Biogeosciences, 8, 2365–2375, 2011
www.biogeosciences.net/8/2365/2011/
doi:10.5194/bg-8-2365-2011

Biogeosciences

Plant-mediated CH_4 transport and contribution of photosynthates to methanogenesis at a boreal mire: a ^{14}C pulse-labeling study

M. Dorodnikov[1], **K.-H. Knorr**[2], **Y. Kuzyakov**[3], **and M. Wilmking**[1]

[1]Institute of Botany and Landscape Ecology, University of Greifswald, Grimmer Str. 88, 17487 Greifswald, Germany
[2]Limnological Research Station and Department of Hydrology, University of Bayreuth, Universitaetsstrasse 30, 95440 Bayreuth, Germany
[3]Department of Soil Science of Temperate Ecosystems, University of Göttingen, Büsgenweg 2, 37077 Göttingen, Germany

Received: 26 March 2011 – Published in Biogeosciences Discuss.: 4 May 2011
Revised: 18 July 2011 – Accepted: 18 July 2011 – Published: 29 August 2011

Abstract. Plant-mediated methane (CH_4) transport and the contribution of recent photosynthates to methanogenesis were studied on two dominating vascular plant species – *Eriophorum vaginatum* and *Scheuchzeria palustris* – at three types of microrelief forms (hummocks – *E*. hummocks, lawns – *E*. lawns and hollows – *S*. hollows) of a boreal natural minerogenic, oligotrophic fen in Eastern Finland. ^{14}C-pulse labeling of mesocosms with shoots isolated from entire belowground peat under controlled conditions allowed estimation of plant-mediated CH_4 flux and contribution of recent (^{14}C) photosynthates to total CH_4. The results showed (i) CH_4 flux increased in the order *E*. hummocks $\leq$ *E*. lawns $<$ *S*. hollows corresponding to the increasing water table level at the relief microforms as adjusted to field conditions. (ii) Plant-mediated CH_4 flux accounted for 38, 31 and 51 % of total CH_4 at *E*. hummocks, *E*. lawns and *S*. hollows, respectively. (iii) Contribution of recent photosynthates to methanogenesis accounted for 0.03 % for *E*. hummocks, 0.06 % for *E*. lawns and 0.13 % for *S*. hollows of assimilated ^{14}C. Thus, microsites with *S. palustris* were characterized by higher rates of transported CH_4 from the peat column to the atmosphere when compared to *E. vaginatum* of drier lawns and hummocks. Contribution of recent photosynthates to methanogenesis was dependent on the plant biomass within-species level (*E. vaginatum* at hummocks and lawns) but was not observed between species: smaller *S. palustris* had higher flux of $^{14}CH_4$ as compared to larger *E. vaginatum*. Therefore, for the assessment of CH_4 dynamics over meso- and macroscale as well as for the implication and development of the modeling of CH_4 fluxes, it is necessary to account for plant species-specific differences in CH_4 production, consumption and transport and the attribution of those species to topographic forms of microrelief.

Correspondence to: M. Dorodnikov
(maxim.dorodnikov@uef.fi)

1 Introduction

Boreal peatlands are large global repositories of organic matter (OM), containing about 15 % of the total terrestrial organic carbon (C) (Turunen et al., 2002). Their plant communities apparently have an important role in ecosystem C dynamics as, first of all, the supplier of organic C. Due to permanently waterlogged anoxic conditions in peatland ecosystems both the recent plant-derived deposits (new C) and previously accumulated OM (old C) in the catotelm decompose resulting in emission of methane (CH_4) to the atmosphere. Because CH_4 is an effective greenhouse gas, which has 23 folds higher global warming potential (based on a 100 yr period) compared to CO_2 (IPCC, 2001), understanding the processes controlling the CH_4 emission in boreal peatlands is critical for estimating current and future global C budgets.

Temperature and water table fluctuations have been identified to be important constraints on the CH_4 emission (reviewed in Lai, 2009), but also the microtopography of peatlands with the respective plant communities could be an effective predictor of the CH_4 fluxes. The surface of a boreal peatland can be differentiated into microrelief subunits – microforms (e.g. hummocks, lawns, hollows) according to their hydrological characteristics (water table level) and the main vegetation communities (Becker et al., 2008). In

turn, vascular plants have been recognized to control the CH_4 flux from wetlands because they affect production, consumption and transport of CH_4 (Joabsson and Christensen, 2001; Lai, 2009). Many studies found a tight correlation of net ecosystem productivity (NEP) and CH_4 emission (Whiting and Chanton, 1993; Dacey et al., 1994; Greenup et al., 2000) and experiments using radiocarbon (Chanton et al., 1995) or ^{14}C-label (King et al., 2002; Christensen et al., 2003; Ström et al., 2005) showed the importance of recent plant photosynthates for CH_4 production. Furthermore, the role of vegetation in CH_4 dynamics might increase in the future due to climate change. Thus, the predicted warming (ACIA, 2005; IPCC, 2007) and elevation of atmospheric CO_2 (IPCC, 2007), which is the substrate for photosynthesis, could enhance the NEP hereby affecting the processes of CH_4 turnover. In light of the importance of the issue, some studies investigated the contribution of recent photosynthates to the CH_4 emission for rice paddies (Minoda et al., 1996; Dannenberg and Conrad, 1999), peatlands of the mid latitude climate region (Christensen et al., 2003) and tundra (King and Reeburgh, 2002; King et al., 2002). However, there is a wide range and variability of estimations of label incorporation into CH_4 during methanogenesis. Thus, for the rice plants the contribution of photosynthates to emitted CH_4 ranged between 3 and 52 % of the total CH_4 flux, depending on the time of the season and treatment (Minoda et al., 1996; Dannenberg and Conrad, 1999). Using ^{14}C labeling, King and Reeburgh (2002) and King et al. (2002) showed that in mesocosms of moist tussock and wet sedge tundra, dominated by *Carex chordorrhiza* and *Eriophorum vaginatum*, 0.05 to 5 % of photosynthesized C contributed to emitted CH_4. Christensen et al. (2003) reported that 0.5 % of $^{14}CO_2$ assimilated by *Eriophorum angustifolium* was emitted as CH_4 during 4-months. The first detection of a label in CH_4 occurred within 2–24 h after assimilation (Megonigal et al., 1999; King and Reeburgh, 2002; King et al., 2002; Christensen et al., 2003), which corresponds to the release of C from recent photosynthates in the rhizosphere of crops (Kuzyakov et al., 2003) and to $^{14}CO_2$ efflux from soil (Kuzyakov and Gavrichkova, 2010). In the current study we attempted to narrow the existing variety of results and to study the mechanisms underlying the fate of recent plant photosynthates in CH_4 production. We conducted a ^{14}C-pulse labeling experiment of intact plant mesocosms of two common boreal peatland species – *Eriophorum vaginatum* and *Scheuchzeria palustris*. *Scheuchzeria palustris*, to our knowledge, has never been investigated in such experiments so far. Furthermore, the abovementioned studies have not considered different location of the species in peatlands' microrelief, e.g. the hummocks, lawns and hollows. Such a combination between plant species and their attribution to microrelief forms distinguishing by water table level, hence by the portion of roots located under anoxic conditions, may be crucial for their contribution to CH_4 flux. Therefore, we consider plant species and microforms as coupled ecological units, which are relevant to the natural environment of boreal peatlands.

Besides providing a source of fresh C for methanogenesis (Hornibrook et al., 1997; King et al., 2002; Ström et al., 2005), vascular plants act as a conduit of CH_4 from the anoxic zone to the atmosphere, bypassing oxidation in the aerobic zone (reviewed in Lai, 2009). *Vice versa*, root ventilation through plant aerenchyma cause leakage of oxygen into the rhizosphere and may lead to inhibition of methanogenesis and oxidation of CH_4 to CO_2 (Chanton and Dacey, 1991; Watson et al., 1997; Joabsson and Christensen, 2001). Water table level varies between microforms increasing in the order hummocks-lawns-hollows, thus resulting in different thickness of the oxidation zone and, as one result, different CH_4 fluxes. Studies using chamber techniques to measure CH_4 emissions generally show the lowest CH_4 fluxes on hummocks and the highest on hollows (Dalva et al., 2001; Johansson et al., 2006; Forbrich et al., 2010). However, for the precise estimation of CH_4 emission, especially for large territories (regional C balance), it is necessary to know species-specific characteristics of microforms (Schimel, 1995; Ström et al., 2005). For example, *Scheuchzeria palustris* dominates the permanently water-logged microforms (hollows) of peatlands and is adapted to grow in anoxic conditions by having well-developed aerenchyma in roots and stems (Watson and Dallwitz, 1992). Hence, this species could promote CH_4 transport to the atmosphere increasing flux of CH_4 from these microforms. For *Eriophorum*, a strong potential for CH_4 release has also been reported, while for this species, CH_4 oxidation in the rhizosphere was found to be low (Frenzel and Rudolph, 1998).

Generally, species-specific plant-mediated CH_4 transport is estimated indirectly by comparison of CH_4 efflux from the surface with different plant communities (vascular/nonvascular) and/or by clear cutting of plants responsible for CH_4 transport (Shannon et al., 1996; King et al., 1998; Kutzbach et al., 2004). The estimated plant-mediated CH_4 flux substantially varies between 33 and 100 % (and even more than 100 % of the total flux, indicating its overestimation) (Schimel, 1995; King et al., 1998; Kutzbach et al., 2004; Koelbener et al., 2010). Thus, direct estimation of plant-mediated CH_4 by separation of plant shoots from the soil/peat is necessary (Schimel, 1995; Frenzel and Rudolf, 1998).

Furthermore, most studies were conducted for the high-latitudes arctic and sub-arctic wetlands (Whiting and Chanton, 1992; Schimel et al., 1995; King et al., 1998; Kutzbach et al., 2004) or for rice paddy soils (Jia et al., 2001, Das and Baruah, 2008). There is much less information available on the plant-mediated CH_4 transport in the boreal region (Frenzel and Rudolf, 1998; Strack et al., 2006). In the current study we present the results of a laboratory ^{14}C-pulse labeling experiment on three microforms (hummocks, lawns and hollows) from an eastern Finnish boreal mire, characterized by two dominant plant species and three water table levels.

We focused on the following research questions:

- What is the contribution of recent photosynthates to the methanogenesis and how fast does new C get incorporated into CH_4?
- What are the rates and amounts of total (labeled and unlabeled) plant-mediated CH_4 flux to the atmosphere in the three microforms?

We tested two hypotheses: (i) contribution of recent photosynthates to methanogenesis occurs fast and depends not only on the amount of plant biomass but on species as well; (ii) the combination of permanently water saturated microsites with the typical plant species such as *Scheuchzeria* at hollows leads to larger plant mediated CH_4 transport to the atmosphere as compared to periodically watered or dry microsites (*Eriophorum* at lawns and hummocks).

2 Materials and methods

2.1 Sampling of peat cores with plants

Cores of peat with plants (mesocosms) were sampled at a natural minerogenic, oligotrophic low-sedge pine fen Salmisuo in Eastern Finland, located in the North Karelian Biosphere Reserve (62°47′ N, 30°56′ E). The site is described in details elsewhere (Saarnio et al., 1997; Becker et al., 2008; Jager et al., 2009; Forbrich et al., 2010). The surface of the site within the peatland was subdivided into three main microform types according to typical vegetation communities and moisture conditions: dry and elevated hummocks (*Eriophorum vaginatum, Pinus sylvesteris, Andromeda polifolia, Sphagnum fuscum*), intermediate lawns (*Eriophorum vaginatum, Sphagnum balticum, Sphagnum papillosum*), and wet hollows (*Scheuchzeria palustris, Sphagnum balticum*). Two of the species dominated at microforms of the experimental site: *Eriophorum vaginatum* at hummocks and lawns and *Scheuchzeria palustris* at hollows. These representative species were chosen for the experiment.

For the extraction of cores from the peatland's microforms a steel corer with handles (diameter 14 cm, length 25 cm) was used. The sampling was done on 25 July 2009, and 36 cores were extracted (24 of *Eriophorum vaginatum* and 12 of *Scheuchzeria palustris*) from randomly chosen hummocks, lawns and hollows. Apart from the vascular plants, the extracted cores included green mosses (*Sphagnum fuscum* and *Sphagnum balticum*) on the top and peat with roots to the depth of 25 cm. Additionally 2 cores of peat with moss but without vascular plants were taken as references. The sampling date corresponded to the peak of vegetation season in this region and the average water table level at the microforms was 12 cm under hummocks, 5 cm under lawns and 0 cm at hollows. No rain or storm events occurred during the sampling. The extracted plant-peat cores were immediately put into polyethylene bags and transferred to the plastic cylinders (diameter 14 cm, length 30 cm) tightly closed from the bottom. A portion of water lost during sampling procedure was compensated with peatland water from the sampling spot to the in situ level of the corresponding microrelief form. All 36 cores were immediately transported to the University of Bayreuth, Germany, where on 28 July 2009 the ^{14}C labeling experiment started. The mesocosms were kept undisturbed (no further destructive manipulations were applied) under controlled conditions with 27/22 °C day/night temperature, a 14-h photoperiod and 800 µmol m^{-2} s^{-1} light intensity (Kuzyakov et al., 2006) corresponding to growth conditions without light and temperature limitations. Water level in peat cores was maintained according to the type of microforms (see above) by adding deionized water during the experiment (18 days). Total plant biomass (shoots, roots) and amount of peat (including moss) in mesocosms increased in the order hollows < lawns < hummocks (Table 1).

2.2 Isolation of plant shoots from entire peat and ^{14}C pulse labeling of mesocosms

To assess the CH_4 plant-mediated transport, we isolated shoots from roots and entire peat in one set of mesocosms. Eighteen randomly chosen cores (6 *Eriophorum* cores of hummocks – *E*. hummocks, 6 *Eriophorum* cores of lawns – *E*. lawns and 6 *Scheuchzeria* cores of hollows – *S*. hollows) were put into Plexiglas containers (inner diameter 15 cm, height 30 cm, volume 5300 cm^{-3}) with tightly fixed bottom and a lid on the top. Each lid had 9 holes (diameter 2 cm), through which all plant shoots were passed (Fig. 1). Then all holes with and without shoots were sealed with silicone rubber (NG 3170, Thauer & Co., Germany), thus no direct connection of a peat core with aboveground shoots existed (Fig. 1). However, containers and lids were tightly closed only during flux measurements, when the brims of containers and lids were fixed with clamps. At other times, lids were loose, allowing gas exchange and preventing overpressure between cores surface and lids. In the remaining 18 cores with vascular plants and the two cores with moss the shoots were not isolated from roots and they were used as references for the peat-shoots isolation experiment.

The ^{14}C pulse labeling was conducted for both isolated and not isolated mesocosms and was done within two subsequent days, as the three different microforms should be labeled separately to avoid different assimilation by different species. The labeling was done according to an established procedure (Gavrichkova and Kuzyakov, 2010; Gocke et al., 2010). Sodium carbonate ($Na_2^{14}CO_3$, ARC Inc., USA) with ^{14}C activity of 1.48 MBq was diluted with de-ionized water in a 30 ml vial. Previously, the water was slightly alkalinized to prevent ^{14}C losses by exchange with atmospheric CO_2. Six isolated and six not isolated mesocosms of *E*. hummocks and *E*. lawns were put into a large Plexiglas chamber (1.5 m^3), which consisted of two halves. The mesocosms were placed on the bottom half and the upper

Table 1. Dry weight (± SE, $n = 12$) and the recovery of ^{14}C label in compartments of mesocosms of *Eriophorum vaginatum* (*E. vaginatum* from hummocks and lawns) and *Scheuchzeria palustris* (*S. palustris* from hollows) after 18 days of the experiment.

Microform type	Plant species	Dry weight, g^{-1}			Recovery of ^{14}C in mesocosms, % from ^{14}C input					
		shoots	roots	peat	shoots	roots	peat	CO_2*	CH_4*	unidentified
hummock	*E. vaginatum*	13.6 ± 6.5^{Ab}	144.9 ± 4.0^{Cc}	45.6 ± 1.8^{Ba}	12.7	11.8	11.2	10.9	0.06	21.4**
lawn	*E. vaginatum*	5.2 ± 1.2^{Ab}	116.3 ± 10.8^{Cb}	38.6 ± 6.3^{Ba}	5.2	2.1	13.6	11.0	0.03	
hollow	*S. palustris*	1.8 ± 0.2^{Aa}	58.2 ± 3.7^{Ba}	71.8 ± 6.6^{Cb}	8.2	37.9	28.6	5.9	0.13	19.2***

* Calculated by linear interpolation of $^{14}CO_2$ and $^{14}CH_4$ fluxes and integration over time using the trapezoidal rule.
** Calculated as a difference between initial input and the sum of all measured ^{14}C compartments of *E. vaginatum* from hummocks and lawns (1st labeling).
*** Calculated as a difference between initial input and the sum of all measured ^{14}C compartments of *S. palustris* from hollows (2nd labeling).

half of the chamber was put on the top into a special slot. This slot was filled with water to seal the connection of two halves. Thereafter, the closed chamber was connected to the vial with label by PVC tubings and $^{14}CO_2$ was introduced inside by adding 3 ml of 5 M H_2SO_4 to the $Na_2^{14}CO_3$ solution. Air with $^{14}CO_2$ was circulated in a closed cycle by a membrane pump (Type SMG4, Gardner Denver Thomas GmbH, Germany) and mixed by fan to allow for homogenous $^{14}CO_2$ distribution. After complete evolution of $^{14}CO_2$ into the chamber atmosphere mesocosms were left for a 2.5-h labeling period. To remove the remaining unassimilated $^{14}CO_2$, the CO_2 from the chamber was trapped afterwards using 10 mL of 1 M NaOH solution. The same pulse labeling procedure with similar activity (1.48 MBq) was done the next day (29 July 2009) for 6 cores of *S.* hollows.

2.3 Measurements of gas fluxes and ^{14}C activity

Fluxes of total CO_2 and CH_4 were measured from 18 unlabeled cores with vascular plants (9 isolated and 9 not isolated from peat) and 2 cores with moss. To measure gas fluxes, transparent Plexiglas chambers (diameter 15 cm, height 30 cm, volume 5300 cm^{-3}) were installed onto containers with isolated and not isolated mesocosms (Fig. 1). We used the transparent chambers also for CH_4 flux measurements, since we aimed to assess plant-mediated CH_4 flux and tried to avoid inevitable plant response to darkening. Air samples were taken with plastic syringes (20 ml, Braun Omnifix, Melsungen, Germany) through outlets equipped with 3-way stopcocks (Sarstedt, Nürmbrecht, Germany) each 30 min during 120 min of chamber deployment (4 times). CO_2 and CH_4 concentrations were measured in collected air samples on a gas chromatograph (SRI 8610, Torrance, USA; FID with methanizer) at the Limnological Research Station of the University of Bayreuth.

Simultaneously to total CO_2 and CH_4, the ^{14}C labeled gas fluxes were measured from the labeled 18 mesocosms (9 isolated and 9 not isolated from peat) according to the following procedure: Plexiglas chambers were installed as described above but left for longer period as compared to unlabeled flux measurements for accumulation of the lowest measurable amount of ^{14}C-CH_4. Depending on plant species, type of microforms and day of the experiment the accumulation time varied between 60 and 180 min. Additionally, a larger volume of air sample (1000–2500 cm^{-3}) needed for ^{14}C-CH_4 analyses was taken by the replacement of the air in a chamber into a foil air balloon (air tight, no pressure required for filling) with a membrane pump. Sampling of ^{14}C-CO_2 and ^{14}C-CH_4 was performed simultaneously on the 1st, 2nd, 4th, 6th, 10th, 11th, 14th and 16th day of the experiment separately for two vascular plant mesocosms (see above).

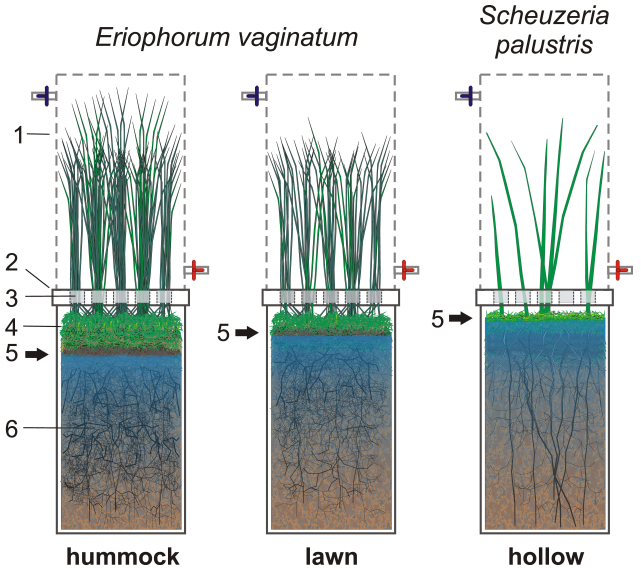

Fig. 1. Isolation of shoots from roots and entire peat cores in mesocosms of *E. vaginatum* and *S. palustris* sampled at hummocks, lawns and hollows of a boreal natural minerogenic, oligotrophic fen Salmisuo in Eastern Finland. Microforms differed by water table level (12-5-0 cm below surface for hummocks, lawns and hollows, respectively) maintained in the laboratory experiment. 1 – chambers used for gases flux measurements, 2 – lid with holes used for isolation of shoots from peat cores; 3 – holes in lids with passed through tillers sealed with silicone; 4 – green moss (*Sphagnum balticum*, *Sphagnum papillosum*); 5 – water table level; 6 – peat with roots.

To measure ^{14}C activity in CH_4, an oxidation line was constructed which converted CH_4 to CO_2 (after King et al., 2002 and personal communication). The combustion device for C/N analysis in solid samples (Feststoffmodul 1300, AnalytikJena, Germany) was adjusted for the purpose by installation of external equipment. Four NaOH traps were connected sequentially by the system of tubings with a combustion chamber of the device and a membrane pump in a way that two of the traps were placed before and two after the combustion chamber. An air sample sucked by the pump entered the first 2 traps where CO_2 was removed and then went to the combustion chamber where CH_4 oxidized to CO_2 at 800 °C. Resulting CO_2 was fixed in the subsequent two NaOH traps. Prior to use, the oxidation line was calibrated for suitable flow rates and tightness with a >95 % of CH_4 recovery as CO_2. Five ml of 1 M NaOH was used in each of the traps. Additionally, to decrease the interference of CO_2 during CH_4 oxidation, the CO_2 was trapped in NaOH during the accumulation time under closed chambers. A vial with 5 ml 1 M NaOH was put to each mesocosm (isolated/not isolated) prior to closing a chamber. The fixation of ^{14}C-CO_2 directly from mesocosms accounted for 55–99 % of total $^{14}CO_2$. The rest 1–45 % of $^{14}CO_2$ was fixed in the first two traps during the procedure of CH_4 oxidation described above. At the end of the experiment – 18 days after the labeling – all labeled mesocosms were destructively harvested and ^{14}C activity was measured in shoots, roots and peat using the same oxidation line but with two NaOH traps. Activity of ^{14}C-CO_2 (including traps with oxidized CH_4) fixed in NaOH was measured in the 1 ml aliquot solution with 2 ml scintillation cocktail (Rotiszint EcoPlus, Carl Roth, Germany) using a 1450 LSC & Luminescence Counter (MicroBeta TriLux, Perkin Elmer Inc., USA). The ^{14}C counting efficiency was at least 70 %; the measurement error did not exceed 3.5 %. The absolute ^{14}C activity was standardized by adding increasing amounts of NaOH as a quencher (Gocke et al., 2010).

2.4 Calculations and statistics

The CO_2 and CH_4 emission rates from unlabeled isolated and not isolated mesocosms were calculated based on the increase in chamber headspace concentration of the respective gases over time (Whalen and Reeburgh, 1988) and are presented as mg CO_2 or $CH_4\,m^{-2}\,h^{-1}$. Estimation of the labelled $^{14}CO_2$ and $^{14}CH_4$ fluxes were performed by extrapolation of the endpoint concentration over the period of gases accumulation under chamber headspace assuming linearity of concentration increase (Forbrich et al., 2010). Fluxes of $^{14}CO_2$ and $^{14}CH_4$ are shown as $kBq\,m^{-2}\,d^{-1}$. To calculate the total amount of label emitted with CO_2 and CH_4 during the experiment, fluxes of $^{14}CO_2$ and $^{14}CH_4$ were linearly interpolated and integrated over time using the trapezoidal rule (King and Reeburgh, 2002; King et al., 2002). This value along with the activity of vascular plants' roots and shoots, as well as peat (including moss in the top layer) was used in the estimation of ^{14}C recovery and presented as percentage (%) from the initial activity. Activity of water samples in mesocosms measured after the finishing of the experiment was close to the background (∼50 dpm) and thus not presented. Plant-mediated CH_4 transport (isolated mesocosms treatment) is shown as % from total (not isolated mesocosms) CH_4 flux of the respective plant species at the respective microforms. Vascular plants' total dry weight was measured at the end of the experiment and was used for estimation of the specific flux of plant-mediated CH_4 (mg g dry weight$^{-1}\,h^{-1}$).

The statistically significant differences of dry weights of mesocosms (shoots, roots, peat) and plant-mediated CH_4 fluxes between species and microsites were determined via multi-variance-ANOVA and Fischer LSD test ($p \leq 0.05$) using STATISTICA 7.0 software (StatSoft, USA).

3 Results

3.1 Fluxes of CO_2, CH_4 and plant-mediated CH_4 from *E.* hummocks, *E.* lawns, and *S.* hollows

Net ecosystem exchange flux of CO_2 (F_{CO_2}) from not isolated mesocosms varied from −2 (negative values indicate C assimilation by mesocosms) to $600\,mg\,m^{-2}\,h^{-1}$ (Fig. 2a). *E.* hummocks and *E.* lawns showed similar patterns of F_{CO_2} being relatively low (−120 to $120\,mg\,m^{-2}\,h^{-1}$) during 13 days with subsequent increase at the end of the experiment (14–16 days) (Fig. 2a). F_{CO_2} at *S.* hollows was similar to *E.*hummocks and *E.* lawns at 1–5th and 12–13th days, whereas during 6–11th it was higher (up to $360\,mg\,m^{-2}\,h^{-1}$) and after 12th day of measurements decreased to $0\,mg\,m^{-2}\,h^{-1}$ as compared to *E.* hummocks and *E.* lawns (Fig. 2a). The net CO_2 flux was lower in isolated vs. not isolated treatment on average of 18 days of measurements. This was especially pronounced for *S.* hollows (Fig. 2b). Reference mesocosms (control) with moss showed the effects of the lack of vascular plants onto gas fluxes: F_{CO_2} was on average higher in two control mesocosms as compared to *E.* hummocks, *E.* lawns and *S.* hollows indicating lower C fixation in mosses biomass (Fig. 2a).

In contrast to F_{CO_2} the CH_4 flux (F_{CH_4}) from not isolated mesocosms showed obvious differences between plants and microrelief forms (Fig. 2c). Average F_{CH_4} increased from 4.3 ± 0.3 through 6.8 ± 0.4 to $9.4 \pm 0.8\,mg\,m^{-2}\,h^{-1}$ at *E.* hummocks, *E.* lawns and *S.* hollows, respectively. As F_{CH_4} was much higher from *E.* hummocks, *E.* lawns and *S.* hollows as compared to the mesocosms without vascular plants, this supported the importance of vascular plants for CH_4 production and transport to the atmosphere (Fig. 2c).

Treatment with isolated vascular plants showed similar patterns of F_{CO_2} as compared to the non isolated treatment (Fig. 2b). In turn, F_{CH_4} in the treatment with isolated vascular plants (Fig. 2d) represented the plant-mediated F_{CH_4}, since F_{CH_4} from the peat surface was excluded. *S.* hollows

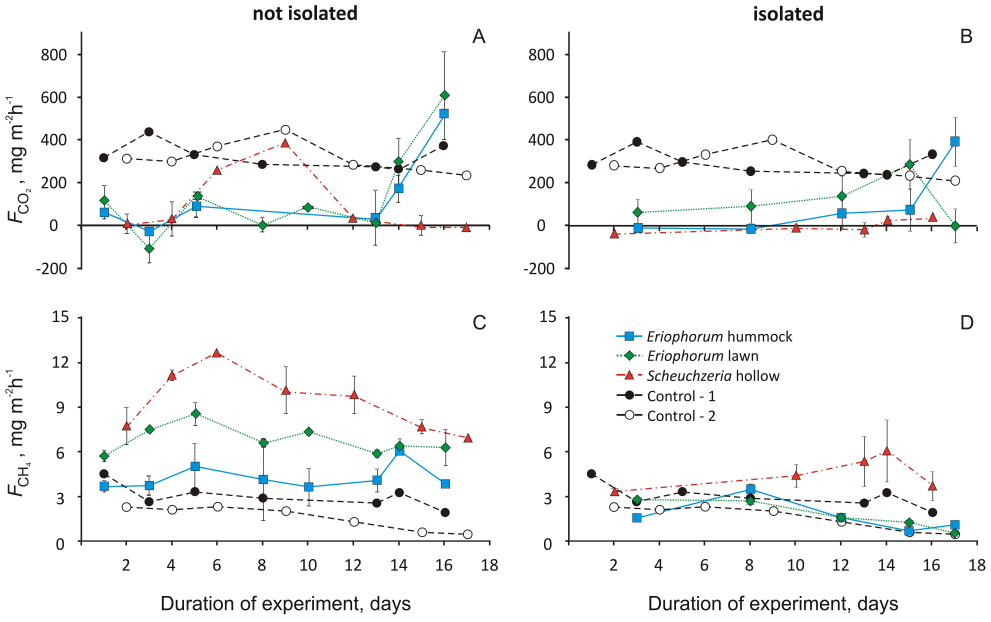

Fig. 2. Fluxes of carbon dioxide (F_{CO_2}); **(A, B)** and methane (F_{CH_4}); **(C, D)** from not isolated **(A, C)** and isolated **(B, D)** mesocosms of *E. vaginatum* from hummocks and lawns, *S. palustris* from hollows and referenced cores without vascular plants during 18 days of the experiment. Errors are standard errors of measurement ($n = 3$).

showed the highest plant-mediated F_{CH_4} in absolute values (Fig. 2d) and this corresponded to 50.5 ± 2.2 % from the total (not isolated) F_{CH_4} (Fig. 3, left y-axis). In turn, plant mediated transport accounted at *E.*hummocks and *E.*lawns was responsible for the 37.9 ± 3.9 % and 31.3 ± 4.6 % of the total F_{CH_4}, respectively (Fig. 3, left y-axis). This effect-was even more pronounced, when the specific F_{CH_4} (per g dry weight of plant biomass, Table 1) was estimated. The specific plant-mediatedF_{CH_4} increased in the order *E.* hummocks $\leq$ *E.* lawns $<$ *S.* hollows (Fig. 3, right y-axis).

3.2 ^{14}C budget and contribution of recent photosynthates to the CO_2 and CH_4 fluxes

Flux of labeled CO_2 (F_{14CO_2}) was first detected 4 hours after labeling from both isolated and not isolated mesocosms and was most intense (500–1400 kBq m^{-2} d^{-1}) in the first 2 days, regardless of the plant species. F_{14CO_2} dropped down on the 3rd day and remained within a range of 5–25 kBq m^{-2} d^{-1} in isolated mesocosms and 20–80 kBq m^{-2} d^{-1} in not isolated mesocosms till the end of the experiment (Fig. 4a, b). The difference in ^{14}C activity between isolated and not isolated mesocosms after the initial flush is most probably attributed to decomposition of recent ^{14}C-labeled rhizodeposits.

In contrast to CO_2, the ^{14}C activity in the CH_4 flux (F_{14CH_4}) was 100 folds lower (0.1–4.2 kBq m^{-2} d^{-1}) (Fig. 4c, d). The earliest appearance of ^{14}C in CH_4 was detected in the *S.* hollows treatment 20 h after labeling. It has to be noted, though, that this might not reflect the actual situation, since the ^{14}C-CH_4 was not measured during first 4 h after the labeling in contrast to CO_2. After 3 days the intensity of F_{14CH_4} strongly decreased especially in the treatments with isolated plants, but the decrease was not that pronounced when compared to F_{14CO_2} (Fig. 4c, d). During the 18 days after the labeling about 11 % of the total added ^{14}C activity was emitted as CO_2 from *E.* hummocks

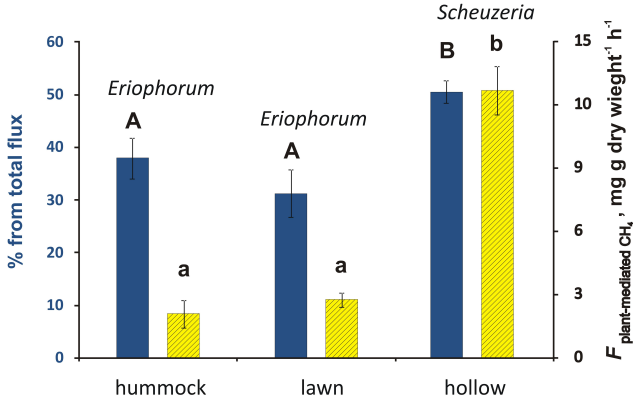

Fig. 3. Plant-mediated CH_4 flux (shown as % from total F_{CH_4}, left y axis) and specific plant-mediated CH_4 flux per unit of biomass (in mg g dry weight $^{-1}$, right y axis) estimated for *E. vaginatum* and *S. palustris* of three microform types as an average during the period of measurements. Errors are standard errors of measurement ($n = 3$). Values followed by the same letters are not significantly different between microform types and plant species (uppercase letters for the left y axis, lowercase letters for the right y axis) at $p \leq 0.05$ according to two-way-ANOVA and Fischer LSD test.

and *E*. lawns each, whereas *S*. hollows emitted 6 % of ^{14}C-CO_2 coinciding with the smallest amount of shoots (Table 1). However, *S*. hollows emitted 2–4 times more ^{14}C-CH_4 when compared to *E*. hummocks and *E*. lawns. The total ^{14}C-CH_4 emission did not exceed 0.13 % of ^{14}C activity in any of the treatment (Table 1). Most of the ^{14}C label was recovered in *S*. roots at hollows (38 %); the shoots and roots of *E*. hummocks and *E*.lawns contained about 32 % of initial label. ^{14}C activity in peat (average of the whole core) varied from 11 to 29 % from the total ^{14}C increasing in the order *E*. hummocks $<$ *E*. lawns $<$ *S*. hollows and was negatively related to plant biomass (Table 1). Approximately 20 % of the total ^{14}C activity applied to each of the three microforms could not be recovered (Table 1). The unaccounted 20 % of ^{14}C were most probably connected with shoot respiration and rapid CH_4 emission events (ebullition), which might occur between measurements in this experiment.

4 Discussion

4.1 Effects of plant species at peatland relief microforms on plant-mediated CH_4 transport

Emission of CO_2 and CH_4 from mesocosms with two plant species attributed to three microrelief forms with typical water table levels under controlled conditions followed the natural pattern observed in situ at the Salmisuo mire complex (Saarnio et al., 1997; Forbrich et al., 2010). Thus, field measurements showed the increase of F_{CH_4} from the surface of relief microforms in the order hummocks $<$ lawns $\leq$ hollows. This pattern was consistent for other sites (Dalva et al., 2001; Johansson et al., 2006). Net ecosystem exchange rates (F_{CO_2}) are in agreement with the data presented by Gažoviè et al. (personal communication) for the peak of season 2007 with similar weather (temperature and precipitation) conditions at the same site and fall into the range typically observed at other sites (Lindroth et al., 2007; Lund et al., 2007; Sottocornola and Kiely, 2010). However, the rate of CH_4 emission in the current laboratory experiment was 1.8-9 folds higher than in situ measurements (Saarnio et al., 1997). Similar range of difference (3.5-9) between laboratory F_{CH_4} and field measurements were reported by King et al. (2002; Table 1) and could be attributed to more optimal growth conditions and higher temperatures (especially soil temperatures) under controlled conditions. This is confirmed by the Q_{10} values for CH_4 production reported in the range from 2 to 20 (Segers, 1998). Furthermore, limited lateral and vertical water movement of porewater in peat columns under controlled conditions favored methanogenesis and/or decreased CH_4 consumption. Comparable CH_4 fluxes for the same plant species (*Eriophorum vaginatum*) were reported by Ström et al. (2005; Table 1). Although the controlled conditions cannot fully reproduce the natural environment, we believe the observed differences between mesocosms reveal the pattern of processes and explain in situ differences between plant species and topographical microforms.

Our results demonstrate the efficiency of *S. palustris* vs. *E. vaginatum* in transmission of CH_4 from the anoxic (methanogenic) zone to the atmosphere: plant-mediated CH_4 transport was 10–20 % more intensive from *Scheuchzeria* mesocosms and 4.5 folds larger on the dry weight basis as compared to mesocosms of *Eriophorum* (Fig. 3). Although we did not control the effect of water table level on the individual species, we studied the plant species and microrelief forms as entire ecological units existing in the peatland complex. Because *S. palustris* was a typical for water saturated hollows and *E. vaginatum* corresponded to drier lawns and hummocks, our finding supports the hypothesis of higher efficiency of vascular plants in CH_4 transport with tolerance to anoxic soil conditions. However, it is necessary to note, that the lower plant-mediated CH_4 flux of *E. vaginatum* could reflect also its higher CH_4 consumption (oxidation) potential against *S. palustris*. However, Frenzel and Rudolph (1998) could not identify significant CH_4 oxidation under *E. vaginatum* despite the highly aerenchymatic root tissues.

Only a few studies have measured plant-mediated F_{CH_4} in peatlands directly by separation of shoots from peat/soil (Schimel, 1995; Frenzel and Rudolf, 1998; Kutzbach et al., 2004). Authors used relatively small chambers (0.5–1 L) fixed around single tillers of *Eriophorum angustifolium* (Schimel, 1995; Frenzel and Rudolf, 1998) and *Carex aquatilis* (Schimel, 1995; Kutzbach et al., 2004). Their estimations of plant-mediated CH_4 transport substantially varied from 30–70 to 150 % (Schimel, 1995; Kutzbach et al., 2004) and up to 3900 % (Frenzel and Rudolf, 1998) of total (reference) flux. Plant-mediated F_{CH_4} assessed by the difference between plots with vascular plants and without them also showed high variability (33–96 %, King et al., 1998; 40–80 %, Christensen et al., 2003; 25–80 %, Koelbener et al., 2010). Although the above mentioned studies did not investigate the same species as in the current experiment, we consider their plant-mediated F_{CH_4} to be generally overestimated (Schimel, 1995 and especially Frenzel and Rudolf, 1998). This is likely because of (i) low representativeness (only some tillers were measured by direct isolation of shoots from soil) and/or (ii) biased or no effects of shoots cutting (Greenup et al., 2000), (iii) weakness of comparison of plots with- and without vascular vegetation (minimized inputs of rhizodeposits, changes of oxidation potentials (King et al., 1998; Koelbener et al., 2010)). Still, because of the uniqueness of individual species for CH_4 turnover (Schimel, 1995; Ström et al., 2005; Koelbener et al., 2010) we cannot extrapolate our result of 30–50 % of plant-mediated CH_4 on other species besides *E. vaginatum* and *S. palustris*. However, the attribution and dominance of these species to microforms of the peatland with specific environmental conditions for growth (mainly, water saturation) may serve as a predictor and provide important information for the assessment and modeling of meso- and macroscale CH_4 fluxes and, hence, C budgets.

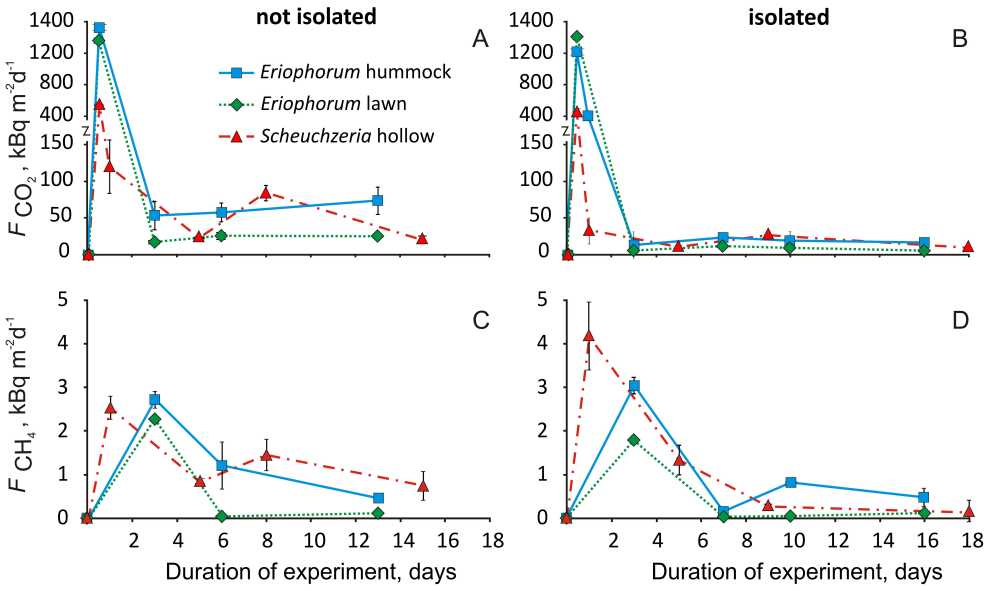

Fig. 4. Fluxes of labeled carbon dioxide (F_{14CO_2}); **(A, B)** and labeled methane (F_{14CH_4}); **(C, D)** from not isolated **(A, C)** and isolated **(B, D)** mesocosms of *E. vaginatum* from hummocks and lawns and *S. palustris* from hollows during 18 days of the experiment. Errors are standard errors of measurement ($n = 3$).

4.2 The fate of recent photosynthates and their contribution to CH_4 production

Pulse labeling of mesocosms allowed tracing the pathways of recent photosynthates of two vascular plant species (and of green moss in the treatment without plant isolation from peat cores). After 18 days of the experiment between 79 % and 81 % of initial ^{14}C activity was recovered in mesocosms of *E.* hummocks, *E.* lawns (1st labeling) and *S.* hollows (2nd labeling) (Table 1). Distribution of the label between soil-plant compartments revealed the strong difference in physiology of *E. vaginatum* and *S. palustris*: recovery of ^{14}C in shoots and roots of *E. vaginatum* was 18 and 14%, respectively, whereas for the *S. palustris* 8 % was recovered in shoots and 38 % in roots indicating intensive allocation of recent photosynthates of *S. palustris* to roots. Although shoots-to-roots ratios of *S. palustris* were similar to *E. vaginatum* (from lawns, Table 1), the root system of *S. palustris* was phenotypically different: its single tap-roots were much thicker, with more developed aerenchyma and probably deeper (since at the bottom of 25-cm peat core roots were still thick) as compared to dense but thin roots of *E. vaginatum* (Fig. 1). Apparently due to such a strong root system with developed aerenchyma *S. palustris* was responsible for the largest total (Fig. 2c), plant-mediated (Fig. 3) and labeled CH_4 fluxes (Table 1).

Overall, 0.03–0.13 % of the initially assimilated ^{14}C was emitted as CH_4 within 18 days of the experiment by two plant species. These results are in agreement with those reported by King and Reeburgh (2002), who found approximately 0.1 % of the ^{14}C-label in CH_4 over a 15 days measurements period of mesocosms with *Eriophorum angustifolium* and *Carex aquatilis* under field conditions. However, in the laboratory experiment with similar mesocosms conducted by the same authors (King et al., 2002) the portion of ^{14}C emitted as CH_4 accounted for 1–5 %. Since total CH_4 flux was more intensive under laboratory vs. field conditions (our observations and King et al., 2002), we expected higher $^{14}CH_4$ efflux. We may have underestimated $^{14}CH_4$ emission probably due to the experimental setup, which did not allow more frequent $^{14}CH_4$ measurements (Fig. 4c, d). In addition, the CH_4 ebullition (Glaser et al., 2004) could account for losses of ^{14}C-CH_4 between flux measurements. However, during measurements of CH_4 fluxes no noticeable events of ebullition were observed in any of the mesocosms. Thus, we could not test the hypothesized fast (within 2–4 h after labeling) conversion of recently fixed plant photosynthates to CH_4 (after King et al., 2002) but we observed the dependence of species-specific plant biomass and the contribution of photosynthates to the methanogenesis (Fig. 5). Several results (Whiting and Chanton, 1993; Dacey et al., 1994; Greenup et al., 2000; Christensen et al., 2003) showed that CH_4 emission rates rise as the net production (or plant biomass) of wetland vegetation increases. Though the authors did not measure the belowground plant-derived C pool directly, they assumed the supply of rhizodeposits (Whiting and Chanton, 1993) and root biomass could best explain CH_4 fluxes (Greenup et al., 2000). Despite we did not measure rhizodeposits on a molecular level, contribution of ^{14}C to the CO_2 and CH_4 fluxes revealed the differences between plant species. Considering *E. vaginatum* alone we did observe the

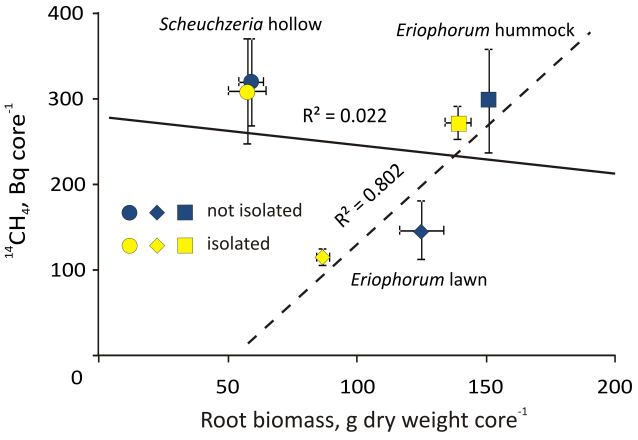

Fig. 5. Total amount of labeled $^{14}CH_4$ emitted during the period of measurements vs. root biomass of vascular plants from isolated and not isolated mesocosms with *E. vaginatum* and *S. palustris* of three microform types. Solid line linear regression of all data presented; dashed line is a linear regression of isolated and not isolated *E. vaginatum* from hummocks and lawns alone. Errors are standard errors of measurement ($n = 3$).

relationship between increasing root biomass and $^{14}CH_4$ flux (Fig. 5, dashed line). However, the comparison of the two species showed weak correlation of root biomass and $^{14}CH_4$ flux, since *S. palustris* with less root- and total biomass (Table 1) was responsible for the largest contribution of labeled plant photosynthates to CH_4 flux (Fig. 5, solid line). These data support results of experiments demonstrating no relationship (Joabsson and Christensen, 2001; King et al., 2002; Ström et al., 2005; Koelbener et al., 2010) or even negative relationship (Bouchard et al., 2007) between CH_4 emission and plant biomass of different species. Thus, the biomass of vascular plants in peatlands cannot alone be a reliable predictor of CH_4 emissions because at least the production (shown by amount of ^{14}C-label) and transport (total and labeled fluxes) of CH_4 were higher for a plant species with small biomass (Ström et al., 2005; Koelbener et al., 2010). It should be considered however, that *E. vaginatum* belongs to microforms with less water saturated conditions (lawns and hummocks) and along with the reported rhizospheric oxidation (Christensen et al., 2003) is likely to increase consumption/oxidation of CH_4 in the upper peat (moss) layer of the respective mesocosms. Almost double amount of emitted ^{14}C with CO_2 from mesocosms with *E. vaginatum* as compared to *S. palustris* hollows might have originated both from respiration and oxidation of CH_4 (Table 1). In addition, oxic conditions and oxygen transport into the rhizosphere could regenerate non-methanogenic electron acceptors such as iron or sulphate oxides (Knorr et al., 2008; Sutton-Grier and Megonigal, 2011), which suppress methanogenesis. This process was reported to be species-specific and did not depend on plant biomass/productivity (Sutton-Grier and Megonigal, 2011).

After all, individual compounds of root exudation (acetate), supply of oxygen and presence of alternative electron acceptors may be responsible for methanogenesis (Ström et al. 2003; Knorr et al., 2008). Since the former parameters are species-specific, a general relation of CH_4 turnover to vegetation biomass may be a too simplistic approach. Therefore, for the assessment of CH_4 dynamics over meso- and macroscales as well as for the implication and development of C modeling of CH_4 fluxes, it is necessary to account for plant species-specific processes of CH_4 production, consumption and transport. The attribution of those species to topographic microforms reflecting environmental conditions may provide more reliable proxies for the estimation of a regional (and global) C balance (King et al., 2002; Kutzbach et al., 2004).

5 Conclusions

Isolation of shoots from entire peat and ^{14}C-pulse labeling of mesocosms of *E. vaginatum* and *S. palustris* attributed to three topographical microforms (hummocks, lawns, hollows) demonstrated the importance of plant communities for CH_4 production and transport in boreal peatlands. Total and plant-mediated CH_4 fluxes as well as tracing of ^{14}C in mesocosms allowed us to conclude:

- F_{CH_4} increased in the order *E.* hummocks $\leq$ *E.* lawns $<$ *S.* hollows corresponding to the increasing water table level of the microrelief forms according to the field conditions.

- Plant-mediated F_{CH_4} accounted for 38, 31 and 50.5 % of total flux at *E.* hummocks, *E.*lawns and *S.* hollows, respectively. These values are among the lowest available in the literature and are original for *E. vaginatum* and *S. palustris*.

- Distribution of the ^{14}C label within mesocosms of two species revealed the strong difference in their physiology: higher recovery of ^{14}C in roots of *S. palustris* (38 % of the total ^{14}C, and only 8 % in shoots) indicated its intensive allocation of recent photosynthates to roots as compared to *E. vaginatum* (14 % in roots and 18 % in shoots).

- Recent photosynthates contributed to methanogenesis of about 0.03, 0.06 and 0.13 % of added activity by *E.* hummocks, *E.* lawns and *S.* hollows, respectively. At the within-species level (*E. vaginatum* at hummocks and lawns) this contribution was depended on the amount of plant biomass. However, there was no dependence of the contribution of recent photosynthates to CH_4 fluxes on biomass of different plant species.

Acknowledgements. Authors greatly acknowledge the staff of the Laboratory for Experimental Ecology, Mekrijärvi research station, University of Joensuu, Finland and personally Taneli Kolström, Matti Lemettinen, Teijo Kortevaara, Eine Ihanus, Risto Ikonen for providing the necessary conditions for work and accommodation. Special thanks to Mrs. Ilka Beil and Nadine Nusko for inestimable help in transport of the samples over Finland and Germany. The study was supported by the DFG Emmy Noether Programm (Wi 2680/2-1) and a Sofja Kovalevskaja Award (M. Wilmking) of the Alexander von Humboldt Foundation.

Edited by: K. Küsel

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