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Master Thesis

臺灣溪頭孟宗竹林之異戊二烯放出特性

Characteristics of Isoprene Emission in a Moso Bamboo Forest, Xitou, Central Taiwan

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口試委員會審定書

臺灣溪頭孟宗竹林之異戊二烯放出特性
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本論文係張庭維君（R03625024）在國立臺灣大學森林環境暨資源學系、所完成之碩士學位論文，於民國 105 年 7 月 5 日承下列考試委員審查通過及口試及格，特此證明

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摘要

異戊二烯(2-甲基-1,3-丁二烯)為一種揮發性有機化合物(Volatile organic compound, VOC，該物質因會間接地造成空氣汙染和強化溫室效應而被關注。在過去研究中指出植物會為減緩熱傷害和暴露於臭氧造成的傷害等目的而製造並放出異戊二烯。因植物放出之異戊二烯總量極大，對於放出量及速度的估計十分重要。過去研究也指出，植物的異戊二烯放出速率受到許多外在環境因子(例如，溫度和光強度)和生理因子(例如，一樹冠層中的位置)。在過去，已有相當多對於植物異戊二烯放出的模型，卻多無考慮竹類之特性，一概以樹木或草地論之；但竹類為東亞地區最重要的森林組成之一，尤其孟宗竹因近年有快速擴張與入侵其他森林而受關注，基於其重要性，應要有針對之研究。因此，本研究以：一、確認孟宗竹是否有異戊二烯放出的能力；二、瞭解孟宗竹林的異戊二烯放出的空間變異；三、瞭解孟宗竹林的異戊二烯放出的時間變異；四、基於實驗資料製作適用於孟宗竹的放出速率模型。本研究利用葉箱法進行異戊二烯採樣。實驗在台灣中部，南投縣溪頭實驗林的竹類標本園及鄰近竹蘆的孟宗竹林進行。在 2014 年 11 月及 12 月，對 14 種竹類進行採樣；其中，綠竹(*B. oldhami*)、孟宗竹(*P. Edulis*)和石竹(*P. lithophila* Hayata) 有可觀的異戊二烯放出速率(32.02, 23.20 and 38.30 nmol m^{-2} s^{-1})；痲竹屬(*Dendrocalamus*)和剛竹屬(*Phyllostachys*)在實驗中的全部物種皆有放出能力；在實驗中，斑葉紅寒竹(*C. marmorea* cv. *Variegata*)、業平竹(*S. fastuosa*)、暹羅竹(*T. siamensis*)和玉山箭竹(*Yushania niitakayamensis*)沒有偵測到放出。在 2015 年 11 月、12 月及隔年 3 月，本研究對不同垂直位置上的放出速率進行測試；然而，在 7 個實驗個體中，僅有一個個體在樹冠層底部與頂部的放出速率有統計顯著差異(P= 0.041)；但若在修除個體差異後將 7 個個體的資料混和測試的話，不同高度是有顯著的放出速率差異的(P= 0.0052)，且由低處到高處放出速率逐漸上升。在 2015 年 9 月到 2016 年 3 月間測試異戊二烯放出速率隨光度的變化和月間變異，本研究發現每個月放出速率都有類似的趨勢隨著光強度增加而上升並在一定的光強度後達到放出速率的飽和狀態，但 2015 年 7 月到 11 月的放出速率明顯高於 12 月到隔年 3 月；在每個月光強度一致(PPFD = 1000 mol m^{-2} s^{-1})的測量中，平均放出速率大致與平均葉溫的趨勢相同，但在 2016 年 2 月和 3 月出現不一致，故可能有其他影響因子造成的季節變異存在。另外，本研究利用月間測量的資料，製作考慮葉溫、光強度影響的孟宗竹異戊二烯放出速率模型；其中，以 Gaussian 分布來模擬葉溫影響並以 Guenther 等人(1993)描述的光強度影響分布來模擬光強度影響有較好的表現；此模型在從 2015 年 9 月到 2016 年 3 月每個月的 RMSE 分別為 38.79、31.26、86.24、46.24、44.16、60.89 和 62.53。整體來說，本研究建立了孟宗竹林樹冠規模的異戊二烯放出估計方法的基礎，並建議為準確估計全年樹冠規模的異戊二烯放出量，在葉溫和光強度以外需考慮樹冠高層間變異和物候和生理因子的影響。

關鍵字：異戊二烯，孟宗竹，冠層變異，模型開發，季節變異

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Abstract

Isoprene (2-methyl-1, 3-butadiene), which is known as a volatile organic compound (VOC), has strong impacts on air pollution and global warming. Former studies indicated that plant can emit isoprene for multiple purposes including enhancing thermotolerance and preventing ozone-exposing damages. According to former estimations, the isoprene emission amount from plants was enormous, suggesting the importance of estimating fluxes of isoprene emission from plants. As well, former studies indicated that environmental factors (e.g., leaf temperature, light intensity) and physiological factors (e.g., position in the canopy) can affect isoprene emissions. Previously, several studies proposed models for estimating isoprene emission from plants, yet they did not consider bamboos. Nevertheless, moso bamboo is one of the dominant species in eastern Asia, currently showing rapid expansion and invasion into other forests. Hence, the objectives of this study were 1) to identify the ability of isoprene emission in moso bamboos and then to clarify 2) spatial and 3) temporal variations in isoprene emission in a moso maboo forest. Also, 4) this study developed a model reproducing the temporal changes in isoprene emission from the bamboos based on the measurements. This study conducted isoprene measurements based on a leaf chamber method in a bamboo specimen garden and a bamboo forest in Xitou Experimental Forest, central Taiwan. First, by checking 14 species of bamboo in November and December 2014, this study revealed that *B. oldhami*, *P. Edulis* and *P. lithophila* Hayata had significant isoprene emission which were about 32.02, 23.20 and 38.30 nmol m^{-2} s^{-1}, respectively. All species of *Dendrocalamus* and *Phyllostachys* showed isoprene emission detected, but the isoprene emissions were not detected in *C. marmorea* cv. *Variegata*, *S. fastuosa*, *T. siamensis* and *Yushania niitakayamensis*. As the result, this study confirmed significance of isoprene emission in moso bamboos. Second, this study examined the pattern of vertical variations in isoprene emission within canopy under the standardized environmental conditions, and only one individual showed significant difference in isoprene emission rates between canopy top and bottom ($P= 0.041$) if we test the significance in each individual; however, if we consider total seven individuals measured, that is, canopy top and bottom tended to show higher and lower isoprene emission rates, respectively ($P= 0.0052$). Third, by measuring isoprene emission rate under fixed light intensity levels, the seasonal variation in isoprene emission during September 2015 to March 2016 increased with light intensity differently between months; where December 2015, January, February and March 2016 have lower emission at the given light level than those of September, October and November 2015. The seasonal variation in isoprene emission rates at the same light intensity (PPFD = 1000 μmol m^{-2} s^{-1}) generally corresponded to that of leaf

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temperature, although some discrepancy was found in February and March 2016, suggesting that there were other factors affecting the seasonal variation. Fourth, to develop a model, this study considered the effect of leaf temperature and light intensity, and better performances found in using the function based on Gaussian distribution for leaf temperature and the function for light-intensity proposed by Guenther *et al.* (1993) in the fitness to the measurements. The RMSE of each month in the model were 38.79, 31.26, 86.24, 46.24, 44.16, 60.89 and 62.53 in September 2015 to March 2016, respectively. Overall, this study established a foundation of estimating total amount of canopy-scale isoprene emission in the moso bamboo forest. For precise estimation, an isoprene emission model for annual canopy-scale should consider not only the effect of leaf temperature and light intensity but also variations in potential emission rates within canopy and phenological and physiological effects in spring.

Key words: Isoprene, moso bamboo, canopy variation, model development, seasonal variation

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Contents

doi:10.6342/NTU201603083

doi:10.6342/NTU201603083

doi:10.6342/NTU201603083

Figure index

doi:10.6342/NTU201603083

doi:10.6342/NTU201603083

Table index

doi:10.6342/NTU201603083

Chapter 1 Introduction

1.1 Importance of isoprene

Isoprene (2-methyl-1,3-butadiene), one of the volatile organic compounds (VOCs), is a highly volatile and reactive hydrocarbon. The oxidation of isoprene and its oxidation products can significantly contribute to the formation of ozone and other oxidants by reacting with nitrogen oxides (Biesenthal *et al.*, 1997). Furthermore, isoprene chemistry may be the main factor of the ozone formation in rural areas (Dreyfus *et al.*, 2002). Isoprene is also a precursor compound of secondary organic aerosols (Claeys *et al.*, 2004). Both ozone and secondary organic aerosol are important pollutants in troposphere. Ozone can cause human respiratory mortality (Anenberg *et al.*, 2010) and also risks for declines of crops and pastures by exposure (Fuhrer, 2009); secondary organic aerosols can cause human health effects such as allergy, asthma, cardiovascular and respiratory diseases (Shiraiwa *et al.*, 2012).

As a highly reactive chemical, isoprene will compete radical (e.g. hydroxyl) with methane, subsequently increase the lifetime of methane by about 15% (Poisson *et al.*, 2000). Scilicet, although isoprene is not a greenhouse gas, it could contribute to greenhouse effect indirectly.

Sindelarova *et al.* (2014) estimated that annual global plant-emitted VOCs (so

doi:10.6342/NTU201603083

called “Biogenic VOCs” or “BVOC”) amount in the last 30 years (from 1980~2010) average was about 760 Tg C yr^{-1}; among the VOCs, isoprene attributed about 523 Tg C yr^{-1}, which accounted for about 70% of the total amount. Such emissions exceeded the global emission of anthropogenic VOCs (142 Tg C yr^{-1}) (Middleton, 1995). Since the isoprene emission of plants is highly related to temperature (Tingey *et al.*, 1981), climate change can chronically influence the isoprene emission amount from plants; the effect of climate change might lead to 1.34 times of isoprene emission amount from plants in 2090 as that in 1990 with the investigation using a global three-dimensional general circulation model coupled to a dynamic vegetation and chemistry models, and resulting an increase of surface ozone level by 20-30 ppbv (Sanderson *et al.*, 2003).

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1.2 Significance of moso bamboo

Moso bamboo (*Phyllostachys edulis*) is a monopodial type bamboo with rapid-growing rhizome, which causes the expansion of moso bamboo forest. Meanwhile, the shoot of moso bamboo has a high shade tolerance which let it can easily invade into intact forests (Wang *et al.*, 2016).

It has been noticed that moso bamboo forests have an expanding tendency. For instance, Okutomi *et al.* (1996) discovered that moso bamboo coverage increased from 24 km^2 to 174km^2 from 1953 to 1985 in Kyoto. A research of aerial photographs analysis found that an invasion phenomenon occurred in some regions of Taiwan (Chiou *et al.*, 2009).

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1.3 Motivation and objectives

Most of the related studies focused on “timber trees” rather than other type of forest such as a bamboo forest, but the emission characteristics of bamboo are still not well understood. However, bamboos are important forest types in Taiwan. A study on black bamboo (*Phyllostachys nigra*) also brought out the issue that bamboos might have strong ability to emit isoprene (Crespo *et al.*, 2013).

To assess the potential impacts of land use changes such as moso bamboo expansion on isoprene emission, models for the better estimation of annual canopy-scale isoprene emission from moso bamboo forests are indispensable. Since some species do not even have an ability to emit isoprene (e.g. Tani and Kawawata, 2008), (1) testing the significance of isoprene emission ability of moso bamboo was the primary objective in this study. Then, to develop the canopy-scale isoprene emission models, understanding spatial and temporal variations in isoprene emission is the key for bottom-up approach estimates (Sindelarova *et al.*, 2014). Thus, the objectives of this study are (2) to clarify the variation of vertical location in emission rate; (3) to clarify the seasonal variation in emission rates and its factors; (4) to develop a model for isoprene emission rate of moso bamboo reproducing the seasonal variations in emission rates. After all, this study aimed to establish the foundation of canopy-scale isoprene emission estimates from a moso bamboo forest.

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Chapter 2 Literature review

2.1 The reason why plants emit isoprene

Since the research of leaf-emitted isoprene had been started for over fifty years (e.g. Sanadze, 1964; Sanadze and Kalandaze, 1966), the reasons why plant emit isoprene is still ongoing. There were many studies hypothesis different reasons, inferred that isoprene emission of plants might have multiple purposes.

The well-discussed theories suggested on the promotion of tolerances to stresses by isoprene. One of the most popular hypotheses is the thermotolerance. For example, Sharkey and Singsaas (1995) indicated that isoprene can promote the tolerance of leaves to thermo-damage, although some evidence did not sustain this hypothesis: Logan and Monson (1999) examined four isoprene-emitted plant species with *in vitro* experiments and found that no significant thermo-damage occurring behavior change between isoprene-exposed leaf discs and non-exposed leaf discs. Singsaas and Sharkey (1998) indicated that the thermotolerance is achieved mainly after short and repeated heat bursts, this might explain the difference of these two studies.

Another hypothesis is that isoprene can prevent damage caused by ozone exposure. According to the thesis of Velikova and Loreto (2001), with studying of a isoprene-emitting plant (*Phragmites australis*), indicated that the individuals which isoprene synthesis were inhibited would be damaged harder than normal individuals

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by ozone. Loreto *et al.* (2001) also demonstrated that non-isoprene-emitting plants which were fumigated with exogenous isoprene reduced the damage to leaves caused by exposure of ozone. The previous study suggested that isoprene played a very strong antioxidant role in plants, not only in isoprene-emitting species but other plants.

The mechanism of both the tolerance might attribute to that membrane lipid bilayers can be strengthened by isoprene (Sharkey, 1996). Further, by using molecular dynamics simulation techniques, Siwko *et al.* (2007) identified that isoprene partitions preferentially in the center of chloroplast membrane bilayer and enhances the packing of lipid tails; as a result, the partition of isoprene in membrane can increase the stability of the membrane under high temperature, dose-dependently.

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2.2 Short and long term factors controlling plant isoprene emission rate

Working with isoprene emission from plant, former studies found that environmental factors can influence isoprene emission rate (Sanadze and Kalandadze 1966; Rasmussen and Jones 1973; Tingey *et al.*, 1979). Reviewing with works of BOVCs, Monson *et al*. (2012) suggested that the principal factors influencing isoprene emission rate can be separated into two sorts: short term factors and long term factors. Short term factors included temperature, light intensity, intercellular CO_2 concentration and stomatal conductance which can instantaneously affect the productivity of isoprene biochemical processes in plants; and long term factors included weather, water stress, position in the canopy and developmental stage of the leaf (Tingey *et al.*, 1981; Kuzma and Fall, 1993; Monson and Fall, 1989; Sharkey and Yeh, 2001; Niinemets *et al.*, 2010a,b; Niinemets *et al.*, 2015) which can affect the potential capacity of isoprene production in plants.

Generally, leaf temperature and light intensity were the most concerned factors in isoprene emission rate from plants; also, these two factors were the most adopted factors in modeling. Numerous studies (Sanadze, 1964; Tingey *et al.*, 1981; Monson and Fall, 1989; Loreto and Sharkey, 1990) tested and verified that a linkage exists between photosynthetic CO_2 assimilation rate and isoprene emission rate; moreover,

doi:10.6342/NTU201603083

the similar response to light processes of the assimilation rate and emission implied that the light intensity can be used on estimation of isoprene emission rate; later, understanding of the biochemical connection between photosynthesis and isoprene biosynthesis directly confirm the linkage (Lichtenthaler *et al.*, 1997; Schwender *et al.*, 1997). Also, several studies found that the emission rate is highly related to temperature, increasing in exponential shape with increasing leaf temperature in first and decreases precipitously after a maximum temperature (e.g. Monson and Fall, 1989; Guenther *et al.*, 1991; Guenther *et al.*, 1993). The relation between temperature and emission rate could be explained with the precursor availability and synthase (enzyme for synthesis) activity in isoprene biosynthesis (Rasulov *et al.*, 2010).

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2.3 Models for estimating plant isoprene emission rate

Tingey *et al.* (1979) modeled the isoprene emission with considering the effects of light intensity and leaf temperature. The model was defined into a general logistic function:

$$\log(E) = \frac{a}{1+\exp[-b\cdot(x-c)]} + d \qquad \text{Equation 1}$$

(E, isoprene emission rate; x, value of light intensity or leaf temperature considered as an independent variable; a, a coefficient that representing the variation between the minimum and the maximum values of E; b, a 'shape parameter' that determines the slope; c, a 'location parameter' that determines the intercept along the x-axis; d, the minimum value predicted by the function). This model defined the response of isoprene emission rate as a general nonlinear fashion, and first increase with light intensity or leaf temperature then saturates. The parameter values for Equation 1 are determined using nonlinear least-squares regression; this means that this model lacking sense of biochemical mechanism, it only fits the form of isoprene emission by considering mathematical strategies.

Guenther *et al.* (1991) developed a model which considered the effect of light intensity, leaf temperature, relative humidity (*RH*) and atmospheric CO_2 concentration; a basal emission capacity (B) can be adjusted by instantaneous changes in the

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environment variables. The value for B was defined as the emission rate at a standard environmental condition. The equation is described below:

$$E = B \cdot L \cdot T \cdot H \cdot C \qquad \text{Equation 2}$$

(L, T, H and C are calculated variables determined by functions linked to light intensity, leaf temperature, *RH* and atmospheric CO_2 concentration, respectively.) Different to Tingey *et al.* (1979), this model considered the biochemical mechanism; furthermore, this model divided the environmental control of E into two parts, including longer-term dynamics determined as B and shorter-term dynamics determined as L, T, H and C. Later works on isoprene emission models usually follow this dividing strategy.

The *RH* and atmospheric CO_2 concentration were shown to be small when considered across the range of conditions encountered by an isoprene-emitting leaf; therefore, in later study (Guenther *et al.*, 1993), the value of E was described and standardized using only light intensity and leaf temperature in later version of isoprene emission rate model:

$$E = B \cdot L \cdot T \qquad \text{Equation 3}$$

Although there are many global scale models for isoprene emission amount have been developed (e.g. Guenther *et al.*, 1995; Schwede *et al.*, 2005; Guenther *et al.*,

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2012), we aimed on the isoprene emission rate of a single species and its determine factors in this study; therefore, we only use the model developed by Guenther *et al.* (1993) for data analysis and exemplary of regression model development.

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Chapter 3 Material and methods

3.1 Research site

This study was conducted in Xitou Experimental Forest of National Taiwan University, central Taiwan (23° 40’ N, 120° 47’E, elevation 1120 m). The long term temperature and precipitation data were acquired by meteorological station in Xitou from 1941 to 2008. According to the data, average annual temperature was about 16 ℃. The highest and the lowest monthly average temperature occurred in July (24.5℃) and December (9℃), respectively. The average annual precipitation was 2614 mm; the dry season occurred from the October to January with the mean monthly, and the rainy season occurred from May to September (Lin, 2015).

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3.2 Sampling of isoprene emission

This study used a photosynthesis system (Li-Cor 6400XT, Li-Cor Inc., Lincoln, NE, USA) to measure environment data including light intensity (expressed in Photosynthetic photon flux density, PPFD, μmol m^{-2} s^{-1}) and leaf temperature, and to collect leaf-emitted air according to Okumura *et al.* (2008). The assembly methods are showed in Figure 1 a, b. For collecting leaf-emitted air, the outlet air flow from the leaf cuvette was divided into two ways by a Teflon T-junction. The air could be drawn into the built-in infrared gas analyzer through the one of the ways; another way would be connected to a stainless steel tube filled with adsorbents (200 mg Tenax and 100 mg Carbotrap, Supelco Inc., Bellefonte, PA, USA) to trap volatile organic compounds (VOCs) including isoprene when a sampling starts. The air supply to the LI-6400XT was drawn from a box and sent through a granular activated charcoal filter to supply VOC-free air. In different canopy locations measurement (Chapter 3.4) and monthly measurement (Chapter 3.5), the original leaf cuvette would be replaced by a cuvette with LED radiation source which can supply stable light intensity (unit in PPFD)(Li-Cor 6400-02B, Li-Cor Inc., Lincoln, NE, USA).

In each sampling, the target leaf would be covered by the leaf cuvette, and a pre-conditioned stainless steel tube filled with adsorbents would be connected to T-junction. Then, the other side of the tube would be connected to a minipump

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(MP-∑30NⅡ, Sibata Inc., Tokyo, Japan). After the connections completed, we would start the minipump at a flow rate of 200 mL min^{-1} for 10 minutes. During the pumping process, the environmental data would be measured once per minute (9 times in a single sampling).

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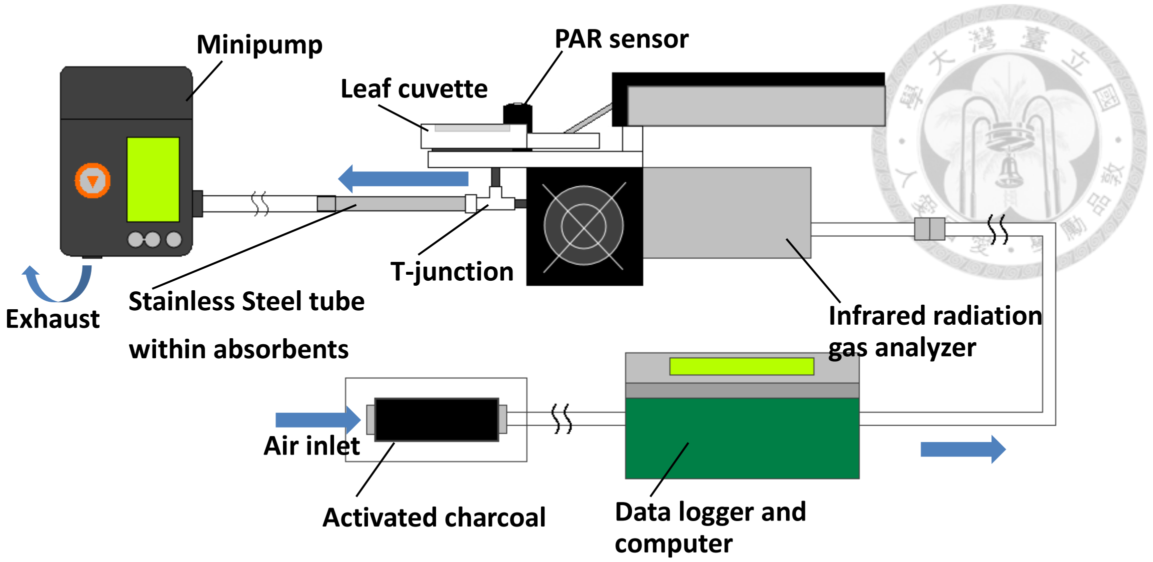
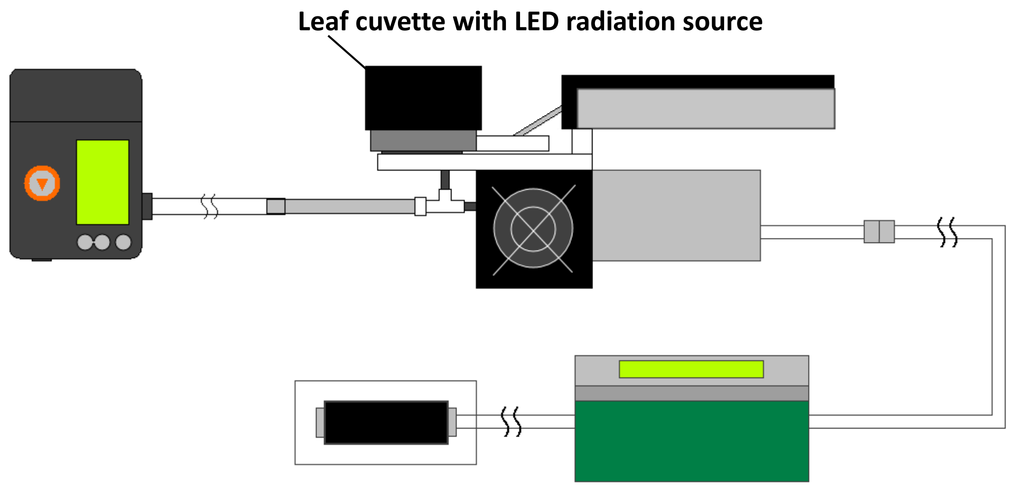


a)



b)

Figure 1 Schematic diagram of instruments (Li-Cor 6400XT) used in this study, including a) without and b) with a LED radiation source (Li-Cor 6400-02B).

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3.3 Screening multiple bamboo species

The measurements were conducted in a bamboo specimen garden in the experimental forest in November 12th, December 14th and 15th, 2014. 14 species or subspecies of bamboo were selected for the screening (Table 1). The measuring month, replication number (*n*), average leaf temperature and PPFD were shown in Table 1. Replication number (*n*) represents the number of sampling in a species. Each sampling was conducted on different leaves on different individuals.

The average air temperatures during measurement in November 12th, December 14th and 15th were 21.8, 17.6℃ and 26.2℃, respectively; the relative humidity was 47.9%, 46.3% and 46.6%, respectively; the PPFDs were 89.6, 174.0 and 867.3 μmol m^{-2} s^{-1}, respectively. During the measurements in November 12th and December 14th, the weather was cloudy; during December 15th, the weather was sunny in morning but became foggy in afternoon.

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Table 1 List of 14 measured bamboo including tribe (from Sungkaew *et al.* (2009)), species, measuring month, replication number (*n*), average leaf temperature (℃) and average light intensity (PPFD: μmol m^{-2} s^{-1}).

Tribe	Species	Month	*n*	Leaf temp.	PPFD
Bambuseae	*Bambusa oldhami*	December	3	20.8	590.8
Bambuseae	*Chimonobambusa marmorea* cv. *Variegata*	December	4	29.8	328.5
Bambuseae	*C. quadrangularis*	November	4	25.5	176.4
Bambuseae	*Dendrocalamus asper*	December	3	31.0	1139.7
Bambuseae	*D. Giganteus*	November	3	22.2	71.8
Bambuseae	*D. latiflorus* Munro. cv. *Mei-nung*	December	3	22.7	269.1
Bambuseae	*D. latiflorus* Munro. cv. *Subconvex*	December	3	31.2	835.3
Bambuseae	*Phyllostachys Bambusoides*	November	3	21.1	59.8
Bambuseae	*P. Edulis*	December	3	20.5	114.4
Bambuseae	*P. lithophila* Hayata	December	2	26.9	170.4
Bambuseae	*P. Makinoi*	November	3	21.1	90.5
Bambuseae	*Semiarundinaria fastuosa*	December	3	17.6	236.0
Bambuseae	*Thyrsostachys siamensis*	December	3	20.3	163.8
Arundinarieae	*Yushania niitakayamensis*	December	3	15.9	107.3

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3.4 Difference between canopy locations

A 70 m^2 experiment plot was established in a pure moso bamboo forest near the bamboo cottage in Xitou experimental forest, and the measurement was conducted on November 14th, December 20th, 21st 2015 and March 15th and 16th 2016. One (Bamboo A), three (Bamboo B, C and D) and three (Bamboo E, F and G) individuals were chosen for this measurement in November, December 2015 and March 2016, respectively. Total 7 bamboos were measured in the measurements. The chosen individuals were cut down, and this study measured the individual height and canopy length before the air sampling.

The measurements were taken on bottom, middle and top location in the canopy of each individual. We determined the bottom location as a range from canopy bottom to 1m above the canopy bottom; the middle location was determined as a range from 0.5m above to 0.5m below the median of the canopy length; the top was determined as a range from the canopy top to 1m below the canopy top. For example, if a canopy is 10m long, bottom, middle and top location will be 0~1m, 4.5~5.5m and 9~10m above its canopy bottom, respectively.

The PPFD of all samplings were set at 1000 μmol m^{-2} s^{-1}. Samples at each location were taken one to three times, each time measurement was conducted on a different leaf. All of the measurements in each individual were completed within 5

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hours after the cutting.

Table 2 Seven individuals of bamboo in the different canopy location measurements with measurement months, replication number (*n*), height, canopy length, and diameter at breast height (DBH).

Individuals	Month	*n*	Height (m)	Canopy length (m)	DBH (cm)
Bamboo A	Nov. 2015	3	15.59	10.06	11.1
Bamboo B	Dec. 2015	1	11.49	7.50	6.6
Bamboo C	Dec. 2015	1	12.65	4.12	8.7
Bamboo D	Dec. 2015	1	12.84	7.60	8.3
Bamboo E	Mar. 2016	3	11.64	8.40	6.7
Bamboo F	Mar. 2016	3	10.22	7.37	5.9
Bamboo G	Mar. 2016	3	13.19	7.38	9.0

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3.5 Monthly measurements for seasonal variations

The measurement was carried out in a managed bamboo forest in front of the 70 m^2 plot (near Bamboo Cottage in Xitou experimental forest) from September 2015 to March 2016. The ambient CO_2 flux was very stable during the whole measurement (ranging in 350-400 μmol m^{-2} s^{-1}, mainly in about 360-380 μmol m^{-2} s^{-1}).

All measurements were taken on the bottom of bamboo canopies. Due to the difficulty of reaching some bamboo canopies, some samplings were taken using excised leaves. The excising method was always conducted by cutting on the first-order branch of the target leaf. Then, the incision would be put in water immediately, and cut again 5 cm or longer from the incision with the new incision be in water for removing air embolisms. A pre-examine showed no significant change on isoprene emission capacity among intact to excised for three hours of leaves.

All samplings were carried out by using a modified photosynthesis system and replaced the original leaf cuvette to a LED radiation-source cuvette which described in Chapter 3.2 in this article (Fig. 1b). Each target leaf was measured 4~6 times for different PPFD levels (one stable PPFD in a time) from 250 to 2500 μmol m^{-2} s^{-1}. All of the measurements in each leaf were completed within 3 hours. In each month, this study measured the isoprene emission rates in relation to PPFD in three to five leaves.

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3.6 Qualification and quantification of VOCs samples

Collected VOCs samples in absorbents were analyzed by an automatic thermal deposition system (TurboMatrix ATD-400, Perkin Elmer Inc., Waltham, MA, USA) combined with a gas chromatography (with a flame ionization detector) (GC-17A/QP5050A, Shimadzu Inc., Kyoto, Japan) in Kyoto University to qualify and quantify isoprene. First, the samples would undergo a two-stage thermal desorption to release compound gas trapped in the adsorbents with the automatic thermal deposition system, and the released compound would enter into the gas chromatography. Compounds would be separated by using an SPB-5 capillary column (length: 60 m, diameter: 0.25 mm, ID, 1 μm, Supelco Inc., Bellefonte, PA, USA) with helium (purity >99.9995%) as the carrier gas. The column temperature was maintained at 30℃ for 5 minutes, raised to 60℃ at 5℃ min^{-1}, and then raised again to 250℃ at 40℃ min^{-1}. The carrier gas pressure, column flow rate, linear velocity, and split ratio were 108.5 kPa, 1.0 mL min^{-1}, 25.7 cm s^{-1}, and 15:1, respectively. An analytical curve was obtained by collecting and analyzing different volumes (10, 20, 40, 60 and 80 mL) of isoprene standard gas (1.03 ppmv) (R=0.999136).

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3.7 Data analysis

3.7.1 Isoprene emission rate calculation

Each isoprene amount should be converted into a flux unit (nmol m^{-2} s^{-1}). Each amount was divided by its sampling period (600 seconds) and in-cuvette leaf area.

There were two situations while determine a leaf area: (1) the leaf area exceeded the cuvette area; (2) the in-cuvette leaf area was smaller than the cuvette area. When the leaf area exceeded the cuvette area, we determine its in-cuvette area as the cuvette area (0.0006 m^2), otherwise, we took the samples back to laboratory and calculated the in-cuvette area by an image processing and analyzing software (Image J, National Institutes of Health, USA).

3.7.2 Standardization of isoprene emission using environmental data

Environmental condition, which could affect the isoprene emission rate, changes among samplings dates. In some measurements (e.g. multiple bamboo species screening, vertical variation of isoprene emission), the environment effects must be corrected in order to compare isoprene emission capacity among different samples. This study used an algorithm which was developed by Guenther *et al.* (1993) and corrected by Monson *et al.* (2012) (hereinafter referred to as "G93 model") to standardize environment condition of plant isoprene emission rate. The algorithm is basically relined on Equation 3 in Chapter 2.3. According to the algorithm, we can

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obtain the estimations of the isoprene emission rate under a basal environment condition of each individual as:

$$B_i = \frac{E_i}{L \cdot T} \qquad \text{Equation 4}$$

Where B_i is the standardized emission rate at a basal condition (the basal condition is set at PPFD = 1000 μmol m^{-2} s^{-1} and leaf temperature = 30℃ or 303K), E_i is the original isoprene emission rate, L and T are calculated variables determined by functions which were related to PPFD and leaf temperature, respectively.

L is defined as:

$$L = \frac{\alpha \cdot C_L \cdot \text{PPFD}}{\sqrt{1+\alpha^2 \cdot \text{PPFD}^2}} \qquad \text{Equation 5}$$

Where α (= 0.0027) and C_L (= 1.066) are empirical coefficients, determined by the measured data from Guenther *et al.* (1993). With a correction developed by Monson *et al.* (2012), we can resolve the problem of having unequal dimension and L becoming invalid when PPFD = 0 in Equation 4. The corrected equation is described below:

$$L = \frac{\alpha \cdot c_{L1} \cdot \text{PPFD}}{\sqrt{1+\frac{\alpha^2 \cdot \text{PPFD}^2}{{c_{L2}}^2}}} \qquad \text{Equation 6}$$

doi:10.6342/NTU201603083

Where c_{L1} is now defined with units in m^2 s μmol^{-1} and an additional coefficient, c_{L2}, is defined with units in μmol m^{-2} s^{-1}. c_{L2} can be set to 1 to fit the original form of Equation 5.

T is defined as:

$$T = \frac{\exp\left\{\frac{C_{T1}\cdot(T_L - T_S)}{R\cdot T_S\cdot T_L}\right\}}{1+\exp\left\{\frac{C_{T2}\cdot(T_L - T_M)}{R\cdot T_S\cdot T_L}\right\}} \qquad \text{Equation 7}$$

Where R is the gas constant (= 8.314 J K^{-1} mol^{-1}). T_M is a constant temperature value (= 314K), T_S is the leaf temperature in basal condition (=303K), T_L is the leaf temperature (unit: K) in the sampling, C_{T1} (= 95000 J mol^{-1}) and C_{T2} (= 230000 J mol^{-1}) are the empirical coefficients determined by the measured data with non-linear best fit method according to Guenther *et al.* (1993).

In the multiple bamboo species screening, we did not use any instrument for adjusting environment condition; therefore, we directly applied the standardization to all of the data in the screening.

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3.8 Developing model for temporal of isoprene emission rate

According to Guenther *et al.* (1993), the instantaneous isoprene emission rate can be estimated with PPFD and T_L using a generic model as mentioned above. However, the model proposed by Guenther *et al.* (1993) was developed with temperate broadleaf species which are genetically far from moso bamboo. Therefore, we should check the applicability, and furthermore, develop a better performance model for moso bamboo's isoprene emission rates.

3.8.1 Effect of the leaf temperature

We used the data in the monthly measurement. First, we selected the data with PPFD of 1000 μmol m^{-2} s^{-1} for fitting the function related to leaf temperature (T) and B_i based on Equation 4. The Equation 4 can be described as:

$$\frac{E_i}{L} = B_i \cdot T \qquad \text{Equation 8}$$

This study assume $\frac{E_i}{L}$ as the isoprene emission rate which is standardized with light intensity, and we defined E_{iL} as $\frac{E_i}{L}$.

$$E_{iL} \stackrel{\text{def}}{=} \frac{E_i}{L} \qquad \text{Equation 9}$$

Then we define $\widehat{E_L}$ as the estimator of E_{iL} and we supposed that $\widehat{E_L}$ can be described as a function with leaf temperature (T_L) as the independent variable. We

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considered $\widehat{E_L}$ using three kinds of distribution functions to derive the better regression for the measurement data. Then, we compared fitness of the three distribution functions using square of coefficient of determination (R^2), root mean square error (RMSE) and small-sample-size corrected version Akaike information criterion (AICc), and decided which distribution had the best fitting among them. The three distributions are: (1) Gaussian distribution, (2) Exponential distribution and (3) G93 leaf temperature distribution. The corresponding function of these three distributions described as:

(1) Gaussian distribution:

$$\widehat{E_L}(T_L) = d \cdot \frac{\exp\left[-\frac{(T_L-b)^2}{2 \cdot a^2}\right]}{a \cdot \sqrt{2c}} \qquad \text{Equation 10}$$

Where *a*, *b*, *c* and *d* are parameters to decide the shape of the distribution function.

(2) Exponential distribution:

$$\widehat{E_L}(T_L) = m \cdot p^{\frac{T_L-o}{n}} \qquad \text{Equation 11}$$

Where *m*, *n*, *o* and *p* are parameters to decide the shape of the distribution function.

G93 leaf temperature distribution:

$$\widehat{E_L}(T_L) = \frac{\exp\left[\frac{C_{T1} \cdot (T_L - T_S)}{R \cdot T_L \cdot T_S}\right]}{1+\exp\left[\frac{C_{T2} \cdot (T_L - T_M)}{R \cdot T_L \cdot T_S}\right]} \cdot B_i \qquad \text{Equation 12}$$

doi:10.6342/NTU201603083

The idea of the distribution function came from original G93 model (Guenther *et al.*, 1993), and this study inferred this equation from Equation 4, Equation 7 and Equation 9. This study followed the parameter design of G93 model, therefore, the definition of C_{T1}, C_{T2}, R, T_s, T_M can refer to Chapter 3.7.2. In this part, we assumed C_{T1}, C_{T2} and B_i as parameters.

To determine the regression functions, we used the least square error method. Notice that the isoprene emission rate estimation, which is one of the main goals of the model, is highly sensitive to the digit. However, the distributions we used were very variable in the digit, therefore, if we used ordinary error (deviation between the actual value and the predicted value), the model would have a serious distortion. So we defined the error as below:

$$\text{error} = \frac{E_{iL}}{\widehat{E_L}(T_L)} - 1 \qquad \text{Equation 13}$$

To fit the parameters in the G93-leaf-temperature function, we should first decide the value of T_M; and to decide the value of T_M, we ran the least square error regression with restriction that $0.99 \leq \frac{\widehat{E_L}(303.15)}{B_i} \leq 1.01$ to a series of T_M value (308, 310, 312, 314, 316 and 318) respectively. When T_M at 312, the regression has the highest correlation coefficient (R) among the series, so we chose the regression result when $T_M = 312$. As well, B_i in G93-leaf-temperature $\widehat{E_L}$ was determined as a parameter based on the least square error regression as the B_i was included in

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Equation 12. On the other hand, B_i for the other two functions, which did not include the B_i, was acquired using the follow equation:

$$B_i = \frac{\widehat{\mathrm{E}_L}(303.15)}{L(1000)}\ ;\ L(1000) \approx 1 \qquad \text{Equation 14}$$

Where $\widehat{\mathrm{E}_L}(303.15)$ and $L(1000)$ represent the function with leaf temperature of 303.15 K (namely, 30℃) and L with PPFD of 1000 μmol m^{-2} s^{-1}, respectively.

3.8.2 Effect of the light intensity

We used the measured data in the monthly measurement which include a series of artificially fixed light intensity from PPFD = 250 to 2500 μmol m^{-2} s^{-1} for the regression. The data were preprocessed with the three acquired functions related to leaf temperature (T) in Chapter 3.8.1 and a re-described Equation 4. We re-described Equation 4 as:

$$\frac{E_i}{T} = B_i \cdot L \qquad \text{Equation 15}$$

Then, we assumed $\frac{E_i}{T}$ as the isoprene emission rate which is standardized with leaf temperature, and we defined E_{iT} as $\frac{E_i}{T}$.

$$E_{iT} \stackrel{\text{def}}{=} \frac{E_i}{T} \qquad \text{Equation 16}$$

Then we define $\widehat{\mathrm{E}_T}$ as the estimator of E_{iT}. We considered $\widehat{\mathrm{E}_T}$ as the distribution function defined by Guenther *et al.* (1993), which can be described below:

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$$\widehat{E_T}(\text{PPFD}) = B_i \cdot L = \frac{B_i \cdot \alpha \cdot C_L \cdot \text{PPFD}}{\sqrt{1+\alpha^2 \cdot \text{PPFD}^2}} \qquad \text{Equation 17}$$

We followed the parameter design of G93 model, therefore, the definition of α, C_L, can refer to Chapter 3.7.2; notice that the value of B_i is determined in Chapter 4.4.1.

To make the best-fit regressions to our data, we used the least square error method and seemed α and C_L as the parameters. The error was defined as the deviation between the actual value and the predicted value since the G93-light-intensity distribution has no such problem of related to digit occurred in leaf temperature distributions functions. The definition of the error described as below:

$$\text{error} = E_{iL} - \widehat{E_L}(T_L) \qquad \text{Equation 18}$$

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Chapter 4 Results and discussions

4.1 Multiple bamboo species screening

Figure 2 shows the standardized isoprene emission rates of each 14 species of bamboo used in the measurements. *B. oldhami*, *P. Edulis* and *P. lithophila* Hayata had relatively high emission rates, which were over 20 nmol m^{-2} s^{-1}. All *Dendrocalamus spp.* species showed emission ability of isoprene though the emission capacities were not as high as those of high-emission species (below 10 nmol m^{-2} s^{-1}). Some species had no isoprene emission rate detected in the measurements, including *C. marmorea* cv. *Variegata*, *S. fastuosa*, *T. siamensis* and *Y. niitakayamensis*.

Most of the species that have higher isoprene emission capacity belongs to specific genus (*Phyllostachys* and *Dendrocalamus*). This implies that there is a relationship between isoprene-emitting significance and phylogenetic relation in bamboos.

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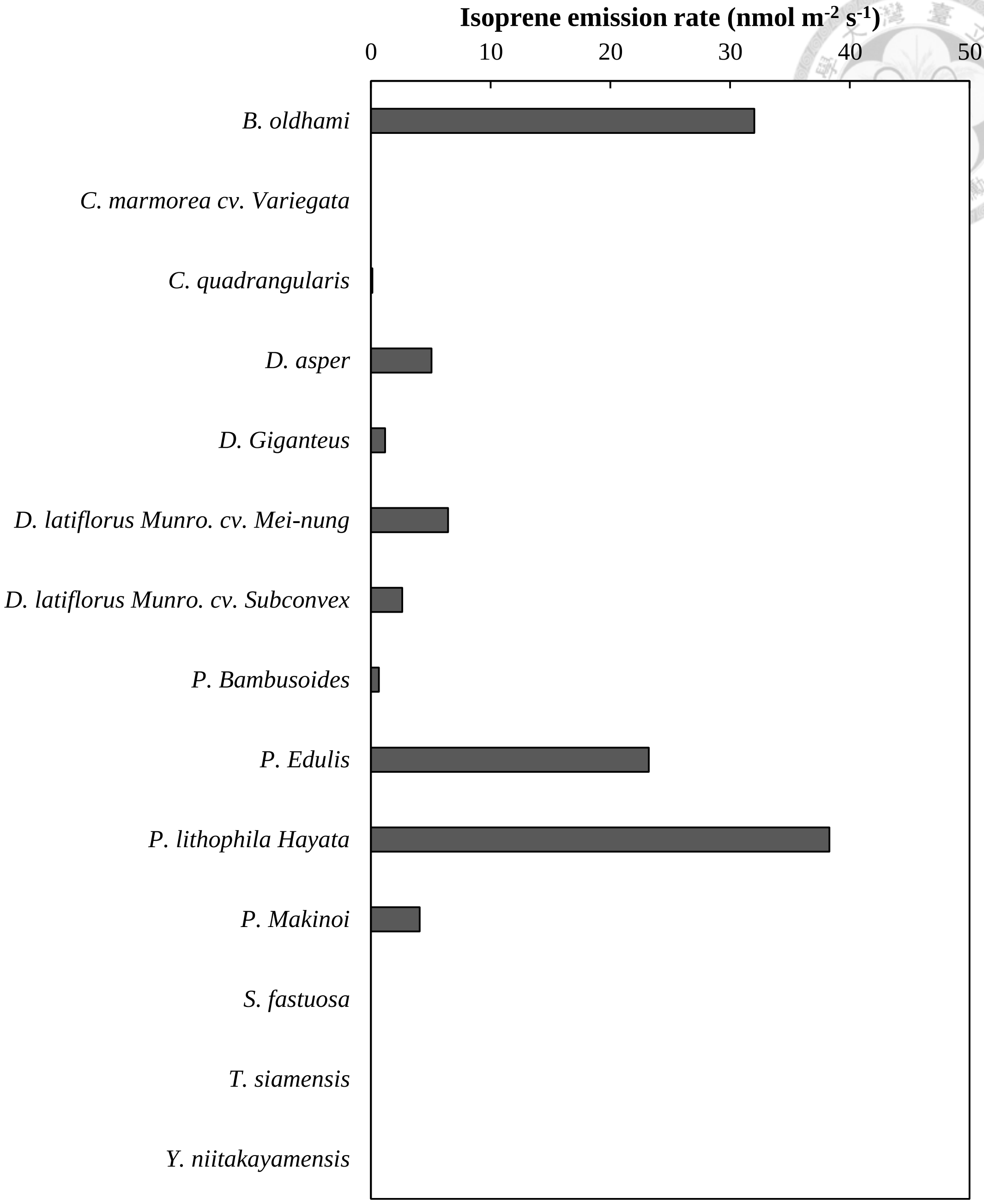

Figure 2 Standardized isoprene emission rates (nmol m^{-2} s^{-1}) of 14 bamboo species.

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Previously, it has been reported that *Quercus spp.* was one of the greatest VOCs emitter (Harley *et al.*, 1999). Previous study examining isoprene emission from 18 *Quercus spp.* species in North America, Geron *et al.* (2001) reported that the emission rates standardized with the same method in this study was about 46 nmol m^{-2} s^{-1}. Another emitter is *Eucalyptus spp.*, of which the basal isoprene emission rate was reported as 3 to 39 nmol m^{-2} s^{-1} with 15 species of *Eucalyptus spp.* measurements in Australia (He *et al.*, 2000). Our measurement demonstrated that bamboos with higher emission capacity: *B. oldhami*, *P. Edulis* and *P. lithophila* Hayata had standardized emission rates of 32.02, 23.20 and 38.30 nmol m^{-2} s^{-1}, respectively. Although the bamboos in this study may not have emission capacities as same as *Quercus spp.* in North America, the isoprene emission of these three species of bamboo are still considerable.

According to this screening, we certified the significance of *P. Edulis* (moso bamboo) in the isoprene emission, suggesting that the investigation of isoprene emission characteristics in moso bamboo is important.

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4.2 Vertical variation of isoprene emission within canopy

Figure 3 shows the standardized isoprene emission rates in relation to height from ground in individuals. We can see that the emission rates slightly increased from lower height to higher height. Bamboo A showed larger emission rate than those of the others, which had longest canopy length and individual height among 7 individuals. This phenomenon cannot be fully attributed to canopy length and individual height because the measuring month of Bamboo A was November 2015, which the leaves had higher isoprene emission capacity in (Chapter 4.3); otherwise, the isoprene emission rates had no determined vertical variations related to the canopy lengths or heights of the individuals.

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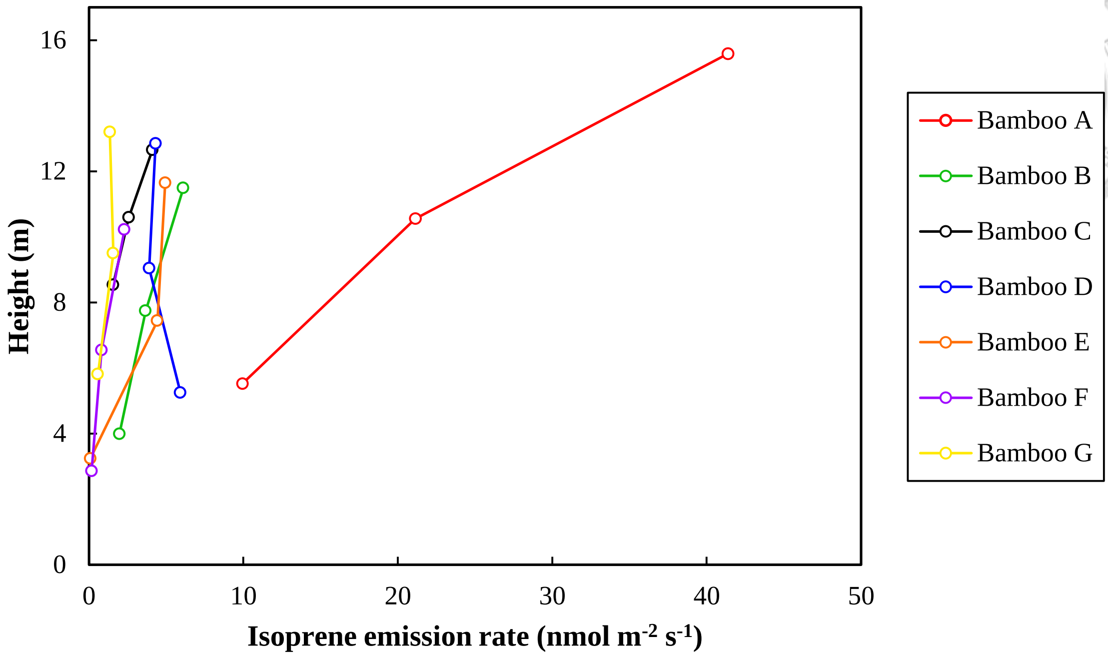

Figure 3 Vertical variations in standardized isoprene emission rates (nmol m^{-2} s^{-1}) of 7 bamboo individuals (open circles with line) with different height (m). Different colors represent data from different individuals (Red, green, black, blue, orange, purple and yellow represent the data from Bamboo A, B, C, D, E, F and G, respectively).

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For checking whether the trend actually exist or not, "relative emission rate" was introduced, which allows us to compare the data among the individuals without differences in isoprene emission capacity. The index was calculated as below:

$$I = \frac{B_{i\text{Location}}}{B_{i\text{Top}}} \cdot 100\% \qquad \text{Equation 19}$$

Where I is the relative emission rate in an individual (relative unit), $B_{i\text{Location}}$ is the standardized isoprene emission rate (nmol m^{-2} s^{-1}) of the bottom, the middle or the top location and $B_{i\text{Top}}$ (nmol m^{-2} s^{-1}) is the standardizing isoprene emission rate of the top location in corresponding individuals. In Figure 4, we can see that lower location had smaller I than that of upper locations. Most of I from the bottom location were 50% lower than that of the top location except Bamboo D. I from the middle location were slightly higher than those of the bottom but 35~90% lower than those of the top except Bamboo G. We used Tukey honest significance test (Tukey's test) to test if there are differences (null hypothesis H_0: no difference between the mean value of two locations; P-value < α to reject null hypothesis; α = 0.05) between each pair of locations. Table 3 shows that the mean value of I in the bottom location was significantly different from that in the top location, but no significant difference between Bottom-Middle and Middle-Top.

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Table 3 The P-value of Tukey's test between each pair of three moso bamboo canopy locations (Bottom, Middle and Top). ("*" sign means P-value < α and reject H_0)

	Bottom	Middle
Middle	0.1590	--
Top	0.0052*	0.2346

When we analyzed the significance of the difference among the locations in individuals (Table 4), we found that only Bamboo E showed the significant difference between the bottom and the top (P-value < 0.05), and the considerable difference between the bottom and the middle (P = 0.062411). The other individuals showed no significance between any pair of locations. Note that statistical tests were not performed in the Bamboo B, C and D due to lack of replications.

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Table 4 The P-value of Tukey's test between each pair of three moso bamboo canopy locations (Bottom, Middle and Top) in four bamboo individuals (Bamboo A, Bamboo E, Bamboo F and Bamboo G). ("*" sign means P-value≦α and reject H_0)

Bamboo A		
	Bottom	**Middle**
Middle	0.821242	--
Top	0.277402	0.548323

Bamboo E		
	Bottom	**Middle**
Middle	0.062411	--
Top	0.041281*	0.940442

Bamboo F		
	Bottom	**Middle**
Middle	0.808466	--
Top	0.171172	0.371374

Bamboo G		
	Bottom	**Middle**
Middle	0.195691	--
Top	0.336813	0.899288

Whether the isoprene emission capacity within the moso bamboo canopy had significant vertical variations, because of the few measurements with higher isoprene emission rates; further studies, measuring vertical profile of emission rate in periods with higher emission rates for relatively lower error, are needed to confirm the variation of canopy locations. Former study reported that the isoprene emission capacity were higher in higher position of canopy in some species of *Populus* and *Salix* (Niinemets *et al.*, 2010b). This phenomenon is reasonable because higher position in canopy has higher temperature, which means that more isoprene is needed to enhance the thermotolerance.

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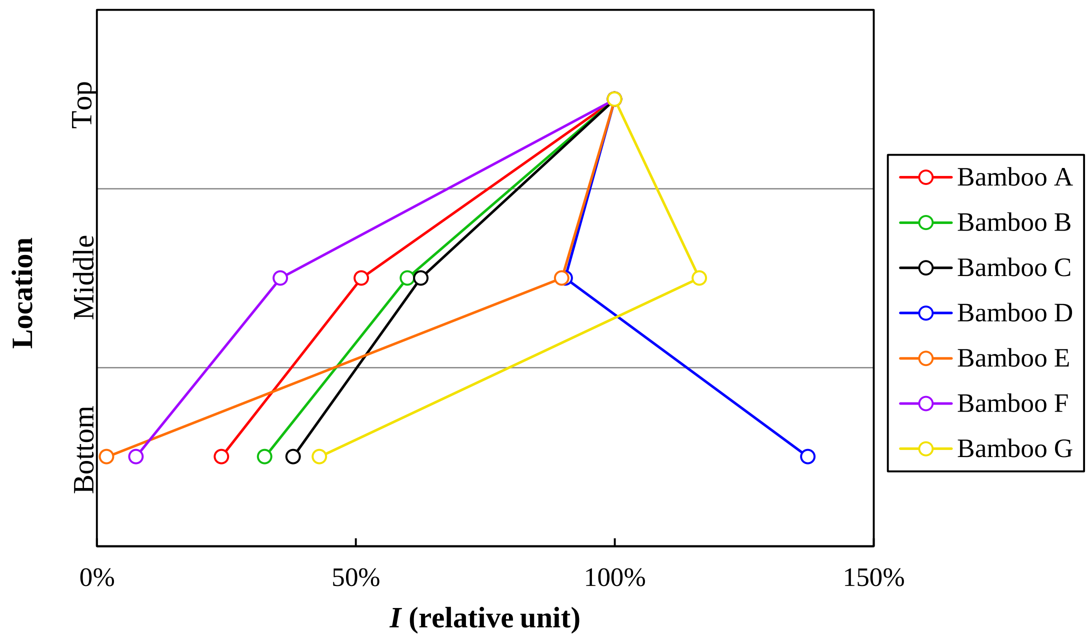

Figure 4 The relative heights (Bottom, Middle and Top) and relative isoprene emission rates (*I*) of 7 bamboo individuals (open circles with line). Different colors represent data from different individuals (Red, green, black, blue, orange, purple and yellow represent the data from Bamboo A, B, C, D, E, F and G, respectively).

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4.3 Seasonal variation of isoprene emission

The data of monthly isoprene emission rates in relation PPFD were shown in Figure 5. The isoprene emission rates increased with PPFD in a manner of logistic-like shape, which were saturated around at PPFD = 1000 μmol m^{-2} s^{-1}. The measurements in September, October and November 2015 showed a relatively higher isoprene emission rates than those in December 2015, January, February and March 2016. According to Tingey *et al.* (1981), isoprene emission rate had a strong relationship with leaf temperature. To confirm the relationship, we plotted the corresponding leaf temperature against the monthly isoprene emission rates with PPFD of 1000 μmol m^{-2} s^{-1} (Fig. 6). The emission rates had an exponential-like trend to the leaf temperature, suggesting the leaf temperature affected the seasonal variation of isoprene emission rate among the months.

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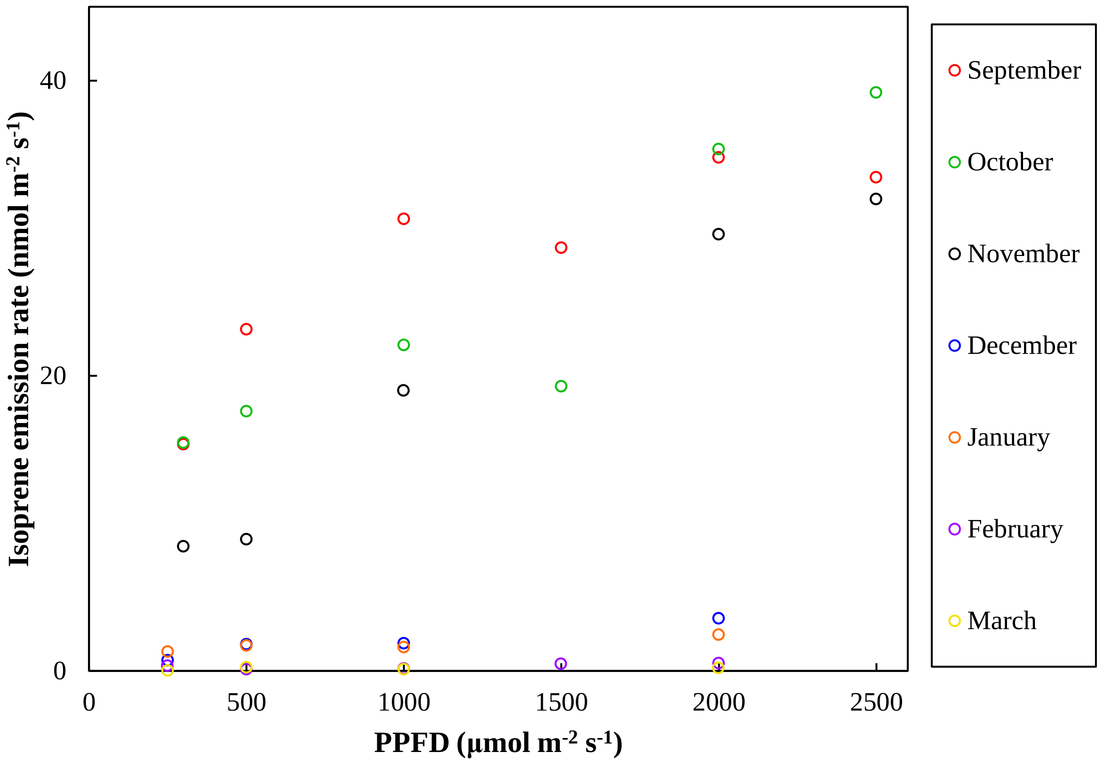

Figure 5 Relationships between the isoprene emission rates (nmol m^{-2} s^{-1}) and light intensities (PPFD, µmol m^{-2} s^{-1}) of monthly measurements (open circles) in 7 months. Different colors represent data measured in different month (Red, green, black, blue, orange, purple and yellow represent the data measured in September, October, November and December 2015, January, February and March 2016, respectively).

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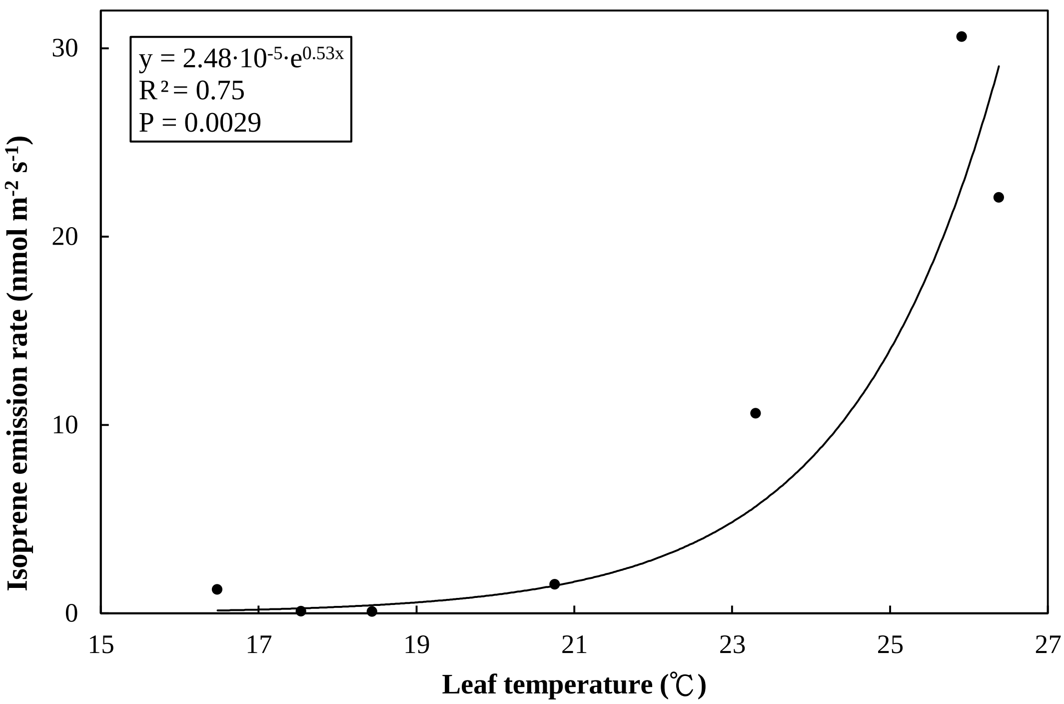

Figure 6 The monthly isoprene emission rates (nmol m^{-2} s^{-1}) and the corresponding monthly leaf temperatures (℃). The solid circle is the monthly isoprene emission rates under artificial light source (PPFD = 1000 μmol m^{-2} s^{-1}), and the solid line is the exponential regression line. The equation, square of coefficient covariance (R^2) with P-value of the regression are shown in box.

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Seasonal variations in the isoprene emission rates and the corresponding leaf temperature were shown in Figure 7. The leaf temperature and the isoprene emission rates showed a similar trend that approximately declining from September 2015 to March 2016. The highest monthly leaf temperature occurred in October 2015 and the lowest monthly average leaf temperature occurred in January 2016; the highest isoprene emission rate occurred in September 2015, and it kept declining from September 2015 to March 2016. On the other hand, the behavior of isoprene emission rates was inconsistent to the leaf temperature during the period between January and March 2016: the leaf temperature of February and March 2016 became higher than that from January, but the isoprene emission rate still declined during the period. Former studies had mentioned about long-term factors that can alter the emission capacity of isoprene emission in plant foliage such as leaf age and developmental stage due to the variation of synthase activity and quantity (Kuzma and Fall, 1993; Niinemets *et al.*, 2015); these implied that there were other factors affecting the biosynthesis processes of isoprene emission in the temporal variation in addition to the leaf temperature.

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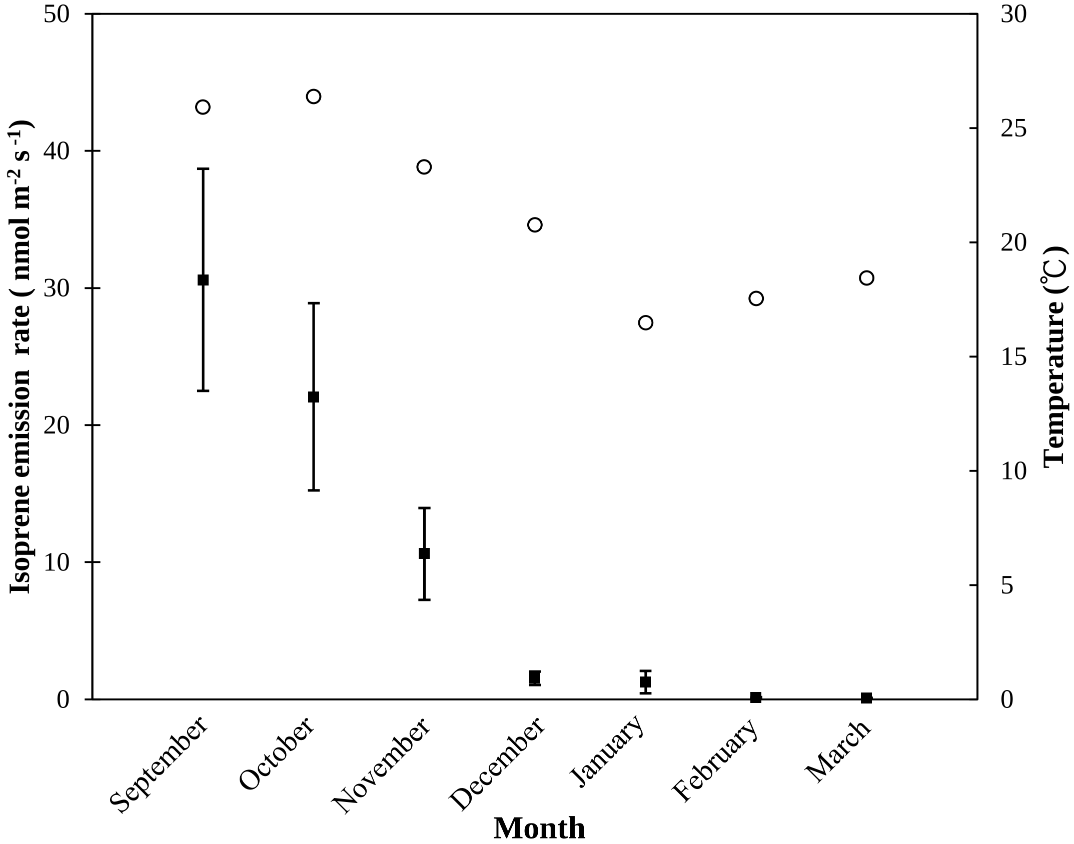

Figure 7 Seasonal variations in isoprene emission rates and the leaf temperatures measured under artificial light source (PPFD = 1000 μmol m^{-2} s^{-1}). Each solid square and error bar represents the average emission rate and standard error of corresponded month from September 2015 to March 2016, respectively. Open circles represent the average leaf temperature of corresponded month from September 2015 to March 2016.

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4.4 Modeling for temporal variation of isoprene emission rate

4.4.1 Effect of the leaf temperature

Figure 8 shows the PPFD-standardized isoprene emission rates in relation to the leaf temperatures and the regression lines of the three distribution functions with the original G93 leaf temperature distribution (Original coefficient values proposed by Guenther *et al.* 1993; where $T_M = 314$, C_{T1} = 95000, C_{T2} = 230000 and $B_i = 42.8$). Isoprene emission rates calculated by the original G93 distribution was lower than those of the three regression lines, when the leaf temperature < about 25℃. On the other hand, the three regression lines increased very much when the leaf temperature > about 26℃. The exponential distribution had the steepest increase in the isoprene emission rates and the Gaussian distribution had the most moderate one. Comparing with the estimation of original G93, the isoprene emission rate of moso bamboo in this study was more "sensitive" to leaf temperature, which means that the moso bamboo has lower emission rate than the estimation of original G93 at first place, then exceeds that in higher leaf temperature; the turning point was about 25℃.

Due to the experimental limitation, this study did not acquire the emission rate data above 30℃; however, plants usually performed an optimum isoprene emission rate at 40-42℃ (Harley *et al.*, 1999) or higher (Niinemets *et al.*, 2010a), and the leaf temperature with optimum isoprene emission rate of moso bamboo obviously

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exceeded the max temperature in this experiment. Therefore, these three regression line may have overestimation of isoprene emission rate in higher leaf temperatures.

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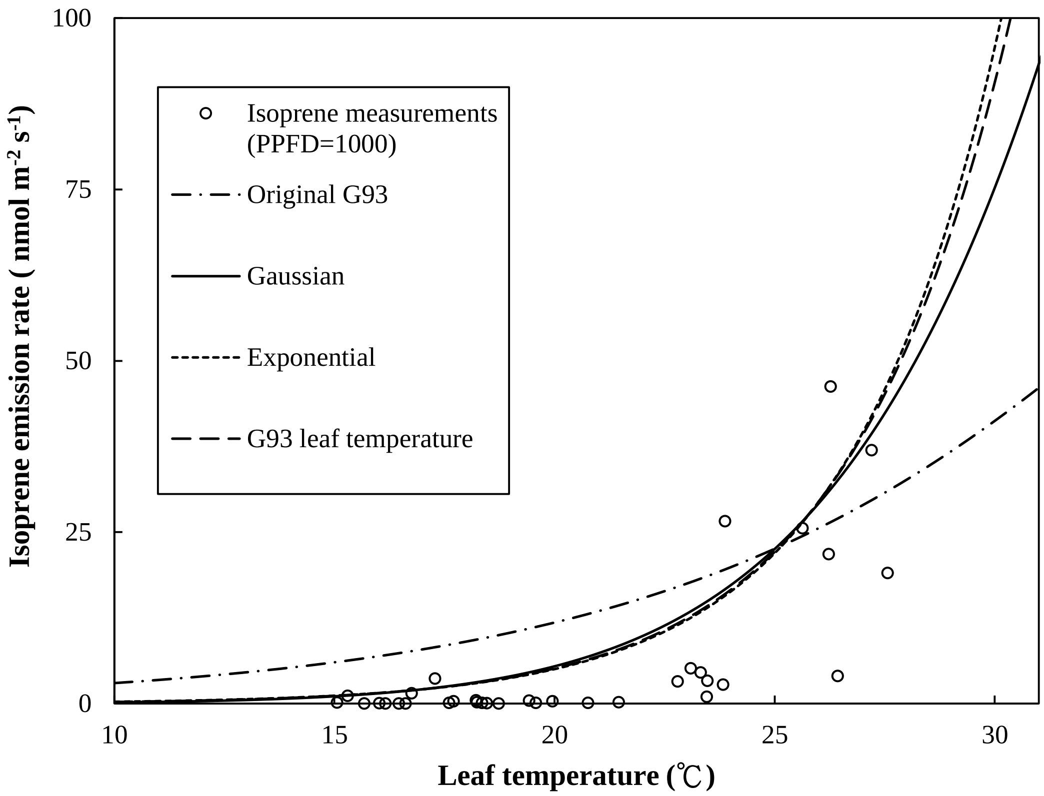

Figure 8 Relationships between the isoprene emission rates and the leaf temperatures. Open circles represent the isoprene emission rates (nmol m^{-2} s^{-1}) under artificial light source (PPFD = 1000 μmol m^{-2} s^{-1}) in monthly measurements. The four fitting curves such as original G93 distribution, the Gaussian, exponential and G93 leaf-temperature distribution regression lines were also shown.

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The determined parameters of the three functions were shown in Table 5 with the parameters of the original G93 function. The Gaussian function showed a little better performance on R^2 and RMSE than that of the others. The G93-leaf-temperature function showed better perform in AICc among the three distribution functions because of the less number of parameters, but it was very close to those of the other two. Overall, the performance of the three distribution functions was better than that of the original G93, but indistinctive differences were found among the three functions.

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Table 5 The values of parameters, basal isoprene emission rate (B_i), squared coefficient of determination (R^2), P-value, root mean square error (RMSE), number of parameters and small-sample-size corrected version Akaike information criterion (AICc) in Gaussian, exponential, G93 leaf temperature and the original G93 leaf temperature distribution functions.

	1st parameter	2nd parameter	3rd parameter	4th parameter	B_i	R^2	P-value	RMSE	Number of parameters	AICc
Gaussian: $d \cdot \frac{\exp\left[-\frac{(T_L-b)^2}{2 \cdot a^2}\right]}{a\sqrt{2c}}$	$a = 10.71$	$b = 328.3$	$c = 2.204 \cdot 10^{-4}$	$d = 266.5$	75.22	0.6135	0	0.8112	4	159.79
Exponential: $m \cdot p^{\frac{T_L-o}{n}}$	$m = 2.016 \cdot 10^{-4}$	$n = 1.662$	$o = 258.8$	$p = 1.632$	95.69	0.6119	0	0.8114	4	161.24
G93 leaf temperature: $\frac{\exp\left[\frac{C_{T1}(T_L-T_S)}{R\,T_L\,T_S}\right]}{1+\exp\left[\frac{C_{T2}(T_L-T_M)}{R\,T_L\,T_S}\right]} \cdot B_i$	$C_{T1} = 212700$	$C_{T2} = 396700$	$B_i = 91.04$	--	91.04	0.6123	0	0.8115	3	158.40
Original G93 leaf temperature:	$C_{T1} = 95000$	$C_{T2} = 230000$	$B_i = 42.80$	--	42.80	0.5687	0.0041	0.8556	3	170.94

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4.4.2 Effect of the light intensity

Figure 9 shows the regression lines determined with leaf-temperature standardized data (E_{iT}) using the three types of T (Gaussian $\widehat{E_T}$, Exponential $\widehat{E_T}$ and G93 leaf temperature $\widehat{E_T}$) as shown in Equation 15 and 16. The Gaussian-standardized regression line saturated at lower PPFD than other two preprocessed regressions; the trends of the exponential-standardized regression and the G93-leaf-temperature-standardized regression were very similar, even so the Exponential-standardized regression line consistently has higher emission rate. Table 5 shows the determined parameters with R^2, P-value and RMSE of the regression. Although the differences were not obvious, the Gaussian-standardized regression showed better performance in p-value; and the Gaussian-standardized regression performed quite better than the others in RMSE. Among the three regressions, the Gaussian-standardized regression showed the best fitting of our data.

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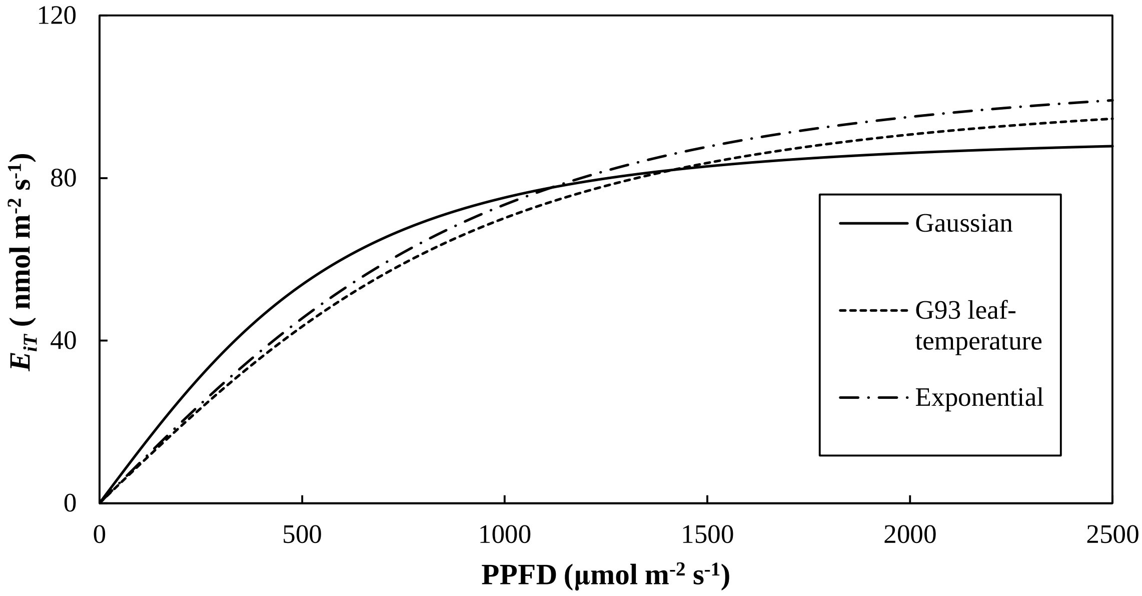

Figure 9 Leaf temperature standardized isoprene emission rates (E_{iT}, nmol m^{-2} s^{-1}) in relation to PPFD (μmol m^{-2} s^{-1}) with the G93 light-intensity regression lines. The standardization was performed using of Gaussian, exponential, and G93 leaf-temperature functions.

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Table 6 The value of parameters (α and C_L), basal isoprene emission rate (B_i), the squared coefficient of determination (R^2), P-value for regression (P-value), and root mean square error (RMSE) in the regression lines of three preprocessed datasets (Gaussian, Exponential and G93-leaf-temperature).

	α	C_L	R^2	P-value	RMSE
Gaussian	0.001463	1.211	0.09864	$7.49 \cdot 10^{-5}$	52.99
Exponential	0.000929	1.128	0.10373	$1.01 \cdot 10^{-4}$	67.63
G93-leaf-temperature	0.000931	1.131	0.10467	$8.24 \cdot 10^{-5}$	63.55

4.4.3 Reproducibility of the model

Since the Gaussian-standardized regression provided better performance in Chapter 4.4.2, this study selected the Gaussian function, and developed the best model consisting with the Gaussian functions for the effect of leaf temperature and the PPFD related function (see Table 5, and 6). Figure 10 shows the leaf-temperature function standardized isoprene emission rate (E_{iT}) measured and calculated with RMSE in each month. The calculations provided better fitting in September, October, December 2015 and January 2016 (RMSE = 38.79, 31.26, 46.24 and 44.16, respectively) compared with other months. In November 2015, February and March 2016, the RMSE were relatively lower (RMSE= 86.24, 60.89 and 62.53, respectively); the

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standardized emission rates of November 2015 were widely spread in higher PPFD, and those of February and March 2016 are obviously lower than the regression line. The reason why the standardized isoprene emission rates of November 2015 widely spread was still unknown. Additionally to Chapter 4.3, the reason why February and March 2016 had lower values of standardized emission rates than the calculations might attribute to the phenology and the physiologic state of the leaves. Nambiar and Fife (1991) had found that the nutrient resorption (retranslocation) can be driven by shoot in conifers. In the study site, growing season of moso bamboo usually occurs in April and May (e.g. Hsieh, 2013), moso bamboo might do nutrient resorption (retranslocation) during February and March from elder leaves, causing low activities in the elder leaves.

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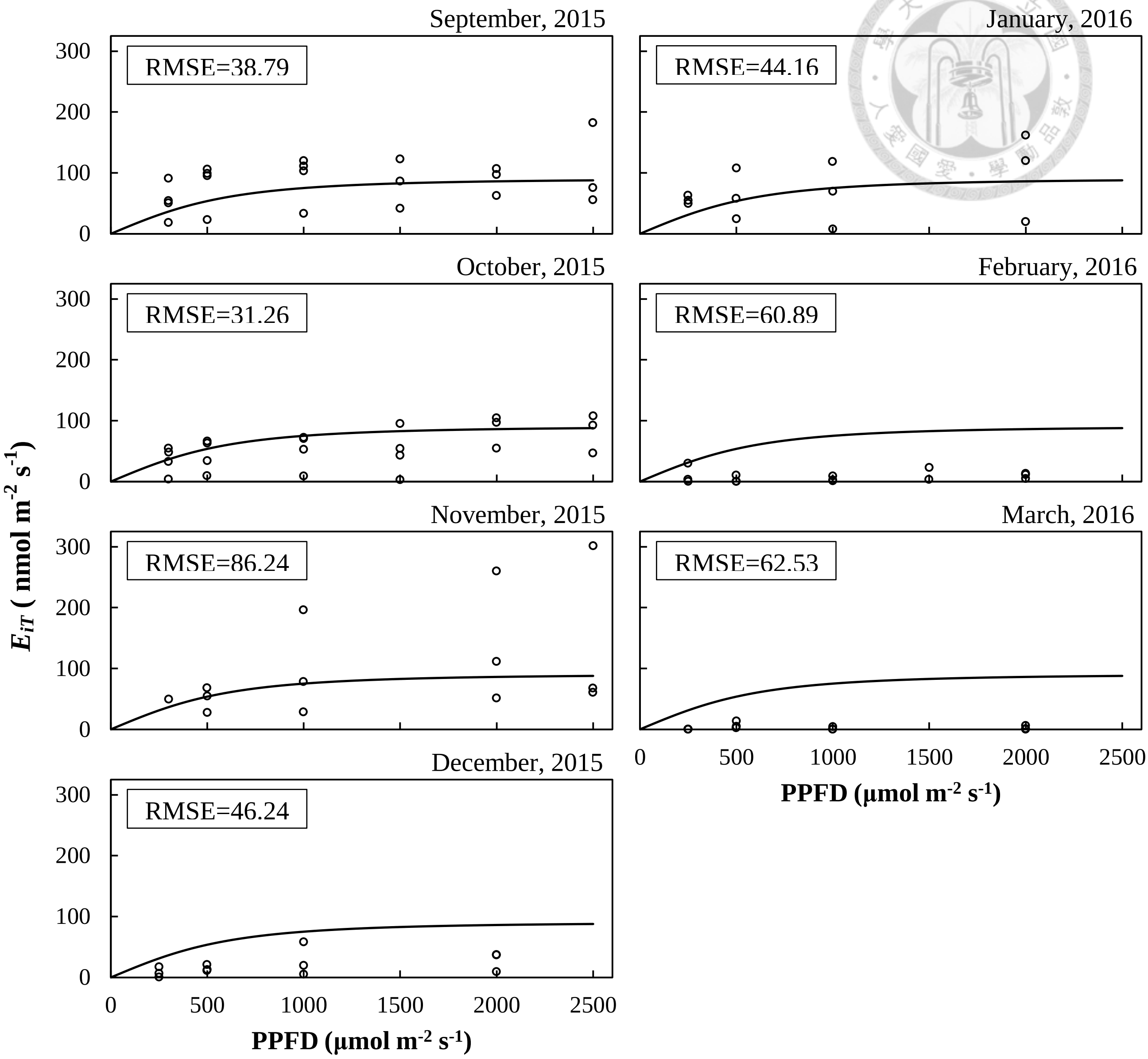

Figure 10 Relationships between Gaussian function based-standardized isoprene emission rates (E_{iT}, nmol m^{-2} s^{-1}) and the light intensities (PPFD, µmol m^{-2} s^{-1}) with the G93 light-intensity regression lines derived in this study for 7 months. Root mean square errors (RMSE) of each month are shown in the boxes.

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Chapter 5 Conclusion

This study conducted 1) for testing the significance of isoprene emission ability of moso bamboo, 2) clarifying the vertical variation and 3) the seasonal variation, and 4) establishing a model for isoprene emission in a moso bamboo forest. Through the understanding of the characteristics of isoprene emission derived in this study, finally, this study established a foundation of total canopy-scale isoprene emission estimates in the bamboo forest.

In this study, isoprene emission had been detected in 10 species in 14 bamboo species. In *Phyllostachys lithophila* Hayata, *Bambusa oldhami* and *P. edulis*, the emission capacities were significant, which were comparable to those of high-emitting plants (*Quercus spp.*). Particularly, the isoprene emission capacity of moso bamboo was considerable (about 23 nmol m^{-2} s^{-1} under Leaf temperature= 30℃, PPFD= 1000 μmol m^{-2} s^{-1}), suggesting the importance of moso bamboos in terms of isoprene emission. In genus *Dendrocalamus* and *Phyllostachys*, all species in our study showed detections of the emission, implying that phylogenetic is related to isoprene emission capacity in bamboos.

The vertical variations of isoprene emission rates had no relation to canopy length or individual height. By individual, no significant differences of isoprene emission capacity among vertical locations were found. However, if we consider total

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7 individuals of bamboo, there might be a trend that higher and lower locations had higher and lower emission rates, respectively. So it was hard to conclude whether the isoprene emission within the moso bamboo canopy had significant vertical variations. Further studies measuring vertical profiles of emission rate in individuals were needed to confirm the vertical patterns derived in this study, particularly in summer seasons with higher emission rates.

The isoprene emission rates of moso bamboos increased with light intensity (PPFD) in a logistic-like distribution. This increasing trend had varied among months; larger emission rates were found during September to November 2016, and lower emission rates were found during December 2015 to March 2016 at a given PPFD. The variation might attribute to the effect of temperature since the monthly isoprene emission rates at PPFD = 1000 μmol m^{-2} s^{-1} basically corresponded to the monthly leaf temperatures. Nevertheless, some discrepancy was found in February and March 2016.

This study developed a best model to reproduce the temporal variations in isoprene emission rates by considering the effect of leaf temperature and light intensity. The models were fitted to the measurement data in the moso bamboos based on Gaussian distribution for the effect of leaf temperature and G93 light-intensity function. According to the RMSE, we found higher reproducibility of the developed

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model in the period September, October, December 2015 and January 2016; however, lower reproducibility was found in November 2015, February and March 2016. The lower isoprene emission rates measured than those of model calculations in February and March 2016 implies effects of the longer term variation, which could not be explained by shorter term factors such as leaf temperature and light intensity. The variation may attribute to the nutrient recycling from leaves before the new bamboo shoot sprouting in the study site, causing the low activities in leaves.

To estimate total amount of canopy-scale isoprene emission in bamboo forests, this study suggested importance of the vertical variations in isoprene emission, and phenological and physiological effects during pre-growing seasons in addition to the leaf temperature and light intensity.

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