<table>
<thead>
<tr>
<th>項目</th>
<th>内容</th>
</tr>
</thead>
<tbody>
<tr>
<td>誌名</td>
<td>農業気象</td>
</tr>
<tr>
<td>ISSN</td>
<td>00218588</td>
</tr>
<tr>
<td>著者</td>
<td>奥村, 智憲, 谷, 晃, 小南, 裕志ほか4名,</td>
</tr>
<tr>
<td>巻/号</td>
<td>64巻2号</td>
</tr>
<tr>
<td>掲載ページ</td>
<td>p. 49-60</td>
</tr>
<tr>
<td>発行年月</td>
<td>2008年6月</td>
</tr>
</tbody>
</table>

農林水産省 農林水産技術会議事務局筑波産学連携支援センター
Tsukuba Business-Academia Cooperation Support Center, Agriculture, Forestry and Fisheries Research Council Secretariat
Isoprene Emission Characteristics of *Quercus serrata* in a Deciduous Broad-Leaved Forest

Motonori OKUMURA*, Akira TANI**, Yuji KOMINAMI***, Satoru TAKANASHI****, Yoshiko KOSUGI***** and Takafumi MIYAMA***

*Graduate School of Energy Science, Kyoto University, Gokasho, Uji, Kyoto 611-0011, Japan
**Institute for Environmental Sciences, University of Shizuoka, Suruga-ku, Shizuoka 422–8526, Japan
***Kansai Research Center, Forestry & Forest Products Research Institute, Fushimi-ku, Kyoto 612–0855, Japan
**** Department of Meteorological Environment, Forestry & Forest Products Research Institute, Tsukuba, Ibaragi 305–8687, Japan
*****Graduate School of Agriculture, Kyoto University, Sakyoku, Kyoto 606–8502, Japan

Abstract

We conducted field measurements of isoprene emissions from sunlit and shaded leaves of *Quercus serrata*, which is one of the major tree species in Japan. The measurements were conducted at the Yamashiro Flux Tower site in a deciduous broad-leaved forest. In June 2006, the isoprene emission rate (*I*), together with the net assimilation rate (*A*) and photosynthetic photon flux density (PPFD), was measured using a leaf cuvette. The experimental results demonstrated that *I* peaked at around noon for both the sunlit and shaded leaves, while *A* of the sunlit leaves peaked in the morning with a subsequent gradual decline. Consequently, the ratio of carbon emitted as isoprene to carbon fixed by photosynthesis (carbon ratio) increased during the afternoon. Data sets obtained at PPFD values higher than 1000 µmol m\(^{-2}\) s\(^{-1}\) revealed that highly correlated with the leaf temperature. The averages of the basal emission rate *I*\(_{b}\), calculated using the Guenther algorithm (G93), were 42.9 and 20.5 nmol m\(^{-2}\) s\(^{-1}\), respectively, for the sunlit and shaded leaves of *Q. serrata*. Our result indicates that *Q. serrata* should be categorized as a strong isoprene emitter. The measured *I* value estimated by the G93 model was consistent with the *I* value within a root-mean-square (RMS) error of 4 nmol m\(^{-2}\) s\(^{-1}\), suggesting that the G93 model can be used to determine the isoprene emission response of *Q. serrata* to PPFD and the leaf temperature.

**Key words:** Carbon budget, Emission model, Isoprene, *Quercus serrata*, Volatile organic compounds

1. Introduction

Biogenic volatile organic compounds (BVOCs) refer to non-methane hydrocarbons emitted from biogenic sources. BVOCs are emitted by many plant species and include terpenoids such as isoprene (C\(_5\)H\(_8\)), monoterpenes (C\(_{10}\)H\(_{16}\)), sesquiterpenes (C\(_{15}\)H\(_{24}\)), alcohols, organic acids, alkenes, and aldehydes. Recently, several attempts to estimate the annual global emission of BVOCs have been conducted. Using the global emission model, Guenther *et al.* (1995) estimated that the annual global emission of non-methane BVOCs ranged from 0.5 to 1.2 Pg carbon per year. Such emissions exceed the global emission of anthropogenic hydrocarbon (0.1 Pg C/year) as estimated by Singh and Zimmerman (1992). It is estimated that over 90% of BVOC emissions are from vegetation (Singh and Zimmerman, 1992). Isoprene is estimated to comprise approximately 50% of the annual global emission of BVOCs (Guenther *et al.*, 1995). The isoprene emission of many tree species is strongly affected by light and leaf temperature (Tingey *et al.*, 1979; Guenther *et al.* 1995).
Terpenoids are highly reactive with ozone and hydroxyl radicals compared with most anthropogenic volatile organic compounds and, therefore, contribute to the formation of ozone and other photochemical oxidants in the lower atmosphere (Yokouchi and Ambe al., 1991). Oxidants in the lower atmosphere (Yokouchi and Ambe al., 1991).

Recently, the effect of BVOC emissions on global carbon budgets has been considered important (Clark et al., 2001). For example, Geron et al. (2002) roughly estimated the BVOC emission offset as comprising 10% of the net ecosystem exchange (NEE) of CO₂ for a lowland tropical wet forest in Costa Rica. Because the majority of BVOCs are decomposed into CO₂ by oxidation, these CO₂ precursors may be considered compounds that affect the global CO₂ concentration.

To estimate forest carbon emissions in the form of BVOCs, it is essential to collect accurate BVOC flux data of major tree species, to identify the effects of environmental factors on the BVOC fluxes, and to develop the BVOC emission model. A reliable BVOC emission model could contribute to establishing more accurate global BVOC emission inventories. Recently, various models have been offered to estimate the BVOC emissions (Guenther et al., 1993; Zimmer et al., 2000). These models describe the photosynthetic photon flux density (PPFD) and leaf temperature dependences of isoprene emission. To date, the G93 algorithm presented by Guenther et al. (1993) has been widely used for isoprene emission estimates. One of the important parameters in the G93 algorithm is the basal emission rate, which needs to be determined from measured emission data sets. In addition, certain other empirical coefficients in the G93 algorithm may vary between species and depend on the plant growth environments. Some previous studies demonstrated that the estimated and measured emission rates were not in good agreement (Pio et al., 2005).

In Europe and the United States, there have been various investigations to identify BVOC emitters and characterize their emissions (Hansen et al., 1997; Steinbrecher et al., 1997). However, little information is available regarding the measured emission rates of Asian plant species (Ohta, 1986; Yokouchi and Ambe, 1988; Tani et al., 2002; Geron et al., 2006b; Tani and Kawawata, in press), and a few studies have been carried out on the BVOC inventories of Asia (Steiner et al., 2002; Zhihui et al., 2003). The estimated emissions in Asia have major uncertainties (> a factor of 5) due to a lack of emission data for major tree species (Chang et al., 2005). In order to establish more accurate Asian inventories, it is necessary to measure BVOC emissions of native tree species in Asia and determine their basal emission rates.

We have been conducting studies to identify terpenoid emitters and investigate their emission characteristics in Japan (Tani and Fushimi, 2005; Tani and Kawawata, in press). Most Quercus trees in Japan are major species in the temperate zones of Asia and have high isoprene emission capacities. Most of them are endemic to Asia. The aim of this study is to investigate the isoprene emission characteristics of Q. serrata, which is one of the major tree species in Japan, and to determine its basal emission rate. We conducted field measurements on isoprene emissions and net assimilation rates of Q. serrata, together with leaf temperature and PPFD, and investigated the relationships between them. We also verified the accuracy of the G93 model for Q. serrata. The ratio of carbon emitted as isoprene to carbon fixed by photosynthesis (carbon ratio) was discussed from the perspective of a carbon budget.

2. Materials and Methods

2.1 Plant materials and Experimental data

Field measurements were carried out in a deciduous broad-leaved forest in Yamashiro, Kyoto (34°47' N, 135°50' E) in June 2006. A 15-m walk-up tower provided access to the canopy top of an oak tree (Q. serrata). The tree was about 12 m high and 40 years old. Measurements were made for sunlit leaves (A1, A2, B1, and B2) on two branches (A and B) around the crown of the tree on June 1 and 4 and for shaded leaves (C1 and C2) on a branch (C) 3 m lower than the branches A and B, on June 2. Sunlit leaves (A1, A2, B1 and B2) faced east, and the shaded leaves (C1, C2) hardly received any direct sunlight throughout the day.

2.2 Isoprene emission measurements

The rates of isoprene emissions (I) and net as-
Fig. 1. A schematic diagram of isoprene sampling using a portable photosynthesis system (LI6400). For measuring the isoprene emission, the outlet air flow from the leaf cuvette was divided into two streams by a Teflon T-junction.  

Simulation (A), stomatal conductance (g), PPFD, and leaf temperatures were measured using a portable photosynthesis system (LI6400, Li-Cor Inc., Lincoln, NE, USA) approximately every 2 hours from 7:00 to 17:00. It was modified to collect isoprene emitted from the leaf in the cuvette (Harley et al., 1997; Pegoraro et al., 2004; Tani and Fushimi, 2005). To expose the leaf to sunlight, a natural light unit was used for the leaf cuvette of the LI6400 system. For isoprene sampling, the outlet tube from the leaf cuvette was replaced by a Teflon tube. The outlet air flow was divided into two streams by a Teflon T-junction. One stream was reconnected to a built-in infrared gas analyzer (IRGA) in the cuvette and the other was used as a sampling port for isoprene (Fig. 1). The flow rate for sampling isoprene was 130 μmol s⁻¹, and the inflow rate to the cuvette was 500 μmol s⁻¹. Further, the outflow rate was 370 μmol s⁻¹. It was confirmed that the decreased flow rate into the IRGA did not affect the IRGA output. A buffer box (30 L) for the air supply to the LI6400 was placed on top of the flux tower to eliminate the influence of a sudden CO₂ concentration change. The air was drawn from the box and sent through a granular activated charcoal filter to remove trace contaminants such as atmospheric BVOCs. H₂O and CO₂ concentrations in the cuvette were not controlled so that these concentrations remained similar to levels in the natural environment. A blank measurement indicated that the cuvette and tube did not adsorb or emit isoprene.

To trap isoprene, adsorbents (200 mg Tenax and 100 mg Carbotrap) packed into stainless steel tubes (φ 1/4 inch×3.5 inch, PerkinElmer Inc., Waltham, MA, USA) were used. The tubes were preconditioned at 300°C for 10 minutes to remove volatile organic compounds and were stored at approximately 5°C in the dark. When sampling isoprene, air was drawn into the tube using a portable pump (MP-Σ30, Shibata Inc., Tokyo, Japan) for 10 minutes at a flow rate of 130 μmol s⁻¹. The sampling was initiated after values of A and g, became almost constant. The samples were brought to the laboratory promptly after collection and stored again at approximately 5°C in the dark until analysis, to prevent any photochemical reactions. The collected samples were analyzed with a GC-MS system (QP5050A, Shimadzu Inc., Kyoto, Japan) within two weeks.

2.3 GC-MS method

GC-MS analytical procedures and parameters have been described in detail elsewhere (Tani and Fushimi, 2005). Isoprene emission from the plant was identified and quantified using GC-MS. The samples underwent a two-stage thermal desorption (TurboMatrix ATD-400, Perkin Elmer), and compound separation was achieved using an SPB-5 capillary column (60 m×0.25 mm, ID, 1 μm, Supelco Inc., Bellefonte, PA, USA). Helium (purity >99.999%) was used as the carrier gas. The column temperature was maintained at 30°C for 5 minutes, raised to 60°C at 5°C min⁻¹, and then raised again to 250°C at 40°C 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. The analytical error was less than 5.5%. Isoprene concentration was determined by the absolute calibration method. An analytical curve was obtained by collecting and analyzing different volumes (0, 2, 4, 6, 8, 10, 20, 40, 60, 80, and 100 mL) of isoprene standard gas (1.03 ppmv). The amount of isoprene in the samples could be completely interpolated within the range of this analytical curve.
2.4 Rate of isoprene emission

The rate of isoprene emission (I, nmol m$^{-2}$ s$^{-1}$) from the leaf was calculated according to the following equation:

$$I = \left[ C_{\text{out}} \left( \frac{1 - w_{\text{in}}}{1 - w_{\text{out}}} \right) - C_{\text{in}} \right] v_{\text{in}} / LA$$  

(1)

where $C_{\text{in}}$ and $C_{\text{out}}$ are the isoprene concentrations (nmol mol$^{-1}$) in the inflow and outflow samples, respectively, and $w_{\text{in}}$ and $w_{\text{out}}$ the water vapor concentrations (mol mol$^{-1}$) in the inflow and outflow samples, respectively. $v_{\text{in}}$ is the flow rate (mol s$^{-1}$) in the cuvette and $LA$ is the enclosed leaf area (m$^2$).

2.5 G93 model calculations

The G93 algorithm (Guenther et al., 1993) describes the PPFD and leaf temperature dependences of isoprene emission as

$$I = I_0 C_L C_T$$  

(2)

where $I$ is the isoprene emission rate at any PPFD $L$ (μmol m$^{-2}$ s$^{-1}$) and temperature $T$ (K), and $I_0$ is the basal emission rate at a standard PPFD (1000 μmol m$^{-2}$ s$^{-1}$) and temperature $T_0$ (303 K). $C_L$ and $C_T$ are correction terms for light and temperature, respectively. $C_L$ is defined as

$$C_L = \frac{\alpha C_{L1} L}{\sqrt{1 + \alpha^2 L^2}}$$  

(3)

where $\alpha (=0.0027)$ and $C_{L1} (=1.066)$ are empirical coefficients, which were determined by the measured data of the four tree species (Guenther et al., 1993). The coefficient $C_{L1}$ was determined to become $C_L$ equal to 1 at the standard PPFD of 1000 μmol m$^{-2}$ s$^{-1}$.

$C_T$ is defined as

$$C_T = \exp \{C_{T1} (T - T_0) / (RT_0 T)\} / \exp \{C_{T2} (T - T_0) / (RT_0 T)\}$$  

(4)

where $R$ is the gas constant (=8,314 J K$^{-1}$ mol$^{-1}$). $T_0$ is also a constant (=314 K), and $C_{T1} (=95,000$ J mol$^{-1}$) and $C_{T2} (=230,000$ J mol$^{-1}$) are the empirical coefficients. Values of $I_0$ for individual leaves were calculated from equation (2) using data sets of the measured emission rates of the leaves.

3. Results

3.1 Diurnal course of the isoprene emission rate

$I$, $A$, $g_S$, PPFD, and the leaf temperatures of the sunlit leaves (A1, A2, B1, and B2) and shaded leaves (C1 and C2) were measured approximately every 2 hours from 7:00 to 17:00 (Fig. 2). The carbon ratio was the ratio of carbon emitted as isoprene to the carbon fixed by photosynthesis. The weather was sunny on June 1 and 4, and cloudy and occasionally sunny on June 2.

The sunlit leaves A1 and A2 were measured on June 1. The PPFD values on the two leaf surfaces rose to over 1000 μmol m$^{-2}$ s$^{-1}$ in the morning, reached a maximum level (1227-1341 μmol m$^{-2}$ s$^{-1}$) at around noon, and decreased to <500 μmol m$^{-2}$ s$^{-1}$ after 15:00. Leaf temperatures demonstrated similar diurnal variations with the maximum of 31.3°C and 31.1°C for leaves A1 and A2, respectively, around noon. For both these leaves, the $A$ value highly correlated with $g_S$. In the case of leaf A1, $g_S$ and $A$ were 0.198 mmol m$^{-2}$ s$^{-1}$ and 14.7 μmol m$^{-2}$ s$^{-1}$, respectively, at 9:30; these values then decreased to 0.055 mmol m$^{-2}$ s$^{-1}$ and 4.2 μmol m$^{-2}$ s$^{-1}$ at 13:00, and rose again to 0.113 mmol m$^{-2}$ s$^{-1}$ and 9.0 μmol m$^{-2}$ s$^{-1}$, respectively, at 16:00. On the other hand, $I$ was almost constant (45.2-48.0 nmol m$^{-2}$ s$^{-1}$) from 9:30 to 13:00 without any obvious decrease observed for $g_S$ and $A$ between 11:30 and 13:00. As a result, the carbon ratio increased from 1.5% at 9:30 to 5.7% at 13:00, owing to the decreased $A$ value in the afternoon. $A$, $g_S$, and $I$ of the sunlit leaf A2 showed tendencies similar to those of the sunlit leaf A1; however, the $g_S$ and $A$ values did not show a decrease greater than those of leaf A1 in the afternoon. Therefore, the carbon ratio was calculated to be 2.7% at 13:00, lower than that of leaf A1.

$A$, $g_S$, and $I$ values of the sunlit leaves B1 and B2 measured on June 4 showed tendencies similar to those of the sunlit leaf A2. However, the leaf temperature and $I$ values of B1 and B2 were lower than those of leaves A1 and A2, and the maximum leaf temperature of leaves B1 and B2 was 27.1°C (around 11:30) and 28.1°C (around 13:00), respectively. The maximum $I$ values of leaves B1 and B2 were 25.5 and 35.9 mmol m$^{-2}$ s$^{-1}$, respectively, observed when the maximum leaf temperature was recorded.

Shaded leaves (C1 and C2) were measured on June 2. The $g_S$ values for both the leaves were less than 0.1 mmol m$^{-2}$ s$^{-1}$. Leaf temperatures, $A$ and $I$ reached maximum levels between 11:00 and 14:00, but, these changes were smaller than those observed in the four sunlit leaves, and in the ranges of 19.9-22.8°C, 0.9-3.9 μmol m$^{-2}$ s$^{-1}$, and 0.4-2.3 nmol m$^{-2}$ s$^{-1}$, respectively.

3.2 Isoprene emission modeling

Since a proportional relationship between $C_L \times C_T$
Fig. 2. Diurnal course of the isoprene emission rate $I$, PPFD, leaf temperature ($T_{leaf}$), stomatal conductance ($g$), net photosynthetic rate ($A$), and carbon ratio of the sunlit (A and B) and shaded (C) leaves measured at approximately 2-hour intervals. The scale of $I$ is different between the sunlit (A and B) and shaded (C) leaves.
and the measured $I$ values could be expected from equation (2), $I_s$ of *Q. serrata* was determined as a slope of the regression line of $I$ against $C_L \times C_T$ (Fig. 3). The $I$ value highly correlated with $C_L \times C_T$ in all the leaves (sunlit leaves: $r^2 > 0.95$, shaded leaves: $r^2 > 0.83$). The calculated $I_s$ values of the individual leaves were in the range of 37.0–48.2 nmol m$^{-2}$ s$^{-1}$ (average: 42.9 nmol m$^{-2}$ s$^{-1}$) for the sunlit leaves. The values for the two shaded leaves were 18.9 and 22.1 nmol m$^{-2}$ s$^{-1}$ (average: 20.5 nmol m$^{-2}$ s$^{-1}$) and these values were half those observed in the sunlit leaves.

To compare the measured $I$ ($I_m$) value with the rate estimated by the G93 algorithm ($I_r$), both the values are plotted together in Fig. 4. $I_m$ values were in close agreement with the corresponding $I_r$ values, within the root-mean-square (RMS) errors of 4 nmol m$^{-2}$ s$^{-1}$ for the sunlit leaves and 0.2 nmol m$^{-2}$ s$^{-1}$ for the shaded leaves. However, there were large relative differences (11%–226%) in the early morning (around 7:30) and late afternoon (around 16:00) for leaves A1 and A2, and in the early morning for leaves B1 and B2. Although the absolute values of the differences

![Fig. 3. Relationships between $C_L \times C_T$ and the measured isoprene emission rate.](image)

![Fig. 4. Isoprene emission rates measured in the experiment ($I_m$) and estimated by the Guenther model (G93) ($I_r$).](image)
were small, the G93 model tended to overestimate the isoprene emission rates of *Q. serrata* in the early morning and late afternoon.

### 3.3 Effect of leaf temperature on isoprene emission

As stated by Guenther *et al.* (1991) and Harley *et al.* (1997), the *I* value of certain other tree species depends significantly on the light intensity and leaf temperature. However, the effect of PPFD on *I* need not be considered when PPFD is greater than 1000 μmol m⁻² s⁻¹ because the *I* value saturates at PPFD values between 500 and 1000 μmol m⁻² s⁻¹ in the case of *Q. serrata* (Ohta, 1986; Tani and Kawawata, *in press*). To examine the effect of leaf temperature on the *I* values within saturated PPFD levels, the *I* value of the sunlit leaves (A1, A2, B1, and B2) was plotted against leaf temperature (Fig. 5). Similar to other studies (Guenther *et al.*, 1991; Harley *et al.*, 1997; Tani and Kawawata, *in press*), the *I* value increased significantly with an increase in leaf temperature when PPFD was greater than 1000 μmol m⁻² s⁻¹. The solid line in Fig. 5 represents an emission curve estimated using the G93 temperature algorithm (equations (2) and (4)), in which the average *I*₅ was determined to be 44.7 nmol m⁻² s⁻¹ and *Cₐ* was assumed to be 1 (when PPFD=1000 μmol m⁻² s⁻¹). The curve was highly consistent with the measured data.

### 3.4 Daytime carbon ratio

To estimate the daytime carbon ratio, the daytime was divided into five periods (7:00-9:00, 9:00-11:00, 11:00-13:00, 13:00-15:00, and 15:00-17:00). The total daytime mass of carbon fixed by photosynthesis and that of carbon emitted as isoprene were individually estimated, assuming *I* and *A* measured during the periods to be the representative values for the corresponding periods. The daytime carbon ratio was calculated from the two total daytime masses of carbon. The ratio of leaves A1, A2, B1, B2, C1, and C2 were 1.63%, 1.21%, 0.79%, 0.86%, 0.33%, and 0.28%, respectively. This ratio did not significantly differ between leaves of identical branches, but it was quite different between branches that were measured on different days. The daytime carbon ratio of the shaded leaves was less than half of that of the sunlit leaves.

### 4. Discussion

#### 4.1 Isoprene emission capacity of *Q. serrata*

The *I* values of *Q. serrata* observed for the sunlit leaves ranged from 2.49 nmol m⁻² s⁻¹ at temperatures ranging from 16°C to 30°C, and the average maximum rate for the four leaves was 42.1 nmol m⁻² s⁻¹. The averages of the basal emission rate *I*₅ estimated using the G93 algorithm were 42.9 and 20.5 nmol m⁻² s⁻¹ for the sunlit and shaded leaves (Fig. 3), respectively. Herley *et al.* (1997) reported that the *I*₅ values of the sunlit and shaded leaves of a white oak (*Q. alba*) that strongly emitted isoprene were 50.8 and 30.5 nmol m⁻² s⁻¹, respectively. Sharkey *et al.* (1996) reported that *I*₅ of the sunlit leaves of *Q. rubra* was 43 nmol m⁻² s⁻¹. The values of the sunlit and shaded leaves did not significantly differ from the *I*₅ values obtained in our study. Although there are non-isoprene emitters of *Quercus* such as the Mediterranean tree species *Q. cerris* and *Q. suber* (Loreto *et al.*, 1998), the majority of oaks have high isoprene emission capacities (Geron *et al.*, 2001). In Japan, Tani and Kawawata (*in press*) identified isoprene emitters of native *Quercus* trees by measuring the *I* value of the seedlings. The *I*₅ value of *Q. serrata* seedlings was 27.8 nmol m⁻² s⁻¹, which is lower than that in our results. As the emission capacity might be significantly lower in potted seedlings than
in field-grown mature trees (Csiky and Seufert, 1999), the difference might also be the case. Based on these results, *Q. serrata* was categorized as a strong isoprene emitter.

Our results revealed that the maximum *I* of branch B (leaves B1 and B2) was 10-20 nmol m$^{-2}$ s$^{-1}$ lower than that of branch A (leaves A1 and A2). All the maximum *I* values were measured at PPFDs greater than 1000 $\mu$mol m$^{-2}$ s$^{-1}$, suggesting that the *I* value saturated against PPFD. This may be because the leaf temperatures of branch B were 2-3$^\circ$C lower than those of branch A, which is supported by the relationships between leaf temperature and *I* as illustrated in Fig. 5. The maximum *I* values of the shaded leaves (C1 and C2) were approximately a twentieth of those of the sunlit leaves. This difference appeared to be due to low PPFDs (less than 100 $\mu$mol m$^{-2}$ s$^{-1}$) measured on leaves C1 and C2, in addition to the low basal emission rate *I*$_{b}$ of branch C (Fig. 3) acclimated to the low light environment.

4.2 G93 model evaluation

From the results of the G93 model evaluation, the *I*$_{c}$ values were in close agreement with the corresponding *I*$_{e}$ values, within the RMS errors of 4 and 0.2 nmol m$^{-2}$ s$^{-1}$ for the sunlit and shaded leaves, respectively. In particular, a better agreement was observed between the two values for the data obtained from late morning to early afternoon (9:00-15:00) (Fig. 4).

Guenther *et al.* (1993) determined the coefficients of the G93 algorithm in equations (3) and (4) by using the measured data (approximately 100 data points) of the four tree species obtained over a short period of time. These coefficients have been widely used for the G93 algorithm and resulted in good agreements between the measured and estimated isoprene emission in many studies. However, several studies showed that the estimated and measured emission rates were not in good agreement with each other (Pio *et al.*, 2005) and, therefore, several values of the empirical coefficients ($\alpha$, $C_{1s}$, $C_{7s}$, and $C_{7r}$) and the constant ($T_{0}$) have been suggested for different tree species (Harley *et al.*, 1997; Hayward *et al.*, 2004). These empirical coefficients might differ, not only based on differences in species, but also on plant growth environments, the age of the leaf, etc. (Guenther *et al.*, 1993).

Our results suggest that the isoprene emission from leaves of *Q. serrata* can be explained by the G93 algorithm using the original empirical coefficients determined by Guenther *et al.* (1993). The *I*$_{s}$ values of *Q. serrata* did not significantly differ between the sunlit leaves. The difference in *I*$_{s}$ values between the shaded leaves was also small, and the averaged *I*$_{s}$ value of the shaded leaves was half that of the sunlit leaves. Therefore, it may be possible to accurately estimate the isoprene emission rate of the whole tree, if the areas of the sunlit and shaded leaves of the tree are known.

4.3 Influence of stomatal conductance on isoprene emission

Isoprene is emitted mainly through stomata (Tingey *et al.*, 1981). For aspen and oak trees, isoprene emission through the cuticule was <2% of that from the stomata (Fall and Monson, 1992). However, the *I* value was reported to be unaffected by the stomatal opening, based on the results of the experiments and numerical computations. Fall and Monson (1992) forced the stomata of *Populus tremuloides* and *Q. alba* to almost close by applying abscisic acid. They found that, under constant environmental conditions of a 30$^\circ$C leaf temperature and 1000 $\mu$mol s$^{-1}$ PPFD, *I* was not affected by *g*$_{s}$. Since the isoprene production rate was constant inside the leaf under constant environmental conditions, they attributed the cause to a new equilibrium of the intercellular isoprene concentration inside the stomata resulting in the emission rate being equal to the production rate. Ninemets and Reichstein (2003) used a vapor-liquid equilibrium model and demonstrated that the intercellular concentrations of isoprenoids with very high Henry's law constants raised and reached a new equilibrium within 1 second after a decrease in the *g* value.

In our study, the *A* value of the sunlit leaves decreased significantly with a decrease in the *g* value. However, no decrease in the *I* value was observed. This phenomenon may be explained by the previous findings described above. Consequently, midday depressions in the *g* and *A* values, which are usually observed in natural environments, and *I* unaffected by *g* could cause an increase in the carbon ratio.

4.4 Carbon ratio

In previous studies, the carbon ratio of many plant species was determined under standard conditions (leaf temperature: 30$^\circ$C, PPFD: 1000 $\mu$mol m$^{-2}$ s$^{-1}$). In Japan, Tani and Fushimi (2005) reported that the carbon ratio of *Edgeworthia chrysantha* ranged from 0.09%-1.40%. In a filed study, the carbon ratios of *Q. alba* and *Q. rubra* for the leaves at the top of the tree canopy were calculated as 4.0% and 7.8%, respectively,
under standard conditions (Sharkey et al., 1996). The carbon ratio of *Psorothamnus fremontii* in the desert region of the western US was reported to be 1%-2% under the standard conditions (Geron et al., 2006a). Based on these results, the carbon ratio of the isoprene emitters appears to range from 0.1 to 10%. In our study, the carbon ratios of the six leaves measured at around 30°C were in the same order of magnitude as the values reported for the other species.

The optimum temperature for photosynthesis in *Q. serrata* is 25-30°C (Kai, 1984), and the optimum temperature for isoprene synthase activity is reported to be 40-45°C (Fall, 1999). This means that the carbon ratio could increase drastically with increasing leaf temperature from 30-40°C. The daytime carbon ratio of *Q. serrata* in summer could be greater than our measurements, because higher leaf temperatures (>35°C) were often observed. An increase in ground-level air temperature caused by global warming might also enhance the daytime carbon ratio of *Q. serrata* and, therefore, the effect of temperature on isoprene emission of the plant must be considered when estimating the carbon balance of forests.

5. Conclusion

The averages of the basal emission rate $I_s$ estimated by the G93 algorithm were 42.9 and 20.5 nmol m$^{-2}$ s$^{-1}$, respectively, for the sunlit and shaded leaves of *Q. serrata*. The result indicates that *Q. serrata* should be categorized as a strong isoprene emitter. The results of the G93 model evaluation showed that the rates estimated by the G93 algorithm were in close agreement with the corresponding measured values, within the RMS errors of 4 and 0.2 nmol m$^{-2}$ s$^{-1}$, respectively, for the sunlit and shaded leaves. From the point of view of the carbon budget, isoprene emission unaffected by stomatal conductance could cause an increase in the daytime carbon ratio under conditions resulting in a “midday depression” of photosynthesis. The isoprene emission rate of *Q. serrata* was strongly dependent on leaf temperature, and the carbon ratio of *Q. serrata* was several percentages under the standard conditions. Consequently, the daytime carbon ratio might be enhanced by an increase in leaf temperature in summer. Global warming might also increase isoprene emission and the annual carbon ratio of *Q. serrata*. Therefore, the effect of temperature on the isoprene emission of the plant needs to be considered when estimating the carbon balance of the forests.

Acknowledgments

The authors are grateful to Tatsushi Iwamoto, Dr. Masako Dannoura, Shogo Hamada and Daichi Suzuki for their assistance with experiments. The authors would also like to thank the anonymous reviewers for their useful comments. This study was supported in part by funds from the Kyoto University 21COE Program “Establishment of COE on Sustainable Energy System.” This study was also partially supported by the Japanese Ministry of Education, Culture, Sports, Science and Technology, Grant-in-Aid for Exploratory Research, 2007, No. 19651009.

References


Geron, C., Harley, P., and Guenther, A., 2001: Isoprene


Kavouras, I. G., and Stephanou, E. G., 2002: Direct evidence of atmospheric secondary organic aerosol formation in forest atmosphere through heteromolec-


M. Okumura et al.: Isoprene Emission Characteristics of Quercus serrata

31 (Suppl. 1), 79–88.
落葉広葉樹林におけるコナラのイソプレン放出特性

奥村智憲・谷 晃**・小南裕志***・高梨 聡****・
小杉緑子*****・深山貴文***・東野 達*

* 京都大学大学院 エネルギー科学研究科
** 静岡県立大学 環境科学研究科
*** 森林総合研究所 関西支所
**** 森林総合研究所 本所
***** 京都大学大学院 農学研究科

要 約

ブナ科コナラ属の植物は何イソプレン放出能が高いことが知られており、アジアにも広く生長し固有種も多い。本研究では、東アジアにおける森林からの揮発性炭化水素放出量の推定とその放出特性の知見を得るために、日本における二次広葉樹林の主要な構成種であるコナラ (Quercus serrata) からのイソプレン放出の野外観測を行った。イソプレン放出速度と、同時に観測した光合成速度や気孔コンダクタンス、葉温、光強度との関係を調べた。さらに、炭素収支の観点からイソプレンとして放出された炭素量と純光合成で固定された炭素量の比 (carbon ratio) を計算するとともに G93 モデルの妥当性についても検討した。陽葉において純光合成速度は気孔開度の影響を受け、朝方に最大となり、それ以降は低下したが、イソプレン放出はその影響を受けず、おおよそ正午を最大とする日変動を示した。そのため、carbon ratio は午後に高まる傾向にあった。陽葉において葉温とイソプレン放出との関係を調べた結果、1000 μ mol m⁻² s⁻¹ 以上の PPFD におけるイソプレン放出速度は葉温と高い相関を示した。一方、陰葉のイソプレン放出は陽葉と同様に正午を最大とする日変動を示したが、その値は陽葉の約 1/20 であった。一日の carbon ratio を求めた結果、陽葉で 0.79 ～ 1.63％、陰葉で約 0.3％であり、コナラの炭素収支を見積もる際に無視できない割合であった。次に、G93 モデルのコナラへの適用を検討した結果、モデルの推定値と実測値は、陽葉で 4 nmol m⁻² s⁻¹ 以下、陰葉で 0.2 nmol m⁻² s⁻¹ 以下の RMS 誤差でよく一致し、コナラのイソプレン放出速度の推定に G93 アルゴリズムを用いることが可能であると示された。観測値を用いて G93 モデルにより計算したコナラの基礎放出速度の平均値 (陽葉: 42.9 nmol m⁻² s⁻¹、陰葉: 20.5 nmol m⁻² s⁻¹) から、コナラはブナ科コナラ属の中でもイソプレン放出能が高い部類に属することが示された。

キーワード: イソプレン、揮発性炭化水素、コナラ、炭素収支、放出モデル