Atmospheric methane removal by boreal plants

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[1] Several studies have proposed aerobic methane (CH_4) emissions by plants. If confirmed, these findings would further increase the imbalance in the global CH_4 budget which today underestimates CH_4 sinks. Oxidation by OH-radicals in the troposphere is the major identified sink followed by smaller contribution from stratospheric loss and oxidation by methano- and methylotrophic bacteria in soils. This study directly investigated CH_4 exchange by plants in their natural environment. At a forest site in central Sweden, *in situ* branch chamber measurements were used to study plant ambient CH_4 exchange by spruce (*Picea abies*), birch (*Betula pubescens*), rowan (*Sorbus aucuparia*) and pine (*Pinus sylvestris*). The results show a net uptake of CH_4 by all the studied plants, which might be of importance for the methane budget. **Citation:** Sundqvist, E., P. Crill, M. Mölder, P. Vestin, and A. Lindroth (2012), Atmospheric methane removal by boreal plants, *Geophys. Res. Lett.*, *39*, L21806, doi:10.1029/2012GL053592.

1. Introduction

[2] The first report of CH_4 emissions by green plants by *Keppler et al.* [2006] proposed global CH_4 emissions by vegetation in the range of 62 to 236 Tg each year, which would comprise 10–30% of the total CH_4 entering the atmosphere [*Lowe*, 2006]. Several subsequent studies supported the findings of aerobic CH_4 emissions [e.g., *Wang et al.*, 2008; *McLeod et al.*, 2008; *Vigano et al.*, 2008; *Messenger et al.*, 2009], but the extrapolation of the results by Keppler using net primary production as a scalar has been criticized. A more conservative estimate was made using biome leaf biomass and photosynthesis as scaling factors, which resulted in emissions in the range of 10–60 Tg yr^{-1} [*Kirschbaum et al.*, 2006]. A number of other extrapolations have been made [*Houweling et al.*, 2006; *Butenhoff and Khalil*, 2007; *Ferretti et al.*, 2007] all resulting in a lower range than that of Keppler et al. Ultraviolet (UV) radiation has been shown to drive an aerobic production of CH_4 from plant tissue and pectin [*McLeod et al.*, 2008; *Vigano et al.*, 2008]. Estimates of global foliar CH_4 emissions from UV-irradiated pectin resulted in a value of 1 Tg yr^{-1} [*Bloom et al.*, 2010]. UV driven demethylation of the methoxyl groups of pectin in the cell wall of the plant has been suggested as a potential source of CH_4 [*McLeod et al.*, 2008; *Keppler et al.*, 2008; *Messenger et al.*, 2009]. UV radiation is indicated to act on a photosensitizer, which generates reactive oxygen species (ROS), which in turn attack pectic polysaccharides so that CH_4 formation occurs [*Messenger et al.*, 2009]. Besides UV-radiation, physical injury of the plant [*Z.-P. Wang et al.*, 2009] and other environmental stress factors might also stimulate ROS activity [*Z.-P. Wang et al.*, 2009; *Qaderi and Reid*, 2011; *Wishkerman et al.*, 2011]. At the same time it is well established that ROS can react with water to form OH [*Logan et al.*, 1981], the principal atmospheric sink of CH_4. The CH_4 emissions from plants have also been suggested to stem from dissolved CH_4 in the water drawn into the plant and subsequently released through diffusion [*Dueck et al.*, 2007] or transpiration [*Nisbet et al.*, 2009].

[3] The importance of the emissions and the mechanisms through which they are released are still discussed [*Bruhn et al.*, 2012]. Some studies have not found evidence for substantial aerobic CH_4 emissions [*Dueck et al.*, 2007; *Beerling et al.*, 2008; *Kirschbaum and Walcroft*, 2008]. There is also little evidence from in-situ studies on plant emission. Comparison of soil chamber measurements between plots with intact vegetation and removed vegetation led to increased production of CH_4 in the intact plot at a tropical savanna [*Sanhueza and Donoso*, 2006] and at two alpine grasslands [*Cao et al.*, 2008; *S. Wang et al.*, 2009]. However Cao et al. also found in their study that alpine shrubs instead consumed CH_4 and *S. Wang et al.* [2009] explained the discrepancy found in their study with differences in soil water content and soil temperature. There have also been a few studies on methane exchange by canopies. *Mikkelsen et al.* [2011] found indications of periodic canopy emissions using a gradient-based method whereas two studies using eddy covariance measurements didn't find any significant emission from the canopy [*Bowling et al.*, 2009; *Smeets et al.*, 2009].

[4] Sphagnum spp. mosses are the only plants so far reported to consume CH_4 by symbiosis with partly endophytic methanotrophic bacteria. Carbon dioxide (CO_2) produced from oxidation of CH_4 is then fixed to the plant during photosynthesis [*Raghoebarsing et al.*, 2005].

[5] Numerous plants have epiphytic bacterial associations, in this case pink-pigmented facultative methyltrophs (PPFMs) that can consume methanol emitted by plants [*Holland and Polacco*, 1994]. One strain of these bacteria, methylobacterium sp. BJ001T that was isolated from poplar tree tissue has been reported to be able to use CH_4 as a sole source of carbon and energy [*Van Aken et al.*, 2004]. This report was not considered definitive [*Dedysh et al.*, 2004].

2. Method

[6] We directly measured CH_4 exchange by boreal plants with the ambient atmosphere in a boreal forest (Table 1).

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Table 1. Details on Measurement Periods[a]

Plant Type	Type of Measurement	Measuring Period	Measuring Frequency	Number of Recordings Available for Analysis (n)	Plant Height (m)	Shoot Leaf Area (m^2)	Temperature Range (°C)	PAR Range (μmol m^{-2} s^{-1})	GPP Range (μmol m^{-2} s^{-1}) for PAR > 2	UV Range (μmol m^{-2} s^{-1})
Spruce1	In situ	13/8–15/9 2009	1/hour	285	~20	0.031	7–19	0–435	−11–0	0–2.8
Birch1	In situ	16/9–19/10 2009	1/ hour	361	~2.5	0.019	−3–16	0–140	−6–4	0–1.5
Spruce2	In situ	7 /7–28/7 2010	1/ hour	399	~20	0.017	13–30	0–117	−7–2	0–1.1
Spruce3	In situ	29 /7–12/8 2010	1/ hour	281	~1	0.026	13–22	0–76	−7–1	0–1
Rowan	In situ	27/8–10/9 2010	1/ hour	279	~4.5	0.008	5–16	0–80	−13–2	0–0.8
Birch2	In situ	10/9–24/9 2010	1/ hour	203	~1	0.011	6–17	0–33	−5–1	0–0.4
Pine1	In situ	29/9–4 /10 2010	1/ hour	97	~0.4	0.003	1–12	0–36	−10–6	0–0.5
Spruce4	Lab	24 hours Feb 2011	4/ hour	65	~0.5	0.008	5–25	0–382	−25–8	-
Spruce5	Lab	24 hours Feb 2011	4/ hour	61	~0.5	0.0147	5–25	0–358	−17–4	-
Spruce6	Lab	72 hours Feb 2011	4/ hour	198	~0.5	0.0168	5–26	0–380	−11–2	-
Pine2	Lab	24 hours Feb 2011	4/ hour	70	~0.3	0.005	5–25	0–327	−25–4	-
Pine3	Lab	24 hours Feb 2011	4/ hour	139	~0.3	0.0019	5–26	0–375	−100–14	-

[a]Information on plant sample and ranges of temperature, PAR, GPP and UV-radiation. 90% of the data fall within the Temperature, PAR, GPP and UV-radiation ranges that are shown in the table.

Semi-continuous field measurements on branches of different plants were made to study direct CH_4 exchange by plants and its dependence on photosynthetically active radiation (PAR), ultraviolet radiation (UV-radiation), temperature and photosynthesis. Because of the strong correlation between different environmental parameters, e.g., radiation and temperature, under natural conditions, additional laboratory measurements were also made to study the controlling factors. The CH_4 exchange measurements were made on spruce (*Picea abies*), birch (*Betula pubescens*), rowan (*Sorbus aucuparia*) and pine (*Pinus sylvestris*) in the 100-year-old Norunda forest stand in central Sweden at 60°5′ N, 17°29′ E. In 2009, the measurements took place in a forest stand that was thinned in 2008, whereas measurements in 2010 were in an untouched part of the forest. The measurements on birch in 2009 were made during the senescent period because environmental stresses had been posited to play an important role in affecting emissions [*Z.-P. Wang et al.*, 2009; *Qaderi and Reid*, 2011; *Wishkerman et al.*, 2011] (see Table 1 for details on measurements periods). Since the branch chamber measurements were integrated in a larger system with measurements of methane oxidation in the soil and methane gradients within the forest, the branches had to be selected within a limited area with the requirement of being reachable from the ground, but in a position that is reached by the sun at least part of the day. This explains the low PAR range for part of the measurement periods.

[7] A temperature controlled, automated branch chamber was used in combination with a high precision off-axes ICOS lazer (LGR-Los Gatos Research) to determine changing mixing ratios of CH_4 in the chamber headspace. The sides of the branch chamber exposed to the sun were quartz glass, which is transparent to UV radiation. The volume of the chamber was 0.0057 m^3. The chamber sealed around the stems of the leaves or needles being studied so that the leaves remained intact throughout the measurements. Changes of headspace concentration were measured after closure of the chamber by recirculating the air through the gas analyzer during a period of 5 min every hour. During closure, the air inside the chamber was kept to within ±1°C of the ambient air, and a fan was used to mix the headspace air. The cooling of the air was provided with a peltier cooler controlled by a CR 1000 data logger (Campell Inc., Logan, USA). The measuring frequency was 0.1 Hz in 2009 and 1 Hz in 2010. Besides CH_4, the analyzer measured CO_2 in 2009 and CO_2 and H_2O in 2010. The flow rate through the analyzer was 1.2 l/min.

[8] Before the measurements started, the chamber was put in an oven for 48 hours at 70°C to prevent possible CH_4 emissions from the chamber itself. The chamber was also run empty, but with equal procedures as the rest of the measurements, for a couple of weeks in 2009 to make sure there is no spurious CH_4 flux. The mean of the CH_4 exchange for this period was not significantly different from zero.

[9] In February 2011, laboratory measurements were made on horticultural specimens of spruce (Picea glauca conica) and pine (Pinus mugo var. pumilio). Samplings of the same species as measured in the field where not available at this time of the year. Exactly the same equipment was used as for the *in situ* measurements. The only difference was that flux measurements were performed four times per hour. The CH_4 exchange was tested at three temperature intervals, 3–7°C, 13–17°C and 23–27°C and four different

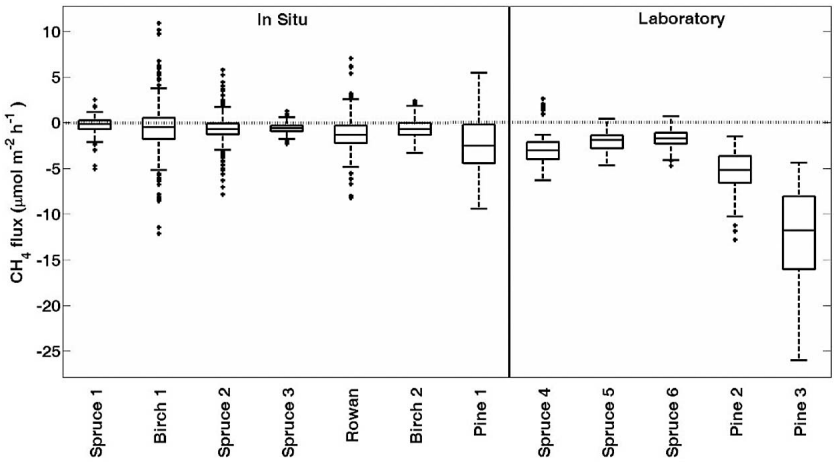

Figure 1. CH_4 exchange (μmol m^{-2} h^{-1}) for 12 measuring periods. The data are expressed per unit (m^2) of leaf area. The middle line of the box and whisker plot represents the median of all recordings including nighttime measurements. The edges of the box are the 25th and 75th percentiles, the whiskers, (black dotted lines) are the extreme values not considered outliers. Values larger than q3 + w (q3–q1) or smaller than q1–w (q3–q1) are considered outliers, where q1 and q3 are the 25th and 75th percentiles, respectively, and w = 1.5 is the whisker length. Negative values represent a flux from the atmosphere towards the branch. The median values are all significantly different from zero at 99% significance level.

intervals of PAR, 0 μmol m^{-2} s^{-1}, 50–150 μmol m^{-2} s^{-1}, 250–350 μmol m^{-2} s^{-1} and 350–450 μmol m^{-2} s^{-1}. The measured CH_4 concentrations had to be corrected for dilution effects by water vapor, but since the water vapor was not measured in 2009 it had to be calculated . We used the Ball-Berry equation, to calculate the stomatal conductance to CO_2, g_s (μmol m^{-2} s^{-1}), as: $g_s = g_0 + \frac{m \cdot A \cdot h}{C_s}$ where $g_0 = 0.01 \cdot 10^6$ (μmol m^{-2} s^{-1}) is the stomatal conductance [*Collatz et al.*, 1991], m = 8.75 (dimensionless) is a fitting parameter [*Xu and Baldocchi*, 2003]. A (μmol m^{-2} s^{-1}) is photosynthesis rate, h (dimensionless) is relative humidity and C_s (μmol CO_2 (mol air)$^{-1}$) is the mixing ratio of CO_2 in air at the leaf surface. C_s is calculated as $C_s = C_a - A \cdot \frac{1.37}{g_b}$ [*Liu et al.*, 2009], where C_a (μmol CO_2 (mol air)$^{-1}$)) is the ambient CO_2 concentration in the air and g_b = 0.075 m s^{-1} is the boundary layer conductance of the shoot, assuming 1 m s^{-1} wind speed in the chamber [*Martin et al.*, 1999]. The transpiration rate E (μmol m^{-2} s^{-1}) is calculated as: $E = g_s' \cdot \frac{(e_s(T_a) - e_a)}{P_a}$, where $g_s' = 1.6 \cdot g_s$ and g_s (μmol m^{-2} s^{-1}) is the stomatal conductance to water vapor, e_s (kPa) is the saturation vapor pressure at air temperature, T_a (°C), e_a (kPa) is the ambient vapor concentration and P_a (kPa) is the air

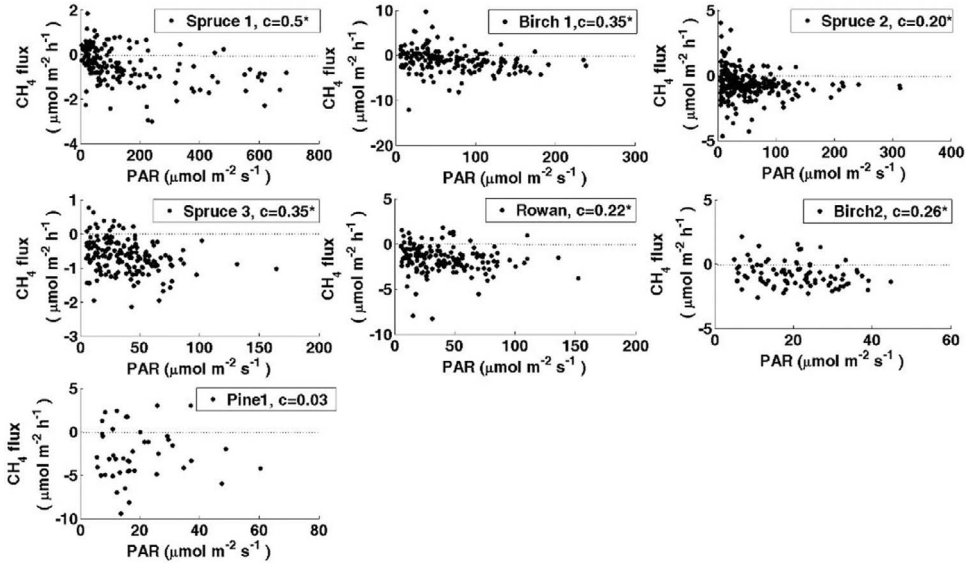

Figure 2. The correlation of CH_4 flux (μmol m^{-2} h^{-1}) with PAR (μmol m^{-2} s^{-1}) for the seven different shoots studied *in situ.* Only PAR values larger than 5 μmol m^{-2} s^{-1} are included in the plots. The c-value is the correlation coefficient. * Indicates that the correlation is significant at 95% significance level.

Table 2. Correlation Between CH_4 Exchange and PAR, CH_4 Exchange and Temperature and CH_4 Exchange and UV Radiation for *in Situ* Measurements[a]

Plant Type	n	Correlation Coefficient, CH_4 and PAR	Correlation Coefficient, CH_4 and Temperature	Correlation Coefficient, CH4 and UV-Radiation
Spruce1	165	−0.5[b]	−0.46[b]	−0.52[b]
Birch1	170	−0.35[b]	−0.25[b]	−0.42[b]
Spruce2	251	−0.20[b]	−0.09	−0.26
Spruce3	173	−0.35[b]	−0.32[b]	−0.42[b]
Rowan	151	−0.22[b]	−0.14	−0.19[b]
Birch2	88	−0.26[b]	−0.016	−0.24[b]
Pine1	44	−0.03	0.04	−0.04

[a]The correlation with PAR and UV is calculated for PAR-values larger than 5 μmol m^{-2} s^{-1}.
[b]Significant at 95% level.

pressure. We then used the measured ambient water vapor mixing ratio in the nearby tower as the initial concentration at time for chamber closure and then we added transpired water to calculate the successively increasing water vapor concentration in the chamber. As the next step, we calculated the dry concentration of CH_4 for each time step as $C_{dry} = C_{wet} \cdot \frac{1}{\left(1 - \frac{w}{1000}\right)}$, where w (mmol mol^{-1}) is the water vapor molar ratio. In 2010 w was measured and the correction could be done directly.

[10] The CH_4 mixing ratio obtained by the analyzer and after dilution corrections, c (μmol mol^{-1}), was then converted to C (μmol m^{-3}) by $C = c \cdot P/(R \cdot T)$, where P = 101325 Pa is the standard atmospheric air pressure, R = 8.314 J mol K^{-1} is the gas constant and T (K) is the chamber temperature.

[11] From the concentration data, a linear fit was made for a two-minute interval beginning immediately after chamber closure to retrieve dC/dt. We calculated the r^2 values for the fits of five different intervals, which were slightly offset to each other and selected the fit with the highest r^2 value. All fluxes with an r^2 value significant at 95% level where kept for further analyses. The CH_4 flux ($J_{CH4flux}$) was calculated as $J_{CH\ 4\ flux} = \frac{dC}{dt}\frac{V}{A}$, where V (m^3) is the chamber volume and A (m^2) is the projected leaf area of the enclosed shoot.

[12] Mean CH_4 exchange and spearman correlations between CH_4 exchange and PAR, temperature, UV and GPP were calculated. The whisker length of 1.5 in the box and whisker plot (see Figure 2) is suggested by *McGill et al.* [1978].

3. Results

[13] The results from the branch chamber measurements show a significant mean uptake of CH_4 by all studied plants (Figure 1).

[14] There was a consistent, small but significant negative correlation between CH_4 exchange and PAR for six of the seven species measured *in situ* with increasing CH_4 uptake for higher values of PAR (Figure 2 and Table 2). The measurements on Pine1 were not significantly correlated with PAR. The correlation coefficients for CH_4 exchange and UV-radiation were similar to those of PAR with increasing CH_4 uptake for higher values of UV-radiation (Table 2). Only three of the seven *in situ* measurements, Spruce1, Spruce2 and Birch1, were significantly and positively correlated with temperature (Table 2). The average CH_4 uptake per unit of leaf area across all species and environmental conditions for the *in situ* measurements was 0.7 μmol m^{-2} h^{-1}.

[15] In the laboratory measurements, CH_4 exchange was significantly (95%) correlated with PAR (range 0–450 μmol m^{-2} s^{-1}) for all measurements with correlation coefficients of −0.23, −0.28 and −0.22 for temperature intervals 3–7, 13–17 and 23–27°C, respectively (Table 3). CH_4 uptake was positively correlated with temperature at 90% significance level with correlation coefficients 0.14 and 0.19 for PAR intervals -5-5 and 250–350 respectively, and negatively correlated with temperature with correlation coefficients −0.01 (p = 0.9), and −0.19 (p = 0.1) for PAR intervals 50–150 and 350–450 respectively (Table 4).

[16] The correlation of CH_4 exchange with GPP was better for the laboratory measurements than for the *in situ* measurements. Of the *in situ* measurements, only Spruce1 and Birch1 showed a significant positive correlation between CH_4 exchange and GPP with correlation coefficients of 0.57 (Figure 3) and 0.52 respectively (Table 5).

4. Discussion

[17] In contrast to earlier studies of CH_4 exchange by plants, we find a net consumption by all plants studied both *in situ* and in the laboratory. The presence of endophytic or epiphytic bacteria with the ability to consume CH_4 would be a possible explanation for this [*Raghoebarsing et al.*, 2005;

Table 3. Correlation Between CH_4 Exchange and PAR at Fixed Temperature Intervals for All Species Measured in Laboratory

Temperature Range (°C)	n	Correlation Coefficient, CH_4 and PAR	p
3–7	109	−0.23	0.02
13–17	119	−0.28	0.002
23–27	80	−0.22	0.05

Table 4. Correlation Between CH_4 Exchange and Temperature at Fixed PAR Intervals for All Species Measured in Laboratory

PAR Range (μmol m^{-2} s^{-1})	n	Correlation Coefficient, CH4 and Temperature	p
−5–5	149	0.14	0.08
50–150	60	−0.01	0.9
250–350	202	0.19	0.01
350–450	74	−0.19	0.1

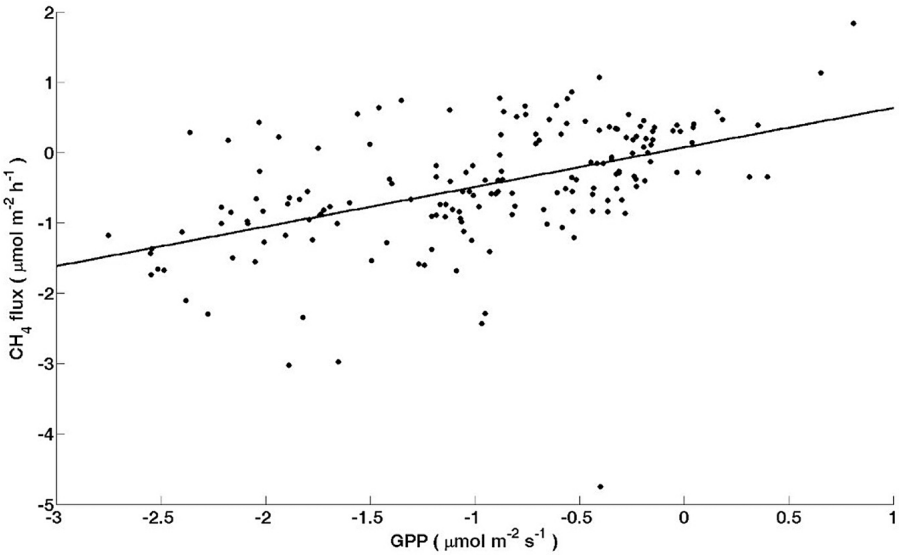

Figure 3. Correlation between CH_4 (μmol m^{-2} h^{-1}) exchange and GPP (μmol m^{-2} s^{-1}) for Spruce1. The correlation coefficient is 0.57. Notice that a negative GPP means uptake from the atmosphere.

Van Aken et al., 2004]. The timescale of the atmospheric OH sink is too large for it to be an explanation.

[18] The strong correlation between PAR and temperature *in situ* makes it difficult to sort out which parameter has the strongest control. The laboratory measurements gave more distinct results: the uptake increased consistently with increasing PAR while there was no consistent control on the uptake by temperature (Tables 3 and 4). This indicates that the CH_4 sink is located somewhere inside the leaves and that the diffusion rate is controlled by the stomatal conductance. Stomatal conductance increases practically linearly with light at the range of PAR encountered in this study. The temperature response found for a several PAR intervals with a decreasing uptake for increasing temperatures could also be explained by a response to vapor pressure deficit (VPD) with stomata responding in the opposite direction, i.e., closing when temperature (and VPD) increases.

[19] What speaks against a microbial process is the negative correlation between CH_4 consumption and temperature found in the laboratory studies since bacterial activities are normally favored by increasing temperatures. However, if it is the diffusion rate through the stomata that is the limiting factor for bacterial consumption, this hypothesis could still be valid.

[20] The emissions of CH_4 by plants that have been reported in several studies are thought to depend on environmental stresses that activate ROS. It is possible that this emission process occurs simultaneously with a consumption of CH_4 by bacteria. High levels of ROS would then control the CH_4 exchange leading to net emissions. Most plants in their natural environment however, might not experience such a high stress level. The absence of UV radiation in the laboratory might explain the higher CH_4 uptake and the higher correlation of the uptake with GPP in this particular environment.

[21] Our observations also contain positive CH_4 fluxes particularly at low GPP (or PAR), but this is mainly attributed to the uncertainty in the measurements. Under the condition of very low fluxes, the uncertainty in measured concentrations caused by signal noise, become significant.

[22] If we scale up our observed *in situ* uptake of CH_4 by multiplying the mean value of 0.7 μmol m^{-2} h^{-1} with the leaf area index of the Norunda forest (4.8) we obtain a value of 3.4 μmol m^{-2} h^{-1}. This is close to the mean CH_4 soil oxidation rate in various forest soils based on 28 studies, which is 4.0 μmol m^{-2} h^{-1} [*Jang et al.*, 2006], this indicates that the canopy might play an equally important role as the soil in the global context.

[23] Two recent studies give alternative explanations to the slow-down in the growth rate of atmospheric methane in the last decades. One of them indicates that it is due to a stabilization of fossil-fuel emissions [*Aydin et al.*, 2011] whereas the other explains it by a decrease in microbial methane sources in the northern hemisphere [*Kai et al.*, 2011]. Our results offer a third explanation: that an increasing amount of CH_4 has been taken up by vegetation during the last decades as a consequence of increased greenness

Table 5. Correlation Between CH_4 Exchange and GPP for All Plants Studied[a]

Plant Type	n-Value	Correlation Coefficient, CH4 and GPP
Spruce1	171	0.57[b]
Birch1	176	0.52[b]
Spruce2	273	0.1
Spruce3	184	0.1
Rowan	162	0.06
Birch2	102	−0.03
Pine1	47	−0.3[b]
Spruce4	49	0.38[b]
Spruce5	47	0.14
Spruce6	144	0.31[b]
Pine2	47	0.51[b]
Pine3	97	0.67[b]

[a]GPP is calculated for PAR > 2.
[b]Significant at 95% level.

[*Myneni et al.*, 1997], NPP [*Nemani et al.*, 2003] and GPP [*Chen et al.*, 2006] as observed by satellite remote sensing.

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References

Aydin, M., et al. (2011), Recent decreases in fossil-fuel emissions of ethane and methane derived from firn air, *Nature*, *476*, 198–201, doi:10.1038/nature10352.

Beerling, D. J., T. Gardiner, G. Leggett, A. R. McLeod, and W. P. Quick (2008), Missing methane emissions from leaves of terrestrial plants, *Global Change Biol.*, *14*, 1821–1826, doi:10.1111/j.1365-2486.2008.01607.x.

Bloom, A. A., et al. (2010), Global methane emission estimates from ultraviolet irradiation of terrestrial plant foliage, *New Phytol.*, *187*, 417–425, doi:10.1111/j.1469-8137.2010.03259.x.

Bowling, D. R., et al. (2009), Soil, plant and transport influences on methane in a subalpine forest under high ultraviolet-B radiation in forests, *J. Ecol.*, *82*, 843–854, doi:10.5194/bg-8-851-2011.

Bruhn, D., I. M. Moller, T. N. Mikkelsen, and P. Ambus (2012), Terrestrial plant methane production and emission, *Physiol. Plant.*, *144*, 201–209, doi:10.1111/j.1399-3054.2011.01551.x.

Butenhoff, C. L., and M. A. K. Khalil (2007), Global methane emissions from terrestrial plants, *Environ. Sci. Technol.*, *41*, 4032–4037, doi:10.1021/es062404i.

Cao, G., et al. (2008), Methane emissions by alpine plant communities in the Qinghai-Tibet Plateau, *Biol. Lett.*, *4*, 681–684, doi:10.1098/rsbl.2008.0373.

Chen, J. M., B. Chen, K. Higuchi, J. Liu, D. Chan, D. Worthy, P. Tans, and A. Black (2006), Boreal ecosystems sequestered more carbon in warmer years, *Geophys. Res. Lett.*, *33*, L10803, doi:10.1029/2006GL025919.

Collatz, G. J., J. T. Ball, C. Grivet, and J. A. Berry (1991), Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer, *Agric. For. Meteorol.*, *54*, 107–136, doi:10.1016/0168-1923(91)90002-8.

Dedysh, S. N., P. F. Dunfield, and Y. A. Trotsenko (2004), Methane utilization by Methylobacterium species: New evidence but still no proof for an old controversy, *Int. J. Syst. Evol. Microbiol.*, *54*, 1919–1920, doi:10.1099/ijs.0.63493-0.

Dueck, T. A., et al. (2007), No evidence for substantial aerobic methane emission by terrestrial plants: A C-13-labelling approach, *New Phytol.*, *175*, 29–35, doi:10.1111/j.1469-8137.2007.02103.x.

Ferretti, D. F., et al. (2007), Stable isotopes provide revised global limits of aerobic methane emissions from plants, *Atmos. Chem. Phys.*, *7*, 237–241, doi:10.5194/acp-7-237-2007.

Holland, M. A., and J. C. Polacco (1994), PPFMS and other covert contaminants: Is there more to plant physiology than just plant?, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, *45*, 197–209, doi:10.1146/annurev.pp.45.060194.001213.

Houweling, S., T. Röckmann, I. Aben, F. Keppler, M. Krol, J. F. Meirink, E. J. Dlugokencky, and C. Frankenberg (2006), Atmospheric constraints on global emissions of methane from plants, *Geophys. Res. Lett.*, *33*, L15821, doi:10.1029/2006GL026162.

Jang, I., S. Lee, J.-H. Hong, and H. Kang (2006), Methane oxidation rates in forest soils and their controlling variables: A review and a case study in Korea, *Ecol. Res.*, *21*, 849–854, doi:10.1007/s11284-006-0041-9.

Kai, F. M., S. C. Tyler, J. T. Randerson, and D. R. Blake (2011), Reduced methane growth rate explained by decreased Northern Hemisphere microbial sources, *Nature*, *476*, 194–197, doi:10.1038/nature10259.

Keppler, F., J. T. G. Hamilton, M. Brass, and T. Röckmann (2006), Methane emissions from terrestrial plants under aerobic emissions, *Nature*, *439*, 187–191, doi:10.1038/nature04420.

Keppler, F., et al. (2008), Methoxyl groups of plant pectin as a precursor of atmospheric methane: Evidence from deuterium labelling studies, *New Phytol.*, *178*, 808–814, doi:10.1111/j.1469-8137.2008.02411.x.

Kirschbaum, M. U. F., and A. Walcroft (2008), No detectable aerobic methane efflux from plant material, nor from adsorption/desorption processes, *Biogeosciences*, *5*, 1551–1558, doi:10.5194/bg-5-1551-2008.

Kirschbaum, M. U. F., et al. (2006), A comment on the quantitative significance of aerobic methane release by plants, *Funct. Plant Biol.*, *33*, 521–530, doi:10.1071/FP06051.

Liu, F., M. N. Andersen, and C. R. Jensen (2009), Capability of the 'Ball-Berry' model for predicting stomatal conductance and water use efficiency of potato leaves under different irrigation regimes, *Sci. Hortic.*, *122*, 346–354, doi:10.1016/j.scienta.2009.05.026.

Logan, A. J., M. J. Prather, S. C. Wofsy, and M. B. Mcelroy (1981), Tropospheric chemistry: A global perspective, *J. Geophys. Res.*, *86*, 7210–7254, doi:10.1029/JC086iC08p07210.

Lowe, D. (2006), Global change: A green source of surprise, *Nature*, *439*, 148–149, doi:10.1038/439148a.

Martin, T. A., T. M. Hinckley, F. C. Meinzer, and D. G. Sprugel (1999), Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches, *Tree Physiol.*, *19*, 435–443, doi:10.1093/treephys/19.7.435.

McGill, R., J. W. Tukey, and W. A. Larsen (1978), Variations of Box plots, *Am. Stat.*, *32*(1), 12–16.

McLeod, A. R., et al. (2008), Ultraviolet radiation drives methane emissions from terrestrial plant pectins, *New Phytol.*, *180*, 124–132, doi:10.1111/j.1469-8137.2008.02571.x.

Messenger, D. J., A. R. McLeod, and S. C. Fry (2009), The role of ultraviolet radiation, photosensitizers, reactive oxygen species and ester groups in mechanisms of methane formation from pectin, *Plant Cell Environ.*, *32*, 1–9, doi:10.1111/j.1365-3040.2008.01892.x.

Mikkelsen, T. N., et al. (2011), Is methane released from the forest canopy?, *iForest*, *4*, 200–204, doi:10.3832/ifor0591-004

Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani (1997), Increased plant growth in the northern high latitudes from 1981 to 1991, *Nature*, *386*, 698–702, doi:10.1038/386698a0.

Nemani, R. R., et al. (2003), Climate driven increases in global terrestrial net primary production from 1982–1999, *Science*, *300*, 1560–1563, doi:10.1126/science.1082750.

Nisbet, R. E. R., et al. (2009), Emissions of methane from plants, *Proc. R. Soc. London B*, *276*, 1347–1354, doi:10.1098/rspb.2008.1731.

Qaderi, M. M., and D. M. Reid (2011), Stressed crops emit more methane despite the mitigating effects of elevated carbon dioxide, *Funct. Plant Biol.*, *38*, 97–105, doi:10.1071/FP10119.

Raghoebarsing, A. A., et al. (2005), Methanotrophic symbionts provide carbon for photosynthesis in peat bogs, *Nature*, *436*, 1153–1156, doi:10.1038/nature03802.

Sanhueza, E., and L. Donoso (2006), Methane emissions from tropical savanna *Trachypogon* sp. grasses, *Atmos. Chem. Phys.*, *6*, 5315–5319, doi:10.5194/acp-6-5315-2006.

Smeets, C. J. P. P., R. Holzinger, I. Vigano, A. H. Goldstein, and T. Rockmann (2009), Eddy covariance methane measurements at a Ponderosa pine plantation in California, *Atmos. Chem. Phys.*, *9*, 8365–8375, doi:10.5194/acp-9-8365-2009.

Van Aken, B., C. M. Peres, S. Lafferty Doty, J. M. Yoon, and J. L. Schnoor (2004), *Methylobacterium populi* sp. nov., a novel aerobic, pink-pigmented, facultatively methylotrophic, methane-utilizing bacterium isolated from poplar trees (*Populus deltoides* × *nigra* DN34), *Int. J. Syst. Evol. Microbiol.*, *54*, 1191–1196, doi:10.1099/ijs.0.02796-0.

Vigano, I., et al. (2008), Effect of UV radiation and temperature on the emission of methane from plant biomass and structural components, *Biogeosciences*, *5*, 937–947, doi:10.5194/bg-5-937-2008.

Wang, S., et al. (2009), Methane emissions by plant communities in an alpine meadow on the Qinghai-Tibetan Plateau: A new experimental study of alpine meadows and oat pasture, *Biol. Lett.*, *5*, 535–538, doi:10.1098/rsbl.2009.0123.

Wang, Z.-P., X.-G. Han, G. G. Wang, Y. Song, and J. Gulledge (2008), Aerobic methane emission from plants in the Inner Mongolia steppe, *Environ. Sci. Technol.*, *42*, 62–68, doi:10.1021/es071224l.

Wang, Z.-P., et al. (2009), Physical injury stimulates aerobic methane emissions from terrestrial plants, *Biogeosciences*, *6*, 615–621, doi:10.5194/bg-6-615-2009.

Wishkerman, A., et al. (2011), Enhanced formation of methane in plant cell cultures by inhibition of cytochrome c oxidase, *Plant Cell Environ.*, *34*, 457–464, doi:10.1111/j.1365-3040.2010.02255.x.

Xu, L., and D. D. Baldocchi (2003), Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature, *Tree Physiol.*, *23*, 865–877, doi:10.1093/treephys/23.13.865.