

Journal of
Plant Ecology

PAGES 1–7

doi: 10.1093/jpe/rts045

available online at
www.jpe.oxfordjournals.org

Variation in the plant-mediated methane transport and its importance for methane emission from intact wetland peat mesocosms

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Abstract

Aims and Methods

Vascular plants are known to influence the production, transport and oxidation of methane in wetland soils, but these processes are not well understood. Using plants grown in intact peat cores, we compared the influence upon methane emissions of 20 forb and graminoid species from European wetlands. We measured plant-mediated transport of methane (conduit or chimney effect) using a novel agar-sealing technique that prevented methane exchange from the bare soil to the atmosphere.

Important Findings

The plant-mediated transport (chimney effect) represented between 30% and almost 100% of the total methane flux, with graminoids exhibiting greater internal transport than forbs. In general, plants with less dense root tissues and a relatively larger root volume exhibited a larger chimney effect. Most species (12 out of 20) significantly reduced methane emissions compared to bare soil and only

one species, *Succisa pratensis*, increased them. We suggest that characterising vegetation in terms of plant functional traits and plant processes offers an effective method for estimating methane emissions from wetlands. However, we found no correlation between the magnitude of the chimney effect and the overall influence of different plant species on methane emissions. Besides introducing a useful tool to study plant-mediated transport, this work suggests that characterising vegetation in terms of functional traits could improve estimates of methane emissions from wetlands, which in turn could help in designing mitigation strategies.

Keywords: functional group • graminoid • forb • agar-sealing • conduit • gas transport

Received: 30 August 2012 Revised: 15 November 2012 Accepted: 5 December 2012

INTRODUCTION

Wetlands are the largest natural source of the important greenhouse gas methane, contributing one-third to global emissions (IPCC 2007). The emission of microbially produced methane from wetland soils is influenced not only by abiotic factors, such as temperature and the water table, but also—in various ways—by plants (Ding *et al.* 2003; Dinsmore *et al.* 2009; Hendriks 2009; Lai 2009; LeMer and Roger 2001; Philippot *et al.* 2009). For example, plants may increase the emission of methane by providing a carbon substrate for methanogenesis in the form of root exudates (Koelbener *et al.* 2010; Neue *et al.* 1996), and by acting as a conduit for transfer

of methane from the soil to atmosphere (Byrnes *et al.* 1995; Cicerone and Shetter 1981; Holzapfelfschorn *et al.* 1986; Whalen 2005). On the other hand, plants may also reduce methane emissions (Heilman and Carlton 2001; Inubushi *et al.* 2001; Ström *et al.* 2005) by providing an oxidising environment in the rhizosphere (Fritz *et al.* 2011; Holzapfelfschorn *et al.* 1986; Jespersen *et al.* 1998). Our understanding of these effects is limited, however, partly because of the difficulty of isolating individual processes (Ding *et al.* 2005; Joabsson and Christensen 2001; Koelbener *et al.* 2010; Neubauer *et al.* 2005; Rothman and Bouchard 2007).

According to some estimates, over half of all methane released from wetlands and rice paddies (Aulakh *et al.* 2000;

Ding *et al.* 2005; King *et al.* 1998; Torn and Chapin 1993) is transmitted through plants. However, knowledge about this plant-mediated transport (also dubbed the conduit or chimney effect) is limited, partly for lack of a convenient method to measure it. The extent and direction of plant-mediated gas transport may be determined by processes such as convective throughflow and diffusion from the transpiration stream through plant surfaces, and these, in turn, are influenced by a variety of factors including atmospheric humidity, temperature, illumination, soil substrate, stomatal rhythm, photosynthetic activity and the presence or absence of aerenchyma structures (Armstrong and Armstrong 1991; Dacey and Klug 1979). Thus, although little is known about interspecific variation, it seems likely that the capacity to transport methane varies greatly among species (Schimel 1995; Sebacher *et al.* 1985).

Some of this variation can be associated with functional plant groups. For example, graminoids have been reported to cause higher methane emissions than shrubs and woody vegetation (Bubier *et al.* 1995; Liblik *et al.* 1997), and some agricultural weeds (forbs) were found to cause higher methane oxidation than rice plants (Holzapfelschorn *et al.* 1986; Inubushi *et al.* 2001). Some of these differences are probably related to specific morphological traits, such as the presence of root aerenchyma. Hence, a functional group approach could contribute to our understanding of the influence of plants on methane emissions.

We compared 20 plant species of wetland habitats for their effect upon methane emissions from peat soil and for their capacity to transport methane from rhizosphere to atmosphere. The species selected included both forbs and graminoids, allowing us to investigate whether some interspecific variation reflects differences at the level of functional groups. The hypotheses of this study were:

- i. The variation among plant species in their effect on methane emissions from wetland soil is related to their functioning as a chimney for methane transport.
- ii. Graminoids have a higher ability than forbs to transport methane from rhizosphere to atmosphere (chimney effect) and hence cause higher methane emissions from soil.

MATERIALS AND METHODS

The experiment was conducted between July 2008 and September 2009 in a greenhouse in Zurich, Switzerland. Peat cores were collected from a protected fen site (at soil layer of 65–91 cm) at Hüttwilersee, near Frauenfeld in Switzerland (47°36′49″N and 8°50′15″E), the same location as used by Koelbener *et al.* (2010). The top 40 cm of soil at this site had been removed in 2005 (i.e. 3 years earlier) as part of a nature restoration project. To obtain homogeneous peat, we selected a uniform area (2.2 × 1.4 m²) and removed the top 25 cm of soil. PVC tubes of diameter 12.5 cm and length 26 cm were

used to collect intact peat cores in a manner similar to that used by Koelbener *et al.* (2010). However, because we wanted to investigate how plants influence methane emissions, we took peat from a layer 25 cm deeper because this was likely to contain less labile carbon (Jorgensen and Richter 1992). The base of each tube was closed with a lid, sealed with gum to make it waterproof (Coltogram; Blattener AG, Zürich), and a transparent tube was inserted into the core to monitor the water level. The peat was saturated with water at the time of collection, and the water level in the tube was maintained at the soil surface throughout the experiment.

Twenty plant species of European wetlands (Table 1) were selected on the basis of their fertility indicator values (Bakkenes *et al.* 2002; Ellenberg *et al.* 1991) with the aim of including species characteristic of both nutrient-poor and nutrient-rich habitats. The species included 9 forbs and 11 graminoids. Plants were grown from seed that was either collected from sites in northeastern Switzerland or purchased from a specialist supplier (Die Wildstaudengärtnerei, Eschenbach, Switzerland). To minimize any variation due to the different origins of the plants, we separated individual seedlings, carefully washed their roots, and planted them in small pots containing sand prior to the main experiment. After 4 weeks, small, uniform plants were transplanted to peat cores contained in pots, taking care to disturb the peat

Table 1: fertility indication for the 20 plant species used in our experiment based on Ellenberg and MOVE N values (Bakkenes *et al.* 2002; Ellenberg *et al.* 1991)

Species	Code	Ellenberg N value	MOVE N value
Forbs			
<i>Succisa pratensis</i>	SP	2	3.20 ± 0.71
<i>Potentilla palustris</i>	PP	2	4.07 ± 0.96
<i>Menyanthes trifoliata</i>	MT	3	4.19 ± 0.96
<i>Lysimachia vulgaris</i>	LV	−99	4.88 ± 1.17
<i>Caltha palustris</i>	CP	−99	5.25 ± 1.03
<i>Mentha aquatica</i>	MA	5	5.34 ± 1.02
<i>Ranunculus lingua</i>	RL	7	5.34 ± 0.77
<i>Lycopus europaeus</i>	LE	7	5.58 ± 0.96
<i>Rumex hydrolapathum</i>	RH	7	5.79 ± 0.72
Graminoids			
<i>Molinia caerulea</i>	MC	1	3.15 ± 1.11
<i>Eriophorum angustifolium</i>	EA	2	2.70 ± 0.95
<i>Eriophorum latifolium</i>	EL	2	—
<i>Carex flava</i>	CF	2	—
<i>Carex curta</i>	CC	2	3.84 ± 0.91
<i>Carex rostrata</i>	CR	3	4.02 ± 1.17
<i>Juncus effusus</i>	JE	4	4.79 ± 1.13
<i>Carex disticha</i>	CD	5	4.92 ± 0.86
<i>Carex acutiformis</i>	CA	5	5.14 ± 0.97
<i>Scirpus lacustris</i>	SL	—	5.85 ± 0.74
<i>Glyceria maxima</i>	GM	9	6.19 ± 0.70

as little as possible. The experiment included eight replicates per species together with unplanted control pots containing only peat. Any plants that died within the first 3 weeks were replaced.

About 2 months after the start of the experiment, plants started to show N deficiency symptoms, and we therefore added nitrogen (as NH_4NO_3 solution)—five weekly doses during summer of 2008 and two doses in spring of 2009, amounting in total 78 mg of N to each pot. Subsequently, the plants grew well, but the pots produced no detectable methane emission, even after an interval of 1 year. Since this was probably due to the very low availability of labile organic carbon in the soil, we added 30 ml of 20 mM glucose solution to each core every week for 6 weeks. Glucose is an intermediate compound in the decomposition process of organic matter to simpler compounds such as acetate and ethanol, which are utilized by methanogenic Archaea to produce methane (Ibba and Fynn 1991). In addition, to ensure an adequate community of methanogens, we inoculated each pot with 30 ml of aqueous extract of soil that was known to produce methane. The form and dosage of carbon substrate and inoculum were based on a test experiment (data not given) conducted on surplus peat cores.

Methane emissions from the pots were measured between 8 and 14 September 2009 using a modified version of the method used by Koelbener et al. (2010) and van Huissteden et al. (2005). Each pot was placed in a transparent plexiglas chamber and incubated for 60 minutes. Gas samples were taken from the headspace of the chamber and analysed immediately using a photoacoustic gas monitor (Type 1412; Innova AirTech Instruments, Ballerup, Denmark). A silica gel filter removed any moisture from the gas sample before it entered the analyser. During each suction, exhaust air was returned from the instrument to the chamber to compensate for the air removed. The monitor measurements were calibrated with gas chromatograph measurements. In preliminary tests with some surplus pots, we made repeated measurements of methane concentrations and found that these increased linearly over the measuring period. In the main study, therefore, we measured concentrations on only two occasions, since this yielded a good estimate of methane emission rates while allowing us to study more species.

To assess the flux of methane through the plant, we developed a method for sealing the soil surface based upon Briggs and Shantz (1911). For sealing, a viscous solution (1% w/v) was prepared by boiling 10 g of agar in 1 l water. The solution was then allowed to cool to around 35–40°C. About 125 ml of this solution was poured into each pot to form a layer of about 1 cm over the soil surface. This agar seal blocked all gas exchange from the soil, ensuring that the flux measured after sealing was coming only through the plant. We saw no sign that the agar treatment affected the plants in any way, and preliminary tests also confirmed that agar itself did not produce methane. Methane emissions were measured first without the agar seal; then the pots were sealed and the

measurement was repeated. The air temperature during the flux measurements was around 25°C, and this value was used to estimate the density of methane (0.656 mg/cc). The mean proportion of the methane flux transported through the plant, i.e. the chimney effect, was calculated as: $\text{Chimney (\%)} = (f_s / f_{us}) * 100$, where f_s means flux from all pots of individual species under agar-sealed conditions, and f_{us} means flux from all pots of same species under unsealed conditions.

The agar was removed as soon as the measurements were complete and plants were harvested. Aboveground and belowground biomass was recorded after drying at 70°C for 48 hours. Root volume was measured using the pycnometer method as described by Jensen et al. (1969); root density was then calculated by dividing the dry root mass by root volume.

The data were analysed using statistical software R, version 2.8.1 (R Development Core Team 2008). Variation in methane emissions among species and controls was tested by means of one-way ANOVA and Tukey test, using log-transformed data. Differences in emissions between unsealed and sealed conditions were compared by T-tests. We calculated linear regressions between methane emission rates and ‘% Chimney’ versus several characteristics of the plants growing in them, both with average values per species and for all pots separately.

RESULTS

For 12 of the 20 species (five forbs and seven graminoids), methane emissions from pots with plants were significantly lower than from unplanted controls, while for seven species there was no significant difference. For only one species, *Succisa pratensis*, were emissions higher than those from the control (Fig. 1). On average, there was no difference between graminoids and forbs in how they affected methane emissions (Fig. 2a).

Sealing the bare soil of the control pots with agar reduced methane emissions by 95% (Fig. 1). In the presence of a plant, however, this sealing generally had a much smaller effect, and for 6 forbs and 10 graminoids, methane emissions were not significantly reduced by sealing of the soil (see % values in Fig. 1).

The proportion of methane flux transported through the plants (chimney effect) varied widely among species (Fig. 1), but was on average greater for graminoids than for forbs (Fig. 2b). This proportion was positively related to root volume for forbs, and negatively related to root density for graminoids (Table 2). There was no significant relationship between the proportion of methane transported through the plant (i.e. the chimney effect) and the total methane emitted from peat cores ($P = 0.258$).

DISCUSSION

Previous studies have shown that plants vary in their capacity to transport methane from the rhizosphere to the atmosphere, and suggested that such variation could cause

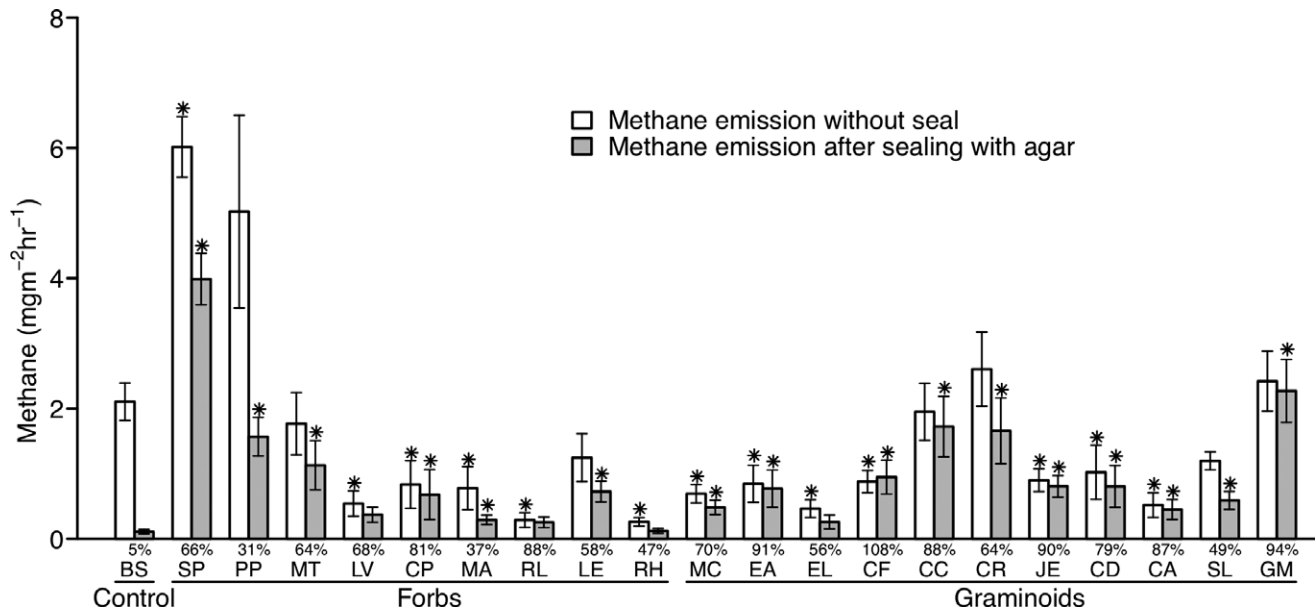


Figure 1: mean CH₄ emission rates from peat cores with different plant species, under unsealed conditions and after sealing the soil surface with agar. The stars (*) above the bars indicate significantly different CH₄ emission rates from cores with plants as compared to the control (bare pots), both for unsealed and sealed, respectively. Percent values below the x-axis indicate the proportion of total methane flux emitted after agar sealing (i.e. the chimney %). The value above 100% falls within the range of measurement error. Species are ordered according to the fertility indication values (N-values) of *Ellenberg et al. (1991)* and *Bakkenes et al. (2002)*; i.e increasing in fertility indication from left to right for both forbs and graminoids respectively (*Table 1*). Graph shows the original data while the significant differences are based on the statistical analysis of log-transformed data

differences in methane emissions among wetlands (*Ding et al. 2005; Morrissey and Livingston 1992; Shannon et al. 1996*). To the best of our knowledge, however, this is the first study to systematically compare the chimney effect in a broad range of wetland species. Our results demonstrate that species do, indeed, vary widely in their transport capacity, with values in our sample ranging from 30% to almost 100% of the total methane flux (*Fig. 1*). However, despite this wide range, the percentage transported was uncorrelated with total methane emissions from the soil, indicating that other mechanisms by which plants influence methane emission from soil, such as the release of carbon compounds and/or oxygen into the soil (*Heilman and Carlton 2001; Neue et al. 1996; Ström et al. 2005*), were also important. This does not mean that the chimney function is ecologically unimportant; indeed, it could contribute substantially to emissions from species mixtures, in which some plants promote the production of methane while others facilitate its transport. However, it does demonstrate that the influence of plant species upon methane emissions is not determined by efficiency of methane transport alone.

We found that graminoids exhibit greater chimney effect than do forbs (*Fig. 2b*), though this does not necessarily imply that methane emission from graminoid-dominated sites are higher than that from sites dominated by forbs or woody vegetation (*Bubier et al. 1995; Liblik et al. 1997*). Moreover, in another experiment we even found a negative relationship ($R^2 = 0.85$, $P = 0.01$) between methane emissions from soil and chimney capability of plant species grown in soil with

water table 5 cm below soil surface (*Bhullar 2011*). Possibly, the differences among functional groups observed in these studies are affected more by the characteristics of sites where particular plant types occur. If so, the chimney capability of plant species may be an important control of methane emissions from wetlands, although a secondary one, as suggested by *Morrissey and Livingston (1992)*. Thus, to understand the role of plant functional groups in methane emissions, we need to consider the combined effect of various mechanisms. This would require more elaborate experiments designed to compare directly the processes of plant-mediated transport, root exudation and radial oxygen loss in relation to plant traits and functional plant groups. Only then could the relative influence of these various mechanisms upon methane emissions from wetlands be quantified.

The difference in transport capabilities of graminoids and forbs may be related to differences in root morphology (*Ding et al. 2005; Hirota et al. 2004; Joabsson and Christensen 2001*). For instance, sedges are thought to be effective in transporting methane because their large root surface represents an effective collection system, while aerenchyma in the root cortex provides a pathway for rapid diffusion (*Torn and Chapin 1993*). Furthermore, we observed that the chimney capability of graminoids was negatively correlated with root density (root mass/root volume), and that of forbs positively correlated with root volume (*Table 2*). This finding is also supported by data from another experiment using four forbs and four graminoids, which revealed a positive relationship

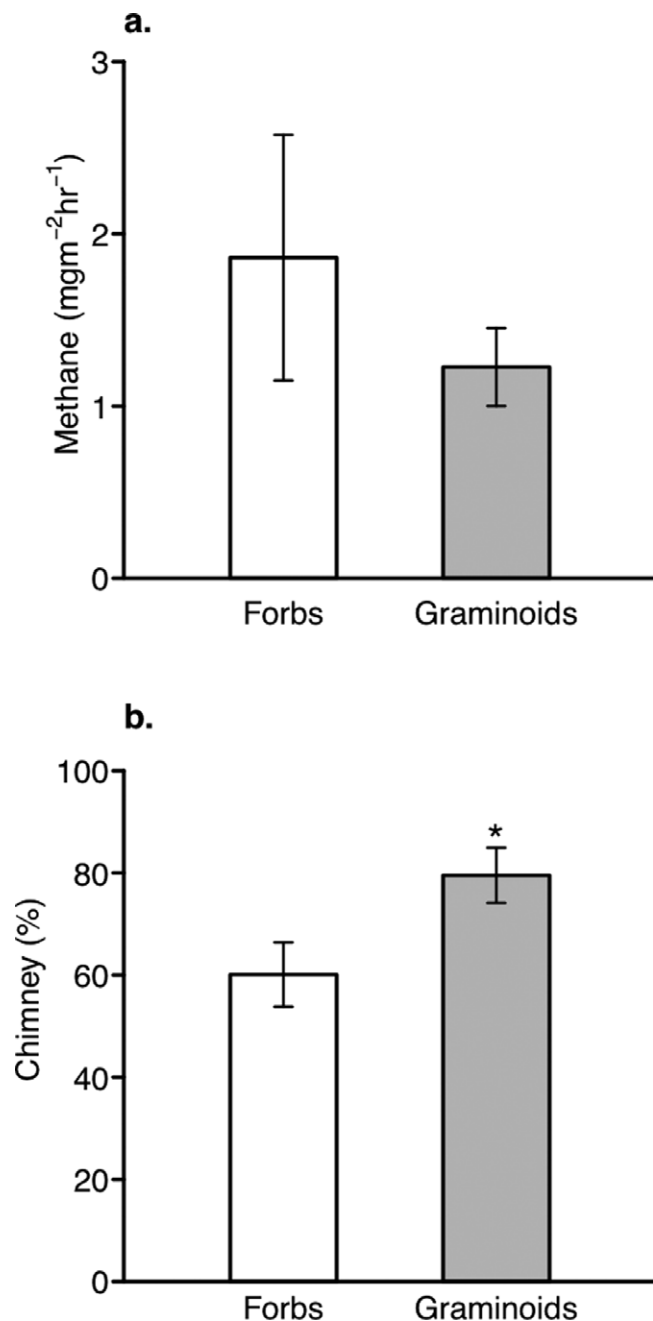


Figure 2: (a) mean methane emissions from peat cores, and (b) capability to facilitate methane transport through plant tissue (% Chimney), averaged for functional plant groups.

($R^2 = 0.58$, $P = 0.028$) between plant-mediated transport and plant root volume (Bhullar 2011). Hence, species with less dense roots—implying a large proportion of air spaces—and a relatively larger root volume in deeper soil layers appear to have a larger potential for methane transport, presumably because they offer a more effective conduit from the deeper anoxic soil to the atmosphere, thereby bypassing the oxidized surface soil (Hendriks 2009).

We had expected the plants to increase methane emissions from peat soil, as has been reported in several studies with wild plants (Joabsson *et al.* 1999; Koelbener *et al.* 2010) and with rice plants in paddy soils (Cicerone and Shetter 1981). However, only one species caused higher emissions, while 12 out of 20 species decreased emissions. The probable reason for this was that our peat cores came from a deeper layer (65–91 cm) than those used by Koelbener *et al.* (2010) (40–59 cm), and were therefore depleted of labile carbon. Thus, unlike in that study, it was necessary to add glucose before any methane was produced. In fact, this was convenient for our purpose, because the standardized additions of labile carbon enabled us to compare plant-mediated transport of different species more precisely. However, the absolute differences in overall methane emission should be interpreted with care because of the manipulations of the carbon and nitrogen conditions we had to make.

The agar-sealing technique was effective in preventing methane exchange across the soil surface (95% reduction), and there was no evidence that it increased methane production; at 108%, the highest emissions after sealing were slightly above those before sealing, but the difference lies within the range of measurement error (Fig. 1). We, therefore, consider sealing with agar to be a simple and effective way to quantify gas transport through plants. It has a clear advantage over the method used by Holzapfelschorn *et al.* (1986), where flux from vegetated area was compared with that from unvegetated area, and over the vegetation removal technique applied by King *et al.* (1998). Exposing the roots to methane-rich gas or solutions (e.g. Aulakh *et al.* 2000; Nouchi *et al.* 1990) creates artificial conditions, which may interfere with transport through the plant. Moreover, the sealing method neither damages the plants, as happens when plants are clipped below the water surface (Ding *et al.* 2005), nor disturbs the substrate, as happens when a tube is inserted (King *et al.* 1998; Torn and Chapin 1993). The use of agar sealing would also simplify the double chamber technique used by Yu *et al.* (1997).

In conclusion, besides introducing a novel method to study plant-mediated transport, this first screening of a large set of plant species suggests that vegetation characterization based on functional traits (such as root system or aerenchyma structure) and plant processes (such as chimney effect and/or radial oxygen loss) could be useful in predicting methane emissions and, therefore, in designing mitigation strategies (Dias *et al.* 2010; Hendriks 2009). First, however, we need more comparative screening experiments, including measurements of rhizosphere oxidation, carbon exudation and methane transport, coupled with plant traits (such as root morphology). Our sealing method could serve as a useful tool for conveniently screening large sets of plant species for their gas transport capabilities.

Table 2: results of linear regression (R^2) between methane emission from the peat core, and characteristics of the plants growing in the peat. Calculations are carried out with mean values per species.

Plant parameter	Forbs			Graminoids			All plants		
	Unsealed	Sealed	Chimney	Unsealed	Sealed	Chimney	Unsealed	Sealed	Chimney
Aboveground biomass	0.02	0.02	0.02	(-)0.39*	0.23	0.04	0.01	0.01	0.00
Belowground biomass	0.21	0.12	0.12	0.00	0.01	0.02	0.11	0.06	0.05
Total biomass	0.13	0.07	0.07	0.15	0.12	0.00	0.13	0.13	0.05
Root/shoot ratio	0.28	0.25	0.02	0.11	0.03	0.11	0.09	0.09	0.00
Root volume	0.12	0.01	(+)0.62*	0.01	0.00	0.05	0.04	0.00	(+)0.39**
Root density	0.17	0.22	0.03	0.02	0.01	(-)0.50*	0.09	0.18	0.15

(+) = positively related; (-) = negatively related; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Sealed: flux measurement from pots after sealing the soil surface with agar; Unsealed: flux measurement from pots without the agar seal.

ACKNOWLEDGEMENTS

We thank Adrian Hartmann, Albert Kölbener, Majid Irvani, Pascal Niklaus, Rajwinder K. Sohal and René Graf for helping with peat collection and flux measurements. This work was supported by ETH Zurich [TH-07 07-3]. We also gratefully acknowledge the anonymous reviewers for their constructive comments, which helped to improve this manuscript.

Conflict of interest statement. None declared.

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