Coweeta Hydrologic Laboratory in mountainous western North Carolina, the Duke University Forest and surrounding areas in the east-central piedmont of North Carolina, and Emerald Isle in Coastal North Carolina from 6 July to 16 September 1997 and on 16 July 1998. Emissions from western *Quercus* species were measured at eight valley and plateau sites in central to southern California from 2 to 11 August 1995, and 16 to 22 May 1996. Isoprene ECs of *Populus* species and hybrids were measured in commercial plantations near Boardman, OR, in June 1995.

Gas exchange of the leaves was monitored using Li-Cor 6400 (Li-Cor, Inc., Lincoln, NE) photosynthesis systems with red or red/blue light-emitting diode (LED) light sources. These systems measure water (H_2O) and CO_2 exchange from leaf surfaces using infrared (IR) gas analyzers and allow control of PAR, leaf and air temperature, humidity, CO_2 concentration, and air flow over

6 cm^2 of enclosed leaf area. Ambient purge air was drawn by the gas exchange systems from open areas 3–5 m away from the trees being studied. This air was passed through a 2 l plastic mixing vessel at a flow rate of 500 $\mu mol\ s^{-1}$ to help stabilize ambient concentrations of isoprene and CO_2.

Cuvette exit air samples were either drawn from the exhaust outlet line using glass 10 ml locking gastight syringes with Teflon plungers (VICI Precision Sampling, Inc., Baton Rouge, LA) or injected directly into the gas chromatograph sample loop for analysis in the field. In some cases, incoming ambient air was scrubbed of isoprene using activated charcoal filters (Supelco Inc., Bellefonte, PA); otherwise ambient air samples for isoprene analysis were drawn from the line between the mixing vessel and the gas exchange system. All syringes were placed in an insulated unrefrigerated box and transported to the laboratory for analysis within 2–4 h. Experiments showed that isoprene loss from the syringes was less than 2% over 24 h, which was considered to be negligible.

Isoprene concentrations in the cuvette exhaust and ambient air were determined using the methods described previously (Greenberg et al., 1993; Harley et al., 1997). Samples collected in the syringes were injected into a 1.9 ml sample loop of an isothermal (130°C) gas chromatograph. Isoprene was separated on a stainless-steel column (1.3 m long × 2 mm i.d.) packed with Unibeads 3S, 60/80 mesh (Alltech Assoc., Deerfield, IL) and measured with a reduction gas detector (RGD2, Trace Analytical, Menlo Park, CA). Zero-grade air was used as the carrier gas instead of nitrogen to minimize baseline disturbance before the isoprene eluted. The carrier gas flow through the column was reversed after isoprene eluted to shorten analysis time. This column backflushing prevented later eluting compounds from interfering with subsequent analysis. After analysis was completed on a given day, the column oven temperature was raised to 170°C overnight to clear the column of less volatile materials. Peak heights were determined using a commercial integrator (Model 3396 Series III, Hewlett Packard, Inc., Avondale, PA). Peak height was determined to be a more consistent and linear indicator of isoprene concentration than peak area. The reduction gas detector system was calibrated daily against a standard cylinder containing 460 ± 2 ppb (v/v) isoprene in air (Scott Specialty Gases, Inc., Plumsteadville, PA). The standard was referenced to the flame ionization detection (FID) response of a gas chromatograph (Model HP5890, Hewlett Packard, Inc., Avondale, PA) which was calibrated to a National Institute of Standards and Technology propane standard (SRM 1660a, 3 ppm propane in air, Rochester, NY). Standard dilutions were performed using a dynamic gas calibration system (Model 146, Thermo Environmental Instruments, Inc., Franklin, MA). Peak height response curves of the RGD were linear between 0.5 and 460 ppbv isoprene concentrations, in agreement with Greenberg et al. (1993). We estimate that analytical error was less than ± 2% as determined by making repeated measurements of the standard gas over this range of concentrations.

Leaf isoprene emission sampling was initiated after allowing leaf gas exchange (internal CO_2 concentration, photosynthesis, and stomatal conductance) to stabilize. This usually occurred within 2–10 min, but occasionally longer if ambient conditions departed significantly from standard light and temperature conditions. Cuvette CO_2 concentration and relative humidity were allowed to vary with leaf performance but were typically stable during the measurement periods. Samples were taken between 950 and 1900 h, and over 90% were taken between 1000 and 1600 h. Solar noon occurred at approximately 1300 h during the study. Three to five successive measurements at 2–4 min intervals were performed on each leaf. Ambient isoprene samples were drawn from the sample line downstream from the 2 l mixing vessel between leaf emission samples.

Leaf mass per unit area (i.e., specific leaf mass, SLM, in $g\ m^{-2}$) was determined on the section of leaf enclosed in the cuvette. These sections were cut and dried at 80°C for 48 h and weighed. If the leaf did not fully cover the opening of the cuvette, the area of the enclosed section was cut and area determined using a portable leaf area meter (Li-3000A, Li-Cor, Inc., Lincoln, NE) prior to drying and weighing.

Isoprene emission rates E ($nmol\ m^{-2}\ s^{-1}$) were calculated as

$$E = f(C_o - C_i)a^{-1}, \quad (1)$$

where f is the flow rate ($mol\ s^{-1}$) into the cuvette, C_o and C_i are the outlet (exhaust air) and inlet isoprene concentrations ($nmol\ mol^{-1}$), respectively, and a is the enclosed leaf area, which was usually 0.0006 m^2 (6 cm^2) in this study. Mass based E ($\mu g\ C\ g^{-1}\ h^{-1}$) could then be calculated by multiplying E from Eq. (1) above by the quantity (216/SLM).

Isoprene emission rates from the leaves were measured under standard conditions, although occasionally leaf temperature differed by as much as 0.5°C from the target of 30°C. In these cases, emission rates were adjusted to standard conditions using the leaf temperature algorithm of Guenther et al. (1993). The primary focus of this paper is on isoprene emission rates measured at a leaf temperature of 30 ± 0.5°C and PAR of 1000 $\mu mol\ m^{-2}\ s^{-1}$.

As each isoprene emission sample was drawn from the cuvette exhaust, leaf environmental and gas exchange data were logged with the photosynthesis system. A hand-held IR thermometer (Model 39800, Cole-Parmer Instrument Co.,Vernon Hills, IL) was used to measure the leaf temperature of some leaves prior to isoprene emission measurement. Above-canopy

meteorological data (1 min measurements of PAR, air temperature, wind speed, and wind direction for 1997) were obtained from the Forest Atmosphere Carbon Transfer Scheme (FACTS1) site at Duke Forest in the North Carolina Piedmont. Hourly meteorological data were obtained from monitoring stations near the isoprene emission measurement sites within the Coweeta Hydrologic Laboratory Experimental Watershed and the Emerald Isle site for several days prior to and during emission measurements.

3. Results and discussion

Although the emission rates reported here are from fully exposed sun leaves, total tree height and height of foliage sample varied from 2 to over 30 m above ground level. To check for differences in ECs due to position on tree (leaf height), isoprene emissions from *Quercus alba* and *Q. falcata* were measured from three sun leaves at each of three levels (approximately 4, 12, and 19 m) on the south facing sides of fully exposed trees approximately 20 m tall. There were no significant differences between ECs with respect to height for either species. A recent study of emissions from *Eucalyptus globulus* (Street et al., 1997) found that saplings emitted substantially more isoprene than older trees. This was not the case in our data. Rates observed from small open-grown *Liquidambar styraciflua*, *Quercus velutina*, *Q. rubra,* and *Q. nigra* seedlings less than 5 years old were not significantly different than those from individuals of the same species which were over 80 years old and in excess of 20 m in height. Four leaves on a North Carolina *Quercus alba* specimen which exhibited chlorosis and root/stem fungal infection were examined during July 1997. Isoprene emission from the four leaves ranged from 16 to 90 μg $C\,g^{-1}\,h^{-1}$, and was highly correlated with photosynthesis rates, which ranged from 0.5 to 7.0 mmol $m^{-2}\,s^{-1}$. This tree died 2 months later, likely from root system stress and subsequent fungal infection induced by Hurricane Fran in September 1996. This was a common cause of tree mortality following the storm. These data were deleted from our analysis. In the oaks examined in North Carolina, a low but statistically significant positive correlation between EC and photosynthesis was observed.

The isoprene ECs from the 25 species are shown in Table 1. In addition, negligible (< 0.1 μg $C\,g^{-1}\,h^{-1}$) isoprene emissions were found from *Carya tomentosa*, *Rhus copallina*, *Smilax rotundifolia*, and *Vitis labrusca* in North Carolina. Mean ECs for the 18 oak (*Quercus*) species ranged from 39 to 158 μg $C\,g^{-1}\,h^{-1}$ (22–79 nmol $m^{-2}\,s^{-1}$). Means for 15 of these fell within the high emitting class (70 ± 35 μg $C\,g^{-1}\,h^{-1}$) of Guenther et al. (1994). Leaves of *Quercus falcata* emitted at somewhat higher rates, while leaves from two *Q. laevis* trees and three *Q. velutina* trees emitted at mean rates in excess of 150 μg $C\,g^{-1}\,h^{-1}$. Three of the four lowest emitting oak species on a dry weight basis also had the highest SLM values (152–186 g m^{-2}) and area-based ECs similar to the other oaks. The other low isoprene emitting oak, *Q. prinus*, was also found to be the lowest emitting species among four studied by Harley et al. (1997). Time of day and growth environment may have also impacted EC estimates from *Q. prinus* (and possibly *Q. rubra* as well) in this study. Measurements were conducted at the cooler western NC site early and late in the day relative to measurements made on other oak species (discussed below). Current emission models such as BEIS2 (Geron et al., 1994; Pierce et al., 1998) assume lower upper canopy SLM values (~ 100 g m^{-2}) than were determined for most oaks (15 of 18 species) during this study. If the mass-based ECs measured here are normalized to a SLM of 100, ECs for 13 of the 18 oaks exceed 85 μg $C\,g^{-1}\,h^{-1}$, and 10 of these exceed 100 μg $C\,g^{-1}\,h^{-1}$. Recent scaling studies (Guenther et al., 1996b, c; Geron et al., 1997) suggest that a value of 100 μg $C\,g^{-1}\,h^{-1}$ may be more appropriate for regional oxidant modeling studies. Table 1 also lists mean emission factors for these species from Benjamin et al. (1996), which summarizes emission rates from branch or seedling enclosure data published prior to 1996 and assigns rates to unstudied species based on taxonomy. The rates measured here are 2 to 28 times higher than those from Benjamin et al. (1996). These differences are attributed not to analytical methods, but rather to differences in leaf developmental environment, phenology, enclosure type (branch or plant enclosure versus leaf enclosure), static versus dynamic flow, and/or lack of (or difficulty in interpreting) environmental measurements associated with some of the earlier branch enclosure measurements. ECs for *Liquidambar styraciflua* are in agreement with those of Guenther et al. (1996a, b). *Populus* values are at the upper end of the range reported for this genus by Guenther et al., 1994. The *Populus* hybrids are interesting in that their ECs are twice those of their parents, and second generation crosses have even greater ECs than the first-generation hybrids. Assimilation rates are similar between the hybrids and parent stock, suggesting that the higher isoprene emission rates of the hybrids represent a greater loss of fixed carbon.

Previous EC measurements for the species *Nyssa sylvatica, Platanus occidentalis, Robinia pseudoacacia,* and *Salix nigra* were lower than measured here. *Robinia pseudoacacia* and *Nyssa sylvatica* were assigned ECs of 14 ± 7 μg $C\,g^{-1}\,h^{-1}$ in Guenther et al. (1994) based on previous measurements. In a later study, Guenther et al. (1996b) reported significantly higher rates from *Robinia pseudoacacia*. Here, ECs from eight fully exposed *Robinia pseudoacacia* leaves on three trees ranged from 118 to 192 μg $C\,g^{-1}\,h^{-1}$. An initial measurement of a partially shaded mid-canopy leaf of *Nyssa sylvatica* yielded an emission rate of 14 μg $C\,g^{-1}\,h^{-1}$, in agreement with

Guenther et al. (1996a) and used in emission models by Guenther et al. (1994). In a later study, a lower value was observed by Guenther et al. (1996b). However, when isoprene was measured from three south facing leaves on two fully exposed *Nyssa sylvatica* trees, much higher values (66–84 $\mu g\ C\ g^{-1}\ h^{-1}$) were observed. This species is thought to be intermediate in shade tolerance early in its development, becoming less tolerant as it approaches canopy height. It is possible that earlier emission rates from this species were determined from more easily accessible partially shaded foliage which developed in a cooler and darker environment. Previous *Salix nigra* and *Platanus occidentalis* emission rates were determined from branch enclosure studies, where canopy position and self-shading within the enclosures could have induced lower emission rates. The higher leaf level values observed from *Salix nigra* are in good agreement with those measured from several *Salix* species by Isebrands et al. (1999). Xiaoshan et al. (2000) reported an emission factor of 80.6 $\mu g\ g^{-1}\ h^{-1}$ from *Platanus orientalis* in China during August using a static branch enclosure system. These authors also report emission capacities of 22.6 and 19.2 $\mu g\ g^{-1}\ h^{-1}$ from *Populus simonii* and *Salix matsudana*, respectively, during early May, and noted that a seasonality strongly affected emission capacity. For instance, *Pendula loud* had an emission capacity of 7.1 $\mu g\ g^{-1}\ h^{-1}$ on 10 May but increased to 63.4 $\mu g\ g^{-1}\ h^{-1}$ in August. It is interesting to note that, if the measurements reported here for *Nyssa sylvatica, Platanus occidentalis, Robinia pseudoacacia,* and *Salix nigra* actually do more closely reflect isoprene emission capacities for these species, then all North American broadleaf forest species summarized by Guenther et al. (1994) fall into either a high (e.g., $70 \pm 35\ \mu g\ C\ g^{-1}\ h^{-1}$) or low (e.g., $<1.0\ \mu g\ C\ g^{-1}\ h^{-1}$) basal isoprene emission rate class for midsummer fully exposed foliage. Collectively, these four species account for about 2.5% of US canopy cover (compared to over 30% for *Quercus*, *Populus*, and *Liquidambar*) and are not concentrated in any single area. Therefore an increase in ECs for these species is not likely to affect regional isoprene emission estimates substantially. However, as noted by Harley et al. (1999), *Platanus occidentalis, Populus spp., Robinia pseudoacacia,* and *Salix nigra*, are included among several high-isoprene-emitting species that are increasingly planted globally as short rotation intensive culture biofuel and wood pulp stocks.

It has been suggested that the basal emission factor may vary with meteorology (temperature and solar radiation "dose") over the previous 10 h to 2 weeks (Sharkey et al., 1999; Geron et al., 2000; Xiaoshan et al., 2000; Petron et al., in press). Diurnal patterns, where ECs peak shortly after solar noon, were also discussed in these studies and by Goldstein et al. (1998). In the North Carolina oak EC data we also see some evidence of a diurnal pattern, where maximum rates observed seemed to peak around midday (data not shown). However, the lowest values observed early and late in the day were from *Quercus prinus*, and it is not clear if this is due to diurnal changes in emission potential, cooler seasonal growth environment, random variability, or possibly a lower genetic emission potential unique to this species. Although the diurnal pattern is difficult to interpret due to high variability within a given hour of the day, the maximum EC pattern we observe is similar to a diurnal pattern observed by Goldstein et al. (1998), where emission potential was derived from canopy level isoprene fluxes. Geron et al. (2000) also derive lower morning EC from eddy correlation isoprene fluxes of Guenther et al. (1998), but see no EC decline in the afternoon. Xiaoshan et al. (2000) report similar diurnal patterns. Further investigation into possible diurnal variation in EC appears to be warranted.

Table 2 shows other recent leaf and branch emission rate measurements published since 1995 (see also the review of Kesselmeier and Staudt, 1999). Except for a single *Nyssa sylvatica* measurement, all leaf level measurements fall within or exceed the highest emission class of $70 \pm 35\ \mu g\ C\ g^{-1}\ h^{-1}$ (roughly equivalent to $32 \pm 16\ nmol\ m^{-2}\ s^{-1}$ on a leaf area basis). Only three individual measurements from branch enclosure measurements (one each from *Liquidambar styraciflua*, *Nyssa sylvatica*, and *Populus trichocarpa*) fell below the corresponding shading-factor-adjusted class of $40 \pm 20\ \mu g\ C\ g^{-1}\ h^{-1}$ suggested by Guenther et al. (1994) for branch enclosure measurements, and it should be noted that these measurements were performed on cut branches (Helmig et al., 1999). Recent European studies (Table 3) can be summarized similarly, although a few measurements, possibly impacted by seasonality, fall into intermediate EC classes.

Recent isoprene emission studies in tropical forests indicate similar patterns. In Puerto Rico, 11 of 38 species screened using a leaf enclosure system emitted isoprene (Lerdau and Keller, 1997). Ten of these emitted at rates in excess of $\sim 23\ nmol\ m^{-2}\ s^{-1}$ under standard conditions, and eight yielded rates from 30 to 100 $nmol\ m^{-2}\ s^{-1}$ (Table 4). The remaining emitter (*Clusia rosea*) emitted at very low rates ($\sim 1\ nmol\ m^{-2}\ s^{-1}$) independent of light and possibly produced isoprene via a non-enzymatic (acid catalysis of dimethylallyl pyrophosphate) process. In Panama, 15 of 51 species studied emitted significant quantities of isoprene, and 14 emitted at rates from 15 to 43 $nmol\ m^{-2}\ s^{-1}$ (Keller and Lerdau, 1999). A canopy crane was used to access upper canopy foliage of 33 species at another lowland site in Panama, where the ECs of 11 of the 12 isoprene emitting species ranged from 11 to 55 $nmol\ m^{-2}\ s^{-1}$ (Lerdau and Throop, 1999). In that study, isoprene emission capacity scaled positively with photosynthesis capacity. Similarly, in South Africa 6 of 14 species tested using a branch enclosure system emitted at rates of 32 to 110 $\mu g\ C\ g^{-1}\ h^{-1}$, while the remaining

Table 2
Summary of emission capacity data at a leaf temperature of 30°C and PAR of 1000 μmol $m^{-2} s^{-1}$ from other recent studies of North American isoprene-emitting vegetation

Species	Ref.[a]	SLM[b]	DW[c]	LA[d]	E[e]	S[f]	Comment
Liquidambar styraciflua	1		70 ± 5		L	N	Upper canopy sun leaves
	2		71		L	N	Upper canopy sun leaves
	2		45		B	N	Upper canopy sun leaves
	3		9.3		B	N	Cut branch
	4			30–70	L	C	Drought experiment
Nyssa sylvatica	2		13		L	N	
	3		4.3		B	N	Cut branch
Populus euroamericana	5		153 ± 10		L	N	Cut branch
Populus balsamifera	6		100 ± 46		B	N	So. British Columbia
Populus fremontii	7			74 ± 9	L	C	29°C
Populus grandidentata	8		95–114		B	N	Peak summer rates
	3		39		B	N	Cut branch
Populus trichocarpa	3		1.9		B	N	Cut branch
Populus tremuloides	9	77	165	59	L	C	Nitrogen/PAR study
	10			68	L	C	Control in CO_2/PAR study
	5		78 ± 10		L	N	Cut branch
	8		92		B	N	Peak summer rates in S. Canada
	3		20		B	N	Cut branch
Quercus alba	9	80	78	28	L	C	Nitrogen/PAR study
	10			33	L	C	Control in CO_2/PAR study
	7			48 ± 15	L	C	29°C
	11		60		P	N	Large tree enclosure
	12	112 ± 6	99 ± 5		L	N	Upper canopy sun leaves
	13	130	100–150	62–96	L	N	Upper canopy sun leaves
	3		77		B	N	Cut branch
Quercus coccinea	12	70–90	115 ± 5		L	N	Upper canopy sun leaves
Quercus falcata	3		29		B	N	Cut branch
Quercus gambelii	1		121 ± 4		L	N	Sun leaves
	14		132 ± 5		L	C	Harley UV-b study
	3		60		B	N	Cut branch
Quercus laevis	2		51		L	N	
	2		35		B	N	
Quercus prinus	12	100–135	71 ± 6		L	N	Upper canopy sun leaves
Quercus rubra	15			38	L	C	
	16	121	77 ± 11	43 ± 7	L	N	Cut branch
	17		> 60		P	N	Large tree enclosure
	5		112 ± 7		L	N	Cut branch
	3		140		B	N	Cut branch
	3		70		B	N	Cut branch
Quercus stellata	2		84		L	N	
	2		41		B	N	
	3		77		B	N	Cut branch
	18			20–40	L	N	Drought/nitrogen study
Q. velutina	12	70–90	97 ± 4		L	N	Upper canopy sun leaves
	3		67		B	N	Cut branch
Salix discolor	5		91 ± 3		L	N	Cut branch
Salix humulis	5		41 ± 1		L	N	Cut branch
Salix nigra	3		56		B	N	Cut branch
Salix petiolaris	5		102 ± 6		L	N	Cut branch
Salix subsericea	5		57 ± 10		L	N	Cut branch

[a] References (1) Guenther et al. (1996b); (2) Guenther et al. (1996a); (3) Helmig et al. (1999); (4) Fang et al. (1996) (5) Isebrands et al. (1999); (6) Drewitt et al. (1998); (7) Fall and Monson (1992); (8) Fuentes et al. (1995); (9) Litvak et al. (1996); (10) Sharkey et al. (1991); (11) Pier and McDuffie (1997); (12) Harley et al. (1997); (13) Geron et al. (1997); (14) Harley et al. (1996); (15) Loreto and Sharkey (1990); (16) Sharkey et al. (1996); (17) Pier (1995); and (18) Harley et al. (1999).

[b] SLM is specific leaf mass in g m^{-2}.

[c] DW is the emission capacity in μg C g^{-1} (dry weight) h^{-1} (± standard error when available).

[d] LA is the emission capacity in nmol $^{-2} s^{-1}$ (± standard error when available).

[e] E is the enclosure type (B = branch, L = leaf, P = whole plant enclosure).

[f] S is the experimental setting (C = controlled study in laboratory or greenhouse, N = natural).

Table 3
Summary of emission capacity data at a leaf temperature of 30°C and PAR of 1000 μmol $m^{-2} s^{-1}$ from recent European field studies where branch enclosures were used

Species	Ref.[a]	DW[b]	LA[c]	Comment
Arundo donax	1	140 ± 70		Spain in early June
Buxus sempervirens	1	20 ± 4.8		France in late June
Cytisus sp.	2	27 ± 24		Italy in June
Erica arborea	2	18 ± 6.2		Italy in June
Erica arborea	3	5.6		Italy in May
Erica multiflora	2	2.0 ± 1.0		Italy in May, October
Erica multiflora	1	2.0		Spain in September
Genista scorpius	1	11 ± 4		France in early October
Myrtus communis	2	137 ± 104		Italy in June
Myrtus communis	3	22 ± 5		Italy in May
Populus nigra	1	63 ± 28		Spain in early June
Populus tremula	4	45		Finland in mid-June
Quercus frainetto	5	118	27	Italy in May
Quercus pubescens	5	80	15	Italy in May
Quercus pubescens	1	78		France in late June, early October
Rhamnus lycoides	1	22 ± 20		Spain in early June
Salix phylicifolia	4	50		Finland in August
Salix spp	1	27 ± 30		Spain in early June
Spartium junceum	2	6.4 ± 0.6		Italy in May
Uvex parvifolia	1	22 ± 20		Spain in early June

[a]References (1) Owen et al. (1998); (2) Owen et al. (1997); (3) Hansen et al. (1997); (4) Hakola et al. (1998); and (5) Steinbrecher et al. (1997).
[b]DW is the emission capacity in μg C g^{-1} (dry weight) h^{-1} (± standard deviation when available).
[c]LA is the emission factor in nmol $m^{-2} s^{-1}$.

8 species all emitted at rates of less than 0.5 μg C $g^{-1} h^{-1}$ (Guenther et al., 1996d). Guenther et al. (1999) re-examined the Central African isoprene emission rate data of Klinger et al. (1998) and estimated that the ECs of those species were more than a factor of 3–10 times higher than previously reported. This was attributed to the same factors that resulted in underestimated ECs for temperate species, and it was noted that accurate characterization of tropical tree isoprene EC is particularly challenging due to difficulties in obtaining appropriate leaf material. He et al. (2000) surveyed 15 common Australian *Eucalyptus* species using a branch enclosure technique. Twelve of these species emitted at rates within or very near the high emitter category (40 ± 20 μg C $g^{-1} h^{-1}$) of Guenther et al. (1994). Plants examined in this study were grown in a greenhouse, and measurements were taken during the southern hemisphere winter season, with PAR and temperature similar to an autumn environment within the greenhouse. The plants had both young expanding and mature leaves. It is interesting to note that the ECs (adjusted to standard conditions using the algorithms of Guenther et al., 1993) reported show a negative correlation with temperature across species.

Our data and results from other recent studies suggest that perhaps true genetic isoprene emission capacities for broad leaf tree species fall into two categories: (1) less than 1.0 μg C $g^{-1} h^{-1}$, representing species where limited amounts of isoprene are produced, possibly via the pathways mentioned by Lerdau and Keller (1997) and Silver and Fall (1991); and (2) 100 ± 50 μg C $g^{-1} h^{-1}$ normalized to a SLM of 100 g m^{-2}. Category 2 corresponds to a leaf-level area-based rate of about 46 ± 23 nmol $m^{-2} s^{-1}$ and a branch-level rate of approximately 56 ± 28 μg C $g^{-1} h^{-1}$. The uncertainty range of ± 50% associated with these ECs is influenced by a variety of growth environment and developmental factors. This variability is likely large enough to obscure most interspecies differences in isoprene emission factors within current databases. This may be further complicated by short-term (hours to days) meteorologically induced temporal variability in basal isoprene ECs from single leaves. The EC variability between *Populus* hybrids indicates that genetic factors within a genus or species could have influence on EC variability similar to that of environmental factors.

Members of the coniferous spruce (*Picea*) genus are also assigned a basal emission rate of 14 ± 7 μg C $g^{-1} h^{-1}$ (Guenther et al., 1994). However, like the oaks in this study which had low mass-based emission factors, their SLM also is very high (> 200 g m^{-2}). Furthermore,

Table 4
Summary of emission capacity data at a leaf temperature of 30°C and PAR of 1000 μmol $m^{-2} s^{-1}$ from recent tropical field studies

Species		
Panama (Keller and Lerdau, 1999)	LA[a]	E[b]
Acrocomia vinifera	20	L
Annona hayesii	9	L
Astroneum graveolens	26	L
Bonamia maripoides	18	L
Cissampelos pareira	28	L
Cnestidium rufescens	26	L
Dioclea guianensis	43	L
Doliocarpus major	32	L
Ficus insipida	37	L
Ficus spp.	16	L
Leuhea seemanii	24	L
Spondias mombin	33	L
Stigmaphyllon hypargyreum	36	L
unknown	33	L
Xylopia frutescens	15	L
Puerto Rico	LA[a]	E[b]
(Lerdau and Keller, 1997)		
Bursera simaruba	32	L
Capparis cyanophollophora	25	L
Capparis indica	23	L
Croton discolor	100	L
Eugenia xerophytical	45	L
Krugiodendron ferreum	30	L
Pictetia aculute	50	L
Pisonia albida	30	L
Reynosia guama	100	L
Thrinax morrisii	35	L
South Africa	DW[c]	E[b]
(Guenther et al., 1996d)		
Acacia nigrescens	110	B
Burkea africana	36	B
Ochna pulchra	32	B
Phragmites mauritianum	35	B
Rhus leptodictya	54	B
Securinega virosa	81	B
Panama	LA[a]	E[b]
(Lerdau and Throop, 1999)		
Brosimum utile	10.7	L
Calophylum longifolium	11.9	L
Dussia munda	30.7	L
Ficus nymphifolia	3.9	L
Lonchocarpus longifolium	53.0	L
Marila laxiflora	11.2	L
Perebea xanthochyma	14.7	L
Protium panamense	46.3	L
Socratea exorrhiza	14.5	L
Symphonia globulifera	16.8	L
Trattinnickia aspera	55.1	L
Virola spp.	13.0	L
Australia (He et al., 2000)	DW[c]	E[b]
Eucalyptus botryoides	4.7 ± 1.4	P
E. camaldulensis	14.6 ± 4.3	P
E. citriodora	48.9 ± 5.4	P
E. cladocalyx	6.1 ± 1.9	P
E. forrestiana	35.8 ± 10.8	P
E. globulus	60.4 ± 30.1	P
E. gomphocephala	15.1 ± 3.7	P
E. grandis	53.9 ± 16.6	P
E. maculata	37.9 ± 33.4	P
E. marginata	25.6 ± 7.4	P
E. robusta	44.0 ± 12.5	P
E. rudis	54.2 ± 15.9	P
E. wandoo	5.3 ± 1.1	P

[a]LA is the emission factor in nmol $m^{-2} s^{-1}$.
[b]E is enclosure type (B = branch, L = leaf, P = whole plant enclosure).
[c]DW is the emission factor in μg C g^{-1} (dry weight) h^{-1}.

the "bottlebrush" type foliage display of spruce shoots results in much of the foliage's being oriented away from the light source in enclosure measurements. If these factors are taken into account, then mean emission factors of 24 μg C $g^{-1} h^{-1}$ recently reported for *Picea glauca* (Isebrands et al., 1999) may also represent higher area-based emission factors. Since isoprene is produced in, and is suspected to protect (Sharkey and Singsaas, 1995; Singsaas et al., 1997) membranes in, chloroplasts, it may be that isoprene emission would be best expressed per unit of chlorophyll. This would account for much of the difference between broadleaf and *Picea* EC; e.g., Middleton et al. (1997) found that midsummer chlorophyll concentrations in *Populus tremuloides* were up to 3 times higher than those for *Picea marianna* and *P. glauca* on a dry weight basis. Such a relationship is also consistent with observed vertical (sun leaf vs shade leaf) patterns in ECs (Harley et al., 1997; Sharkey et al., 1996) and could be used in combination with recent remote sensing techniques which offer satellite-based estimates of chlorophyll density.

In a recent review, Kesselmeier and Staudt (1999) warned that using phylogenetic schemes to extrapolate emission factors from one species to another, even within a genus, could result in invalid rate assignments. This was the case in using North American *Quercus* ECs for non-isoprene-emitting European *Quercus* species. The results presented here and in other recent studies also indicate that emission rates from species derived from branch/plant enclosure data, with limited environmental data, or from plants grown in laboratory or shaded environments should be regarded cautiously when formulating regional BVOC emission estimates, especially when estimating emissions during hot summer conditions conducive to high photochemical activity. Use of such ECs may cause flux estimates to be biased low. This

could be the case for model estimates of isoprene for European and North American regions where such isoprene emission rates have been used in the past.

In future studies of isoprene emission capacity, we recommend that several steps be taken to ensure that isoprene emission potential of plants is appropriately assessed. Environments during leaf development, phenology, recent (past 24 h to 2 weeks) climate, leaf age, and measurement techniques should all be carefully evaluated before measurement or assignment of measured rates to plant species. If possible, foliage at the tops of mature crowns/canopies should be examined. Enclosures of individual leaves allow more precise environmental control and less complicated interpretation of emission rate data. Leaf plasticron indices (Isebrands et al., 1999) should also be considered when studying indeterminate species such as *Populus*, since leaf flushing and growth can occur on such plants throughout the growing season. Use of gas exchange systems which allow accurate estimates of photosynthesis and stomatal behavior provides physiological information useful in interpreting isoprene emission rates.

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