Full Paper

J. Agric. Meteorol. 68 (1): 25-33, 2012

Methane flux of leaves in a tropical rainforest and a temperate conifer forest

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Abstract

We measured methane (CH_4) fluxes of leaves growing in a tropical rainforest and a temperate conifer forest using the closed static chamber method. Leaf samples were chosen from the canopy and forest floor of a tropical rainforest at Pasoh Forest Reserve, Peninsular Malaysia and a temperate forest at Kiryu Experimental Watershed (KEW), central Japan. At Pasoh, we sampled four species from the canopy (*Xanthophyllum stipitatum*, *Dipterocarpus sublamellatus*, *Ptychopyxis caput-medusae*, *Neobalanocarpus heimii*) and four species from the forest floor (*Alphonsea maingayi*, *Rinorea anguifera*, *Macaranga lowii*, *Neobalanocarpus heimii*). The leaves of *Elaeis guineensis* were also sampled at an oil palm plantation near the forest reserve area. At KEW, we sampled the leaves of *Chamaecyparis obtusa*, from both the top (18 m) and middle (16 m) of the canopy as well as leaves of *Eurya japonica* at the forest floor. Incubation experiments revealed that CH_4 was emitted from leaves of the tested species sampled at two sites, although CH_4 fluxes showed variations on a daily basis. These results suggest that tree leaves both at Pasoh and KEW might function as a small CH_4 source, but their contribution to the CH_4 exchange of the total forest ecosystem is very small compared to the soil CH_4 flux.

Key words: Closed static chamber, Flux, Incubation, Leaf, Methane.

1. Introduction

Methane (CH_4) is the second most important greenhouse gas after CO_2 (Forster *et al*., 2007), with a radiative potential 26 times more effective than CO_2 (Lelieveld and Crutzen, 1992). Global anthropogenic sources of CH_4 include fossil fuel-related industries, waste management, enteric fermentation, rice agriculture, and biomass burning and amount to 360 Tg $year^{-1}$ (Le Mer and Roger, 2001). Concerning natural sources, wetlands emit up to 115 Tg $year^{-1}$. Upland ecosystems are considered to be net sinks for CH_4 with consumption by soils amounting to 30 Tg $year^{-1}$. Oxidation by OH^- radicals in the troposphere amounts to 470 Tg $year^{-1}$. Global CH_4 budgets estimate a missing source of about 10 Tg $year^{-1}$, which might be explained by unexpected emissions from upland ecosystems or adjustments to any of the known CH_4 sources and sinks (Megonigal and Guenther, 2008).

Based on incubation experiments under solar radiation, Keppler *et al*. (2006) reported that leaves of tree and grass species native to temperate and tropical regions emit CH_4 under aerobic conditions, and extrapolations from laboratory measurements to the global scale indicated that CH_4 emissions from plants could constitute a large fraction of the total global emissions of CH_4 (amounting to about 149 Tg $year^{-1}$), although scaling the measurements up to global magnitude involves inherent uncertainty (Kirschbaum *et al*., 2006, 2007; Parsons *et al*., 2006; Butenhoff and Khalil, 2007). If large CH_4 efflux from leaves as argued by Keppler *et al*. (2006) were true, CH_4 emissions from

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Received; March 25, 2011.
Accepted; August 25, 2011.

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plant leaves may have an important effect on global warming as a net source of CH_4. Because Keppler *et al.*（2008）suggest the methoxyl group of plant pectin as a precursor of aerobic CH_4 in which production from the pectin component of plant cell walls can be evoked by ultraviolet（UV）radiation, Vigano *et al.*（2008）showed that CH_4 emissions from dry and detached fresh matter of temperate and tropical plants can be stimulated by UV radiation and/or heating.

In addition to temperate and tropical plant species, Kitaoka *et al.*（2007）observed CH_4 emissions from fresh leaves of typical tree species native to cool-temperate forests in Hokkaido in northern Japan using incubation experiments with a PPFD of 350 μmol m^{-2} s^{-1}. Wang *et al.*（2008）conducted laboratory incubation experiments using detached leaves and stems of hydrophytes and xerophytes indigenous to the temperate Inner Mongolia Steppe. They found that some herbaceous hydrophytes emitted CH_4 from stems, but not from detached leaves; also, some xerophytes emitted CH_4 from detached leaves but not from stems. However, using a highly accurate, traceable online analytical system, no evidence for substantial aerobic CH_4 emissions from photosynthesizing and dark-respiring leaves of C_3（*Nicotiana tabacum* L.）and C_4（*Zea mays* L.）grass species was provided by Beerling *et al.*（2008）. Dueck *et al.*（2007）also reported no detectable $^{13}CH_4$ emissions from either C_3 or C_4 grasses labeled with the heavy stable isotope carbon ^{13}C to allow detection of subsequent CH_4 emissions that are isotopically distinct from background values using highly sensitive photoacoustic spectroscopy. Therefore, the issue of CH_4 emissions from plants remains open from the perspective of various data on CH_4 fluxes using different approaches, and the physiological mechanisms responsible for CH_4 emission under aerobic conditions are unclear. Evaluating whether CH_4 emissions from plants affect CH_4 exchange between the forest ecosystem and the atmosphere is important.

The objective of this study was to describe whether CH_4 fluxes of detached fresh tree leaves growing in a tropical rainforest and a temperate forest watershed have impacts on total CH_4 flux in each forest ecosystem. Methane flux in tropical forests greatly impacts global climate. Tropical forests are the habitat for termites that are known to produce CH_4（Zimmerman *et al*., 1982; Frankenberg *et al*., 2005）, whereas tropical forest soils almost always consume CH_4（Keller *et al*., 1986）. In temperate forest watersheds, wetlands reportedly function as large sources of CH_4（Itoh *et al*., 2007）. We investigated CH_4 fluxes of detached fresh leaves using incubation experiments and then compared the results to those of other studies conducted under different experimental conditions and soil CH_4 fluxes, which represents an active area of CH_4 flux research.

2. Materials and Methods

2.1 Site and materials

The study was conducted at the Pasoh Forest Reserve of the Forest Research Institute Malaysia（FRIM）, near Simpang Pertang in Negeri Sembilan, Peninsular Malaysia（2°58´N, 102°18´E）and the Kiryu Experimental Watershed（KEW; 34°58´N, 136°00´E）in the southeast of Shiga Prefecture, central Japan.

The core area is composed of primary forest（600 ha）in the Pasoh Forest reserve（2450 ha）and is covered with a primary lowland mixed dipterocarp forest（tropical evergreen broadleaf forest）, consisting of various species of *Shorea* and *Dipterocarpus.* The continuous canopy height is about 35 m, although some emergent trees exceed 45 m. The soil A horizon is thin（0-5 cm）and lateritic gravels are abundant below 30 cm（Yamashita *et al*., 2003）. This forest has two rainy periods that occur from March to May and from October to December, although monthly rainfall shows considerable interannual fluctuations（about 200 mm $month^{-1}$, Kosugi *et al*., 2008）. The annual mean air temperature during 2002-2007 measured at the top of the tower（52 m）was 25.5℃, and the annual mean rainfall measured with a tipping bucket rain gauge at an observatory located 430 m from the tower was 1754 mm. The oil palm plantation near the forest reserve area was also selected as a study site because different dominant（forest, oil palm, or sago ecosystem）underlying environmental factors in tropical peatland affect the exchange of CH_4 between ecosystems and the atmosphere（Melling *et al*., 2005）. At Pasoh, we sampled leaves of four tree species from the canopy [*Xanthophyllum stipitatum* Benn., *Dipterocarpus sublamellatus* Foxw., *Ptychopyxis caput-medusae*（Hk.f.）Ridl., *Neobalanocarpus heimii*（King）Ashton] and four tree species from the forest floor [*Alphonsea maingayi* Hook. f. et Th., *Rinorea anguifera* O. Ktze., *Macaranga lowii* King ex Hook f., *Neobalano-*

carpus heimii（King）Ashton.] three times in the rainy season（December 11, 2007 and October 13-14, 2008）. Canopy trees were accessible from a triangle canopy corridor 31 m high. The leaves of *Elaeis guineensis* Jacq. vat. dura Beet. were also sampled at the oil palm plantation near the forest reserve area four times in the dry and rainy seasons（on June 9-10, 2008 and October 14-15, 2008, respectively）. According to Keppler *et al.*（2006）and Kitaoka *et al.*（2007）, irradiation may affect CH_4 emission from leaves. To examine the effect of solar radiation on CH_4 flux of leaves, leaf sampling was conducted both at dawn（07：00-08：30）and in the late afternoon（15：00-16：00）. Three branches of each species were cut and immediately soaked in distilled water.

KEW（5.99 ha）is about 99.3％ covered by the evergreen conifer Japanese cypress（*Chamaecyparis obtusa* Sieb. et Zucc.）, which was planted in 1959（average height: 13.9 m, maximum height: 21.1 m）, and 0.67％ covered by distinct wetland in riparian zones. The soil texture is sandy or sandy silt（Itoh *et al.*, 2009）. The annual mean air temperature and rainfall during 2008, measured at an open site observatory, was 13.0℃ and 1635 mm, respectively. At KEW, we sampled leaves of *C. obtusa* from both the top（18 m）and middle（16 m）canopy and collected leaves of *Eurya japonica* Thunb. at the forest floor five to eleven times during the period from May 2008 to January 2009. Three branches of both species were cut and soaked in distilled water in the late afternoon（around 15:00-16:00）.

2.2 Methane flux measurements

The CH_4 fluxes of leaves were measured using the closed static chamber method. In the laboratory, leaves from three samples were detached and put in glass vial chambers（50, 100 ml）, sealed with a silicon septum or PVC-chambers（330, 450, 670 ml）and incubated in the dark for 16 h at 30℃. To avoid the effect of pressure change on CH_4 concentration in the chamber, CH_4 flux measurements were conducted only before and after incubation. At KEW, 0.5-2.0 ml of air in the chamber was collected with a gastight syringe, then the CH_4 concentration was measured with a gas chromatograph（GC; GC-14BPF; Shimadzu, Kyoto, Japan）equipped with a flame ionization detector（FID）and a Porapak Q column（2 m×3 mm diameter; Shinwa Chemical Industries, Kyoto, Japan）using N_2（flow rate, 50 ml min^{-1}）as the carrier gas. At Pasoh, 5 or 10 ml of air in the chamber was collected in a vacuum glass vial, and CH_4 flux measurements using a GC were conducted in the laboratory at Kyoto, Japan. Blank samples were also measured with the GC. Measurements of CH_4 concentration were conducted within 10 days after air sampling at Pasoh and within 24 h at KEW. After GC analysis, leaf area was measured using a portable area meter（LI3000-A, Li-Cor Inc., Lincoln, Nebraska, USA）. Dry weights of leaves were obtained after drying at 40℃ for a minimum of 48 h. Methane flux of leaves per unit leaf area（ϕ_{LA}, ng cm^{-2} h^{-1}）was calculated from the linear regressions of the concentration versus time curves from the chambers as follows:

$$\phi_{LA} = \frac{\rho V}{A}\frac{dc}{dt} \qquad (1)$$

where A is the leaf area（cm^2）, ρ is air density in the chamber（ng cm^{-3}）, V is the chamber volume（cm^3）, and dc/dt is the linear change in gas concentration within the chamber（mol mol^{-1} h^{-1}）. The air density was adjusted for the air temperature measured at the time of sampling. Similarly, CH_4 flux of leaves per unit leaf dry weight（ϕ_{dw}, ng g_{dw}^{-1} h^{-1}）was calculated as follows:

$$\phi_{dw} = \frac{\rho V}{DW}\frac{dc}{dt} \qquad (2)$$

where DW is the dry weight of leaves（g_{dw}）. Positive fluxes indicate emission of gas from the leaf to the atmosphere; negative fluxes indicate net absorption of gas from the atmosphere by the leaf.

2.3 Statistical analysis

Tukey tests were used to determine any differences among the means of CH_4 flux of leaves for the different sampling dates（$p < 0.05$）.

3. Results

3.1 Methane fluxes of tree leaves at Pasoh（tropical rainforest）

At Pasoh, 0.25±0.21 ng CH_4 g_{dw}^{-1} $h^{-1}$was emitted from leaves of canopy tree species（mean±SD; Fig. 1a）. Small CH_4 absorption was observed from leaves of *X. stipitatum* and *D. sublamellatus* sampled at dawn in October 2008（−0.07±0.09 and −0.13±0.12 ng CH_4 g_{dw}^{-1} h^{-1}, respectively）, although no clear temporal variation of CH_4 fluxes was detected from leaves of the other two species. The CH_4 fluxes of *A. mainga-*

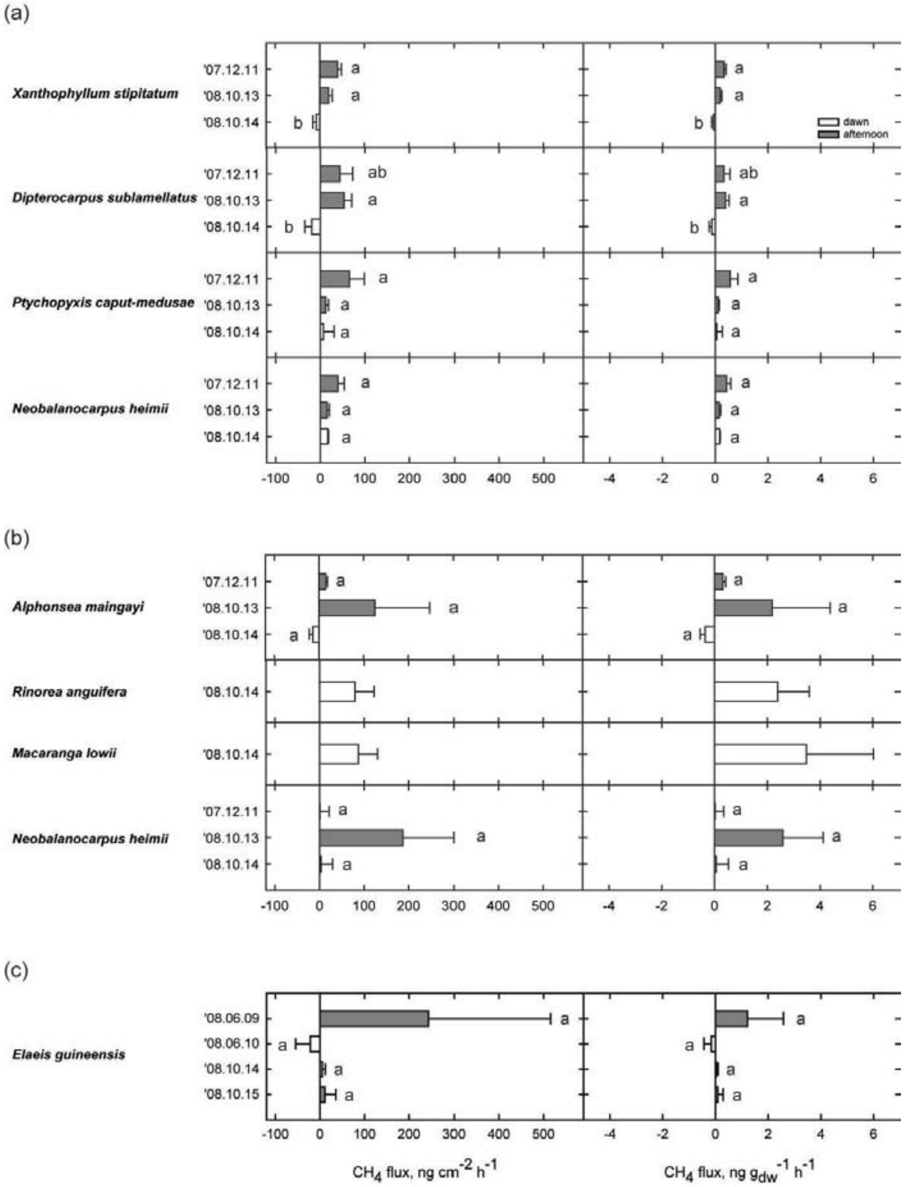

Fig. 1. Methane fluxes of tree leaves sampled from the canopy（a）, forest floor（b）, and oil palm plantation（c）at Pasoh. Methane fluxes were standardized per unit leaf area（ng cm^{-2} h^{-1}, left side）and per unit leaf dry weight（ng g_{dw}^{-1} h^{-1}, right side）. Within each graph, the bars labeled with lower-case letters differ significantly [Tukey test: $p < 0.05$].

yi and *N. heimii* at the forest floor varied on daily basis, with mean rates ranging from −0.36 to 2.18 and from 0.01 to 2.59 ng CH_4 g_{dw}^{-1} h^{-1}, respectively, but no significant difference was observed between sampling dates（Fig. 1b）. The leaves of *E. guineensis* also showed day-to-day variations in CH_4 fluxes, with mean rates ranging from −0.17 to 1.22 ng CH_4 g_{dw}^{-1} h^{-1}, but no significant difference was detected（Fig. 1c）. Methane fluxes of leaves from each tree species were several orders of magnitude smaller than those from unsaturated soil（Fig. 3a）. 1.55±2.62 mg CH_4 m^{-2} day^{-1} was emitted and 0.98±0.72 mg CH_4 m^{-2} day^{-1}

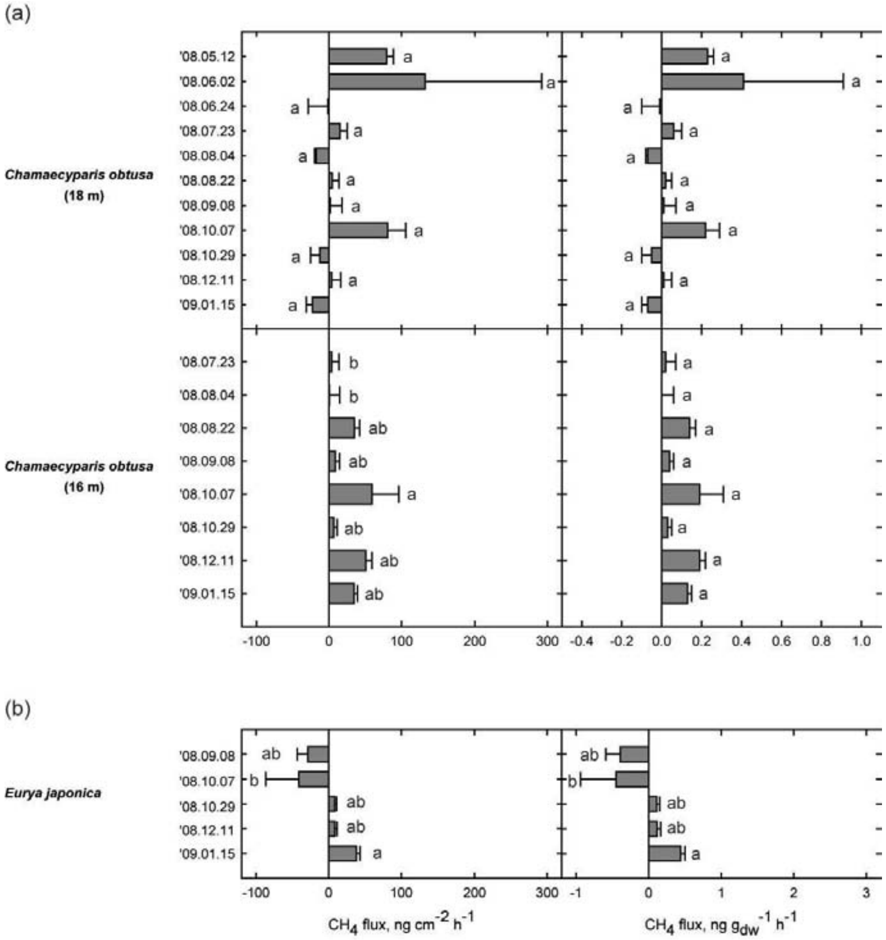

Fig. 2. Methane fluxes of *Chamaecyparis obtusa* leaves sampled from the top（18 m）and middle（16 m）of the canopy（a）, and *Eurya japonica* leaves sampled from the forest floor（b）at KEW. Methane fluxes were standardized per unit leaf area（ng cm^{-2} h^{-1}, left side）and per unit leaf dry weight（ng g_{dw}^{-1} h^{-1}, right side）. Within each graph, the bars labeled with lower-case letters differ significantly [Tukey test: $p < 0.05$].

was absorbed in unsaturated soil, whereas（7±10）×10^{-7} mg CH_4 m^{-2} day^{-1} was emitted and（4±6）×10^{-7} mg CH_4 m^{-2} day^{-1} was absorbed in tree leaves.

3.2 Methane fluxes of tree leaves at KEW（temperate forest）

At KEW, both emission and absorption of CH_4 from *C. obtusa* leaves at the top of the canopy（18 m）were observed, with mean rates ranging from −0.07 to 0.41 ng CH_4 g_{dw}^{-1} h^{-1}, but no seasonal change of CH_4 fluxes was detected（Fig. 2a）. Methane emissions per unit leaf area from *C. obtusa* leaves at the middle of the canopy（16 m）were significantly larger on October 7, 2008（59.10±45.32 ng CH_4 cm^{-2} h^{-1}）. However, a clear difference in CH_4 emissions per unit leaf dry weight was not observed between sampling dates, with mean rates ranging from 0 to 0.19 ng CH_4 g_{dw}^{-1} h^{-1}. In *E. japonica* leaves from the forest floor, CH_4 absorption on October 7, 2008（−0.45 ng CH_4 g_{dw}^{-1} h^{-1}）and CH_4 emission on January 15, 2009（0.44 ng CH_4 g_{dw}^{-1} h^{-1}）were prominent（Fig. 2b）. Methane fluxes of leaves from *C. obtusa* and *E. japonica* were several orders of magnitude smaller than those from both wetlands and unsaturated soil（Fig. 3b）. 44.05±139.68 mg CH_4 m^{-2} day^{-1} was emitted and 0.35±0.23 mg CH_4 m^{-2} day^{-1} was absorbed in soil, whereas（8±11）×10^{-7} mg CH_4 m^{-2} day^{-1} was emitted and（4±6）×10^{-7} mg CH_4 m^{-2} day^{-1} was absorbed in tree leaves.

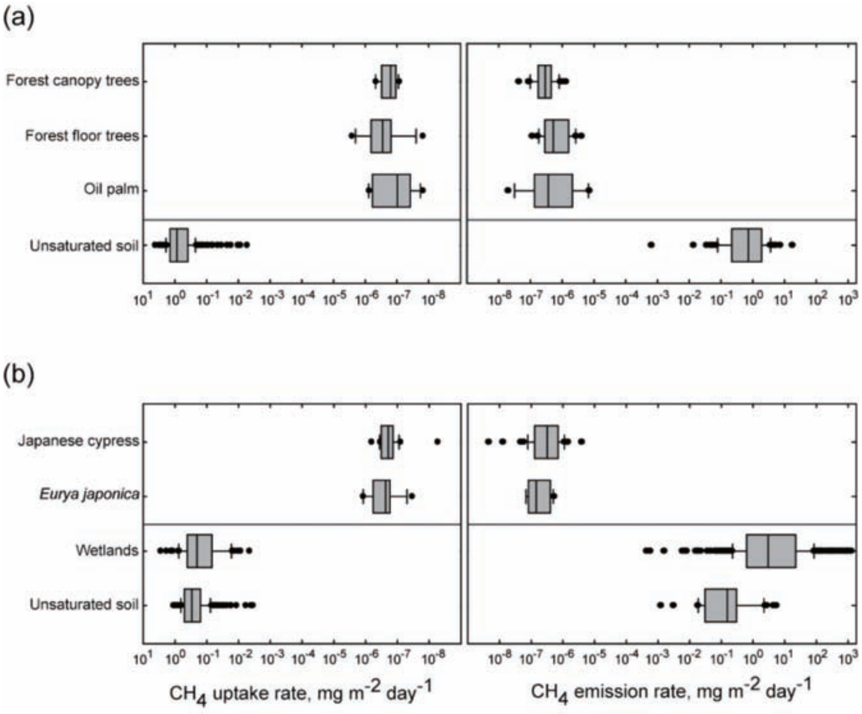

Fig. 3. Comparison of CH_4 fluxes of tree leaves with soil CH_4 fluxes at Pasoh（a）and KEW（b）. Using leaf area index（LAI）, CH_4 fluxes from tree leaves were standardized per unit plot area（mg m^{-2} day^{-1}）. The box plots show the median, interquartile range, and extreme cases of individual variables. Soil CH_4 flux data at Pasoh were from Itoh（unpublished data）, which were measured at five points in the 2-ha plot near the a triangle canopy corridor. Soil CH_4 flux data at KEW were from Itoh *et al*.（2007, 2009）, which were measured at nine points in both wetlands and unsaturated soil plots.

4. Discussion

In this study, small CH_4 emissions from leaves were found for each of the representative tree species at Pasoh and KEW（Figs. 1 and 2）. The averaged CH_4 fluxes from leaves of each species showed day-to-day variations, but no temporal and seasonal trends were detected. These results suggest that environmental factors such as solar radiation and air temperature did not affect CH_4 fluxes from leaves. The range of values in CH_4 fluxes per unit leaf dry weight observed in this study was much smaller compared to some recent incubation experiments（Table 1）and was within the fluctuation range of CH_4 fluxes, which was not significantly different from zero when measured with a high-accuracy, traceable online analytical system（Beerling *et al.*, 2008）. These findings suggest that tree leaves growing at Pasoh and KEW may have the potential to emit and in some cases absorb CH_4, but the mechanism is unknown and the amount is not significant. In both sites, CH_4 fluxes from tree leaves were several orders of magnitude smaller than those from the soil（Fig. 3）. Although studies have reported that soil CH_4 fluxes at Pasoh and KEW are significant（Itoh *et al.*, 2009, Itoh, unpublished data）, the contribution of CH_4 fluxes from foliage to the CH_4 exchange of the total forest ecosystem at both sites is far smaller than that from soil.

Note that the amount of CH_4 emission from plant leaves reported recently is highly variable among measurement conditions（Table 1）. Comparing CH_4 emission rates from leaves among studies, longtime incubation（up to 72 h）, high temperature（35-40℃）, and UV irradiation induce remarkable CH_4 emissions（Kitaoka *et al.*, 2007; Vigano *et al.*, 2008）. Vigano *et al.*（2008）and Keppler *et al.*（2008）reported that temperature and UV mediate the formation of CH_4, which is produced from fresh and dry organic matter, as well as several structural plant components. If UV is an important factor for CH_4 release from plants, then CH_4 emissions may be suppressed in the absence of

Table 1. Comparison of methane emission rates of plants.

Plants	Methane emission rates, ng CH_4 dw^{-1} h^{-1}	Experimental conditions	References
C_3-leaf 'temperate regions'	0.19-21.6*	Incubation experiments with solar radiation（for 16 h at 30 or 40℃）	Keppler *et al.*（2006）
C_3-leaf 'tropical regions'	0.09-17*		
C_4-leaf	0.21-10.1*		
C_3-intact plant	12-873*	Chamber experiments	
C_4-intact plant	55-762		
C_3-leaf 'cool-temperate regions'	9.1-31.3	Incubation experiments with PPFD of about 350 μmol m^{-2} s^{-1}（for up to 72 h at 35℃）	Kitaoka *et al.*（2007）
C_3-'hydrophyte'	6.78-13.50*	Incubation experiments（for 10-20 h at 20-22℃）	Wang *et al.*（2008）
C_3-'xerophyte'	0.55-3.39*		
C_4-'xerophyte'	0.48*		
leaves of terrestrial plants（including moss, grass, and trees）	0-4300	Incubation experiments with UV radiation（at 20-40℃）	Vigano *et al.*（2008）
C_3-leaf（Tobacco）	n. d.	A high-accuracy traceable online analysis with photosynthetically active radiation	Beerling *et al.*（2008）
C_4-leaf（Mays）	n. d.		
C_3-leaf 'crops'（grown under different temperature, CO_2 concentration and watering regime）	85.6-115.5	Incubation experiments（for 2 h at ～22℃）	Qaderi and Reid（2011）
leaves of tropical trees	−0.55- 6.02	Incubation experiments（for 16 h at 30℃）	This study
leaves of temperate trees	−0.94-0.91		

* including the data that no CH_4 emission was detected or was too weak to quantify change in CH_4 concentration.

UV wavelengths, as confirmed by Dueck *et al.* (2007) and Beerling *et al.* (2008). Also, irradiation treatment during incubation has also been suggested to enhance CH_4 emission from leaves (Keppler *et al.*, 2006; Kitaoka *et al.*, 2007), but a significant difference in CH_4 fluxes between leaves sampled in the afternoon and those sampled at dawn was observed in only two tree species at Pasoh. Thus, the effect of solar radiation on CH_4 fluxes from leaves of plants under natural conditions may not be as large as previously reported. A possibility exists of aerobic CH_4 release from plants via a biophysical rather than an enzymatic process (Kirschbaum *et al.*, 2006).

To estimate the impact of CH_4 fluxes of plants on its exchange between the forest ecosystem and atmosphere, the most important factor is whether plants can be a net CH_4 source under field conditions. Although some studies have estimated total CH_4 emissions from terrestrial plant communities (Megonigal *et al.*, 2004; Keppler *et al.*, 2006; Kirschbaum *et al.*, 2006), large variations in CH_4 fluxes from plant leaves caused by different measurement conditions will result in serious errors in estimating total CH_4 fluxes from terrestrial plant communities under aerobic conditions. Some studies indicate that tree leaves in a floodplain forest can transport CH_4 from an anaerobic root zone to the atmosphere through woody tree parts (Terazawa *et al.*, 2007; Qaderi and Reid, 2011). In such tree species, gases such as ethylene (C_2H_4) and CH_4 can move from roots to shoots either via the transpiration stream or through aerenchyma, which slowly develop as a result of flooding. If plants do not have a known biochemical pathway to synthesize CH_4 but rather take up this gas produced by microbial activities under aerobic conditions, the growing conditions of plants will largely affect CH_4 emission from terrestrial parts. To evaluate whether the forest canopy is a net CH_4 source, the monitoring of diurnal and seasonal changes in CH_4 fluxes from living plants under field conditions is urgent.

Acknowledgments

This research was partially supported by the Japan Society for the Promotion Science (JSPS), Grant-in-Aim for Scientific Research.

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