

Interaction of fertilization and soil water status determine C partitioning in a sedge wetland

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ARTICLE INFO

Keywords:

¹³C₂ pulse labelling
Rhizodeposition
Phospholipid fatty acids (PLFAs)
Fertilization
Water status
Carbon partitioning

ABSTRACT

Photosynthetic carbon (C) fixation and its partitioning in the plant-soil system are responsible for soil C sequestration and nutrient cycling. These microbially-mediated biogeochemical processes are impacted strongly by soil nutrient availability and soil moisture, which are being altered by global environmental change. We studied the interactive effects of fertilization (fertilized vs unfertilized) and water regime (high-water vs low-water level) on plant C fixation and rhizodeposition, and the subsequent microbial processing of plant-derived C substrates in mesocosms planted with the wetland sedge *Carex acuta*. We used a ¹³C₂ pulse-labelling approach to track assimilates in plants, microbial phospholipid fatty acids (PLFA) and soils for 7 days. Fertilizer × water regime interactions affected the dynamics of root ¹³C efflux, microbial utilization and final ¹³C sequestration in the soil. Plants growing in high-water unfertilized soils rapidly exuded a greater proportion of ¹³C into the rhizosphere, but the temporal increase in soil ¹³C was lower than in the other treatments. In contrast, the greatest temporal increase in soil ¹³C was observed in high-water fertilized systems. This occurred because fertilized plants were more productive and fixed more C, which resulted in larger root biomass with faster turnover and consequently larger amounts of ¹³C immobilized in the high-water fertilized soils than high-water unfertilized soils. The composition of microbial communities processing the C rhizodeposits was dynamic during the 7 d study. Initially, the exuded ¹³C was processed mainly by bacteria, while fungal PLFA became progressively more enriched after 7 d. This indicates that fungi were the main recipients of C in rhizodeposits at this time, regardless of nutrient availability or soil water regime. In summary, fertilization of the *C. acuta* sedge wetland stimulated above- and belowground production and selected for a smaller but more active microbial community dominated by fungi. Fertilization enhanced soil C sequestration of recently fixed photosynthates in this wet sedge grassland.

1. Introduction

Wetlands play an indispensable role in the global carbon (C) cycle and C sequestration. Wetland soils store approximately 2300 Pg of soil organic C, the amount corresponding to 20–30% of the terrestrial organic C pool (Davidson and Janssens, 2006; Mitsch and Gosselink, 2007). The potential of wetland soils for C sequestration is determined by plant productivity, microbial activity and C partitioning in the plant-soil-microbial system (Mitsch and Gosselink, 2007; Bardgett et al., 2013). These plant-microbial interactions are mediated via rhizodeposition, the flux of organic compounds released from the living roots into the soil (Jones et al., 2004). Rhizodeposition serves as a primary source of energy and C for soil microorganisms, which regulates the composition of soil microbial communities (Paterson et al., 2006), microbial

growth, decomposition of pre-existing soil organic matter (SOM) (Blagodatskaya and Kuzyakov, 2008; Blagodatskaya et al., 2009), release of nutrients in forms available for plants (Kuzyakov, 2010; Kaštovská et al., 2015), and formation of new SOM (Paul, 2016; Kögel-Knabner, 2017).

Rhizodeposition is primarily determined by inherent plant characteristics such as species, plant age and ontogenetic phase (Kuzyakov and Domanski, 2000; Jones et al., 2004; Baptist et al., 2015). Additionally, N availability and soil moisture are crucial external factors impacting plant rhizodeposition (Jones et al., 2004; Badri and Vivanco, 2009; Atere et al., 2017; Holz et al., 2018) and plant-microbial interactions (Treonis et al., 2004; Yao et al., 2012; Tian et al., 2013; Ge et al., 2017). Fertilized plants are more productive aboveground as well as belowground (Mitsch and Gosselink, 2007; Liu and Greaver, 2010;

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<https://doi.org/10.1016/j.soilbio.2019.03.031>

Received 17 October 2018; Received in revised form 29 March 2019; Accepted 31 March 2019

Available online 04 April 2019

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Kaštovská et al., 2017) with higher tissue nitrogen (N) content, turnover and altered root morphology (Bardgett et al., 2014; Holz et al., 2018). Plants growing in nutrient-luxury conditions usually increased the inputs of root-derived C to the soil (Baptist et al., 2015; Ge et al., 2017) and shifted its composition by enhancing the contribution of compounds derived from root turnover (Kaštovská et al., 2017). The soil microorganisms responded to N fertilization by increased C mineralization rates (Dietrich et al., 2017), altered community composition (Geisseler and Scow, 2014) and microbial biomass, where both negative (Treseder, 2008, Rousk and Bååth, 2011) and positive (Geisseler and Scow, 2014) effects were reported. Despite of an increased rhizodeposition flux, lowered microbial processing of root-derived C was observed in fertilized systems (Wang et al., 2016; Ge et al., 2017). Unlike fertilization, waterlogging decreased plant nutrient uptake (Atere et al., 2017) and C allocation below ground, which was complemented by decreased microbial processing of rhizodeposited ^{13}C and label incorporation into microbial PLFA (Yao et al., 2012; Tian et al., 2013; Atere et al., 2017). The lower microbial activity in water-saturated soils (Bapiri et al., 2010) together with lower investment into exudation may further result in lowering N availability for plant uptake (Kaštovská et al., 2015). Soil moisture and N availability thus importantly interact in affecting plant C acquisition and its partitioning in the plant-microbial-soil systems. This was already shown in the study of Atere et al. (2017), where the authors documented the largest flux of root-derived C and its stabilization in fertilized soils exposed to drying-rewetting cycles compared to flooded-fertilized or unfertilized systems.

Most studies aiming to assess the effects of soil water regime, fertilization or their interactions on partitioning of C in wetlands have focused on agricultural paddy soils, considering the economic and ecological importance of rice fields as an important source of human diet (FAO, 2009), but also greenhouse gas emissions (Le Mer and Roger, 2001). Until now, little attention has been paid to C partitioning in semi-natural oligo- or mesotrophic lowland wetlands, ecosystems that play an indispensable role in water retention and C sequestration (Mitsch and Gosselink, 2007). Natural wetlands differ from paddy systems by extensive management, natural fluctuation of soil water level and by the presence of perennial graminoids with large root system and intensive C allocation belowground (Edwards, 2015; Kaštovská et al., 2015, 2017). Even though these differences imply different functioning and C balance compared to intensively-used artificial wetlands, studies examining the interactive effects of fertilization and soil water regime on the partitioning of assimilated C in the plant-microbial-soil continuum in natural oligotrophic wetlands are missing. Since excessive nutrient loading as well as climate change effects on the water balance and draining of wetlands are projected to become increasingly important drivers of wetland deterioration in the next 40 years (Millennium Ecosystem Assessment, 2005), such studies are urgently needed for reliable predictions of ecosystem behaviour in the future.

We present a study of the interactive effect of fertilization and soil water regime on the partitioning of recently assimilated C within a wetland plant-microbial-soil system. We uniquely linked the responses of plants (changes in productivity and allocation of recently fixed C to growth and rhizodeposition) and the soil compartment, focusing on total microbial biomass as well as on the community actively processing rhizodeposited C and, finally, on C stabilization in the soil. We worked in well-established mesocosms planted with *Carex acuta*, a species representative of oligotrophic wet grassland systems, which nowadays often face eutrophication resulting from management practices on surrounding agricultural lands and decreased water level and in which we lack an understanding of the mechanisms driving their response to ongoing changes. A ^{13}C pulse-labelling approach was used to track the label into plant tissues, soil and microbial PLFAs immediately after plant labelling and after 7 days. The two sampling times allowed us to compare the role of different soil microbial groups in the processing of simple exudates released from roots shortly after fixation and of more

complex compounds deposited to the soil later after fixation. Based on previous studies in paddy systems, we hypothesized that C allocation below ground, investments to exudation and label incorporation into microbial biomass will be lower under water-saturated conditions compared to water-unsaturated conditions (Tian et al., 2013; Atere et al., 2017) and that the fertilized soils will host a larger and more active microbial biomass associated with larger root systems compared to unfertilized plants (Wang et al., 2016). We further focused on the contribution of fungi and bacteria to the processing of root-derived C and assumed that the fungal role will decrease under both water-saturated and fertilized conditions compared to water-unsaturated and unfertilized treatments (De Vries et al., 2006; 2007; Tian et al., 2013). Therefore, we expected unique patterns of C partitioning, rhizodeposition flux and microbial processing of new C entering the soil under individual treatment combinations.

2. Material and methods

2.1. Mesocosm study

The mesocosms were established in April 2009: 48 pots (40 × 40 × 35 cm LxWxD, respectively) were filled with 20 cm of sand overlaid by 15-cm of a mineral soil (20 kg soil dry weight per pot) and each planted with four plants of *Carex acuta*. The soil was a cambisol gathered from a meadow containing $1.17 \pm 0.10\%$ C_{TOT} , $0.11 \pm 0.01\%$ N_{TOT} , and with pH (H_2O) of 6.08 ± 0.01 . The planted pots were randomly distributed in groups of six into larger basins in order to easily control water and nutrient levels, and subjected to different combinations of fertilization and water treatments, with two replicate basins for each treatment combination in a full-factorial design. For the fertilization treatment, all pots in randomly selected basins received either no fertilizer (UF) or 300 kg NPK fertilizer $\text{ha}^{-1} \text{yr}^{-1}$ (15% of N in the form of NH_4NO_3 , 15% of P_2O_5 and 15% of K_2O , w/w; N:P:K ratio 2.3:1:2) (F), which was added in two half doses every year, at the beginning of the growing season in late April - early May (2010–11) and at the time of maximum aboveground biomass in July (2009–11). The pots in each basin were subjected to either the high water (HW) treatment, in which the soil was kept saturated but not flooded, or the low water (LW) variant (30 cm below the soil surface). Water was added to the basins when needed in order to maintain the desired water levels, which were regulated through holes drilled in the side walls of the basins at appropriate heights above the bottom. At the time of the labelling experiments after two years, the pots were fully vegetated and the canopy was closed independent of the treatment.

2.2. Labelling experiment

The pots were pulse-labelled by $^{13}\text{CO}_2$ in May 2011 (third growing season) in the period of intensive plant growth, 14 days after NPK fertilization. On May 10, four pots from each treatment combination were randomly chosen (16 together) and placed into two basins according to their original water level treatment. On May 11, both basins were covered by a plastic foil held in place by a supporting wooden frame and equipped with an efficient fan. The ends of the foil were placed into the water in the basin. In this way, two closed chambers of the same headspace volume (1.0 × 2.0 × 0.8 m) were established. When the CO_2 concentration in the chambers decreased below 200 ppm, 400 ml of $^{13}\text{CO}_2$ (99.9 at%) were added into each chamber near the operating fan using a syringe with needle, which increased the inside CO_2 concentration by about 200 ppm. Then the concentration of the inside CO_2 was kept between 300 and 400 ppm (checked by gas chromatography) by regular addition of $^{13}\text{CO}_2$. The labelling lasted 4 h. After two hours of the labelling period, both chambers were uncovered for 5 min to ventilate the vapour and keep the inside temperature close to external conditions. The pots were returned to their original basins immediately after labelling.

2.3. Plant and soil sampling

Plant and soil materials were sampled immediately after the ^{13}C labelling finished (on May 11, T0) and again after 7 days (T7). The soil and vegetation in all pots was cut into two halves with a big knife and, in each sampling campaign, half of each pot was destructively sampled for measuring above- (AG) and belowground (BG) plant biomass and contents of C and ^{13}C in the plant biomass and soil. First, we clipped a representative sample of the AG (green, living) plant biomass and took four soil core samples (5 cm diameter). We immediately separated roots and rhizomes from the soil by hand. The cleaned plant material and a part of the soil were dried at 60 °C for 48 h, weighed, milled and analysed for C and N contents and their isotopic composition. The rest of the soil was immediately frozen at –80 °C for phospholipid fatty acid (PLFA) analyses. Then we collected, dried and weighed all the remaining AG (living and dead) and BG (roots and rhizomes) plant biomass from the half-pot. Finally, data on plant biomass were combined from both sampling times to obtain the representative plant biomass for the whole pot. On May 13, whole control unlabelled pots (two for each treatment, 8 altogether) were processed in the same way to determine ^{13}C isotope natural abundance in plant and soil materials.

2.4. Plant and soil analyses

The C and ^{13}C contents in the plant and soil samples were analysed on a CHNS Elemental analyser Vario Micro Cube (Elementar, Germany) connected to an isotope ratio mass spectrometer (IR-MS Delta X Plus, Finnigan, Germany). Subsamples of fresh homogenized soil from each pot (10 g) were extracted by 0.5 M K_2SO_4 (40 ml), the extracts were filtered and dissolved organic C (DOC) and N (DN) were analyzed on a LiquiC TOC II (Elementar, Germany).

2.5. Microbial community composition and ^{13}C incorporation into microbial PLFA

PLFA profiling was used to describe the microbial community composition. The utilization of root deposits by soil microorganisms was assessed by tracing the ^{13}C assimilated during pulse labelling in individual microbial PLFAs. Lipid samples were prepared according to Frostegård et al. (1993) with minor modifications (see Kotas et al., 2016 for details). The concentration and isotopic composition of the resulting methyl esters were determined using a Trace GC 1310 coupled with GC IsoLink II and interfaced via ConFlo IV with DELTA V (Thermo Scientific, Bremen, Germany). The gas chromatograph was equipped with a TG-5MS column (30 m, 0.25 mm ID, 0.25 µm film thickness; Thermo Scientific). The reactor was seed oxidized after each combustion. The isotope ratios were calculated with ISODAT 3.0 relative to the pulse of reference CO_2 gas that was characterized by repetitive measurement of three international standards (IAEA-CH3, IAEA-CH6, IAEA-600 purchased from IAEA, Vienna, Austria) using on-line combustion in an elemental analyser (Flash 2000 by Thermo Scientific) coupled to the same mass spectrometer. Methyl-nonadecanoate was used as the internal standard for PLFA quantification. The concentration and isotopic composition of each PLFA were corrected for C added during methylation. Only PLFAs detectable in all soil samples in sufficient concentrations allowing accurate determination of their isotopic composition were considered. PLFAs i16:0, i17:0, a17:0 were used as markers of Gram-positive bacteria (G+); 16:1ω7, 16:1ω5, cy17:0, 18:1ω7 as markers of Gram-negative (G-) bacteria and 18:2ω6,9 as the marker of fungi (Frostegård and Bååth, 1996). Total bacterial biomass was calculated as the sum of the above-mentioned bacterial markers and general bacterial markers 17:0 and 18:1ω5. The PLFAs 16:0, 18:0, 20:0, 19:1ω8 and 18:1ω9 were considered as non-specific microbial markers (Kaiser et al., 2010). The PLFA 18:1ω9 is often used as a fungal marker, but we decided to assign it as non-specific since it was similarly correlated with both G- PLFAs and fungal marker 18:2ω6,9 thus its

affiliation to fungi was uncertain (see Frostegård et al., 2011).

2.6. Calculations

A binary mixing model was used to calculate the amount of pulse-derived ^{13}C in shoot and root biomass, soil and individual PLFAs:

$$^{13}\text{C} (\mu\text{g g}^{-1}) = [(\text{at}\%_{\text{sample}} - \text{at}\%_{\text{control}}) / (99.90 - 1.10)] \times \text{C pool size} (\mu\text{g C g}^{-1})$$

where $\text{at}\%_{\text{control}}$ is the ^{13}C natural abundance in the control samples, $\text{at}\%_{\text{sample}}$ is the ^{13}C abundance in the samples after labelling, 99.90 is the pulse ^{13}C $\text{at}\%$ and 1.10 is the ambient $\text{at}\%$ of the CO_2 in the atmosphere. Net C fixation of the system ($\text{mg } ^{13}\text{C pot}^{-1}$) was calculated as the sum amount of ^{13}C in the shoots, roots, and soil after the 4-h labelling period. Differences between net ^{13}C fixation and the amount of ^{13}C remaining in the system after 7 days were considered as respiration losses (Fig. 2). For both samplings, the ^{13}C distribution in the plant-soil system was expressed on an absolute as well as a relative basis (% net C fixation).

2.7. Statistics

All data were checked for normality and homoscedasticity, and log-transformed if necessary to improve the normality of the residuals. The differences in particular plant, soil and microbial parameters between the treatments and between the two sampling times were tested by two-way ANOVA with interaction, complemented with Tukey-HSD post hoc tests, in Statistica 13 (StatSoft, USA). Pearson correlation coefficients were used to assess how tightly different variables were related to each other. The interactive effect of water level and fertilization on ^{13}C partitioning in the plant-microbial-soil systems was tested by redundancy analyses (RDA) and a Monte Carlo simulation with 1999 permutations. We did no standardization by samples but centering and standardization by variables because the variables were not always measured on the same scale (Šmilauer and Lepš, 2014). Only the adjusted explained variation is referred to in the results. Principal component analysis (PCA) with supplementary variables (treatments) was used to depict the variability of the experimental mesocosms and correlations between treatments and variables representing the ^{13}C partitioning. All variables were log-transformed prior to evaluation by multivariate statistics. Multivariate statistical analyses were performed with CANOCO for Windows version 5.0 (Ter Braak and Šmilauer, 2012). All statistical tests were considered significant at $P < 0.05$.

3. Results

3.1. Plant biomass

Total plant AG and BG biomass were correlated across all pots ($r = 0.727$, $P < 0.05$), with BG exceeding AG biomass in all treatment combinations (Fig. 1). The AG biomass (both living and dead) was enhanced in the F versus UF pots ($F = 173.3$, $P < 0.001$). HW level further increased the living AG biomass in the F pots (W^*F , $F = 6.6$, $P < 0.05$). The BG biomass was also larger in the F than UF pots ($F = 33.5$, $P < 0.001$), but the HW level reduced it in comparison to the LW treatment ($F = 7.9$, $P < 0.05$). Therefore, the LW-F treatment had the largest BG biomass (Tukey HSD test $P < 0.05$, Fig. 1). Plant biomass C and N concentrations and biomass C/N ratios were not affected by any of the treatments.

3.2. Soil chemical characteristics

Fertilization and water level did not affect total soil C and N contents and their C/N ratio, but influenced the smaller and more labile C and N pools (Table S1). Fertilized pots contained significantly more soil

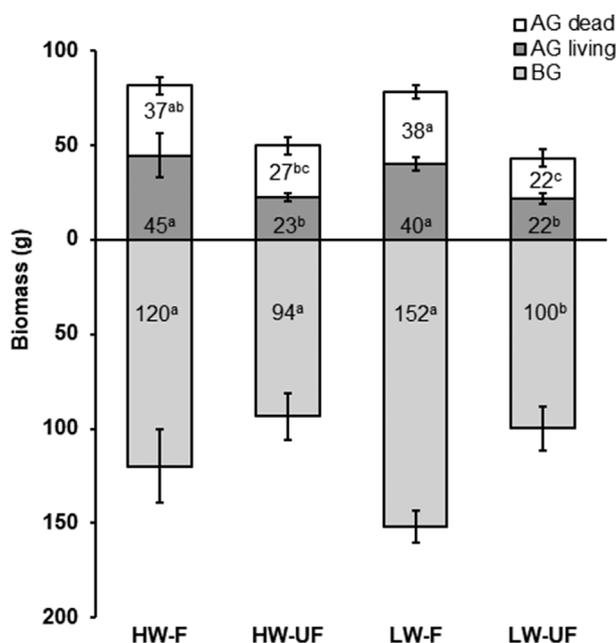


Fig. 1. Aboveground (AG living and dead) and belowground (BG) plant biomass in mesocosms with different fertilization (F – fertilized, UF – unfertilized) and water level (HW – high water, LW – low water) treatments (mean ± SD, n = 4). Superscripts indicate significant differences in plant biomass among treatments revealed by Tukey-HSD test ($P < 0.05$).

DOC ($F = 24.7, P < 0.001$) and DN ($F = 10.0, P < 0.01$) than unfertilized pots. HW level decreased the soil DN pool ($F = 15.8, P < 0.001$), which resulted in the lowest DN concentration in the HW-UF pots among all treatments (Tukey HSD test, $P < 0.05$).

3.3. Microbial biomass and PLFA profile

Both microbial biomass (PLFAtot) and community composition were significantly influenced only by fertilization but did not change with water level or time (immediately after labelling or 7 days later). Fertilization significantly decreased microbial biomass in comparison to UF pots (Table 1) and shifted the microbial PLFA profile (RDA, $P = 0.002$, pseudo- $F = 5.5$; Fig. S1). The proportion of bacterial PLFA decreased from $28 \pm 3\%$ in the UF to $22 \pm 2\%$ in the F treatment ($F = 16.31, P = 0.002$), while the proportion of fungal PLFA remained stable across the treatments ($28 \pm 4\%$ PLFAtot; mean ± sd, n = 16). This difference led to an increased F/B in F compared to UF pots ($F = 6.69, P = 0.023$), while the lowest F/B ratio was found in LW-UF treatment (Table 1). Within bacterial PLFA, the relative abundance of those specific for G- bacteria highly exceeded G+ markers (G-/G+ ratios 6.7 ± 1.2 ; mean ± SD, n = 16). Both were negatively affected by fertilization and markers of G- bacteria decreased more ($F = 16.55, P = 0.001$) than markers of G+ bacteria ($F = 8.25, P = 0.014$).

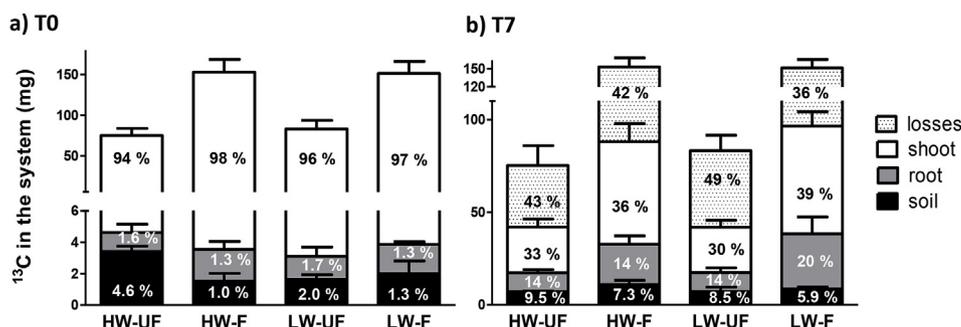


Fig. 2. Distribution of ^{13}C in plant-soil systems at a) T0 – immediately after labelling and b) T7 – 7 days after labelling in mesocosms with different fertilization (F – fertilized, UF – unfertilized) and water level (HW – high water, LW – low water) treatments. The heights of columns show the absolute amounts of ^{13}C in particular pools (mean ± SD, n = 4), while the values in columns show the relative contribution of ^{13}C in the pools to the net ^{13}C fixation, equal to the total ^{13}C in the system at T0.

3.4. ^{13}C fixation and distribution in the plant-soil system

The mass-specific ^{13}C fixation per g of living AG biomass was comparable across the treatments. The system net ^{13}C fixation was therefore driven by plant biomass and the F pots with larger plant biomass fixed significantly more ^{13}C than the UF systems ($F = 93.3, P < 0.001$, Fig. 2). At T0, a majority of ^{13}C was still present in the AG biomass ($\geq 94\%$ of net fixed ^{13}C) in all treatments (Fig. 2a). However, plants in the HW-UF pots allocated the fixed C below ground and to the soil faster than in other systems (F*W interaction, $F = 13.7, P = 0.003$; Table 2). Consequently, shortly after fixation the HW-UF soils contained the largest absolute as well as relative ^{13}C amounts from all the treatments ($4.6 \pm 0.8\%$ of net fixed ^{13}C in comparison to only 1–2% of net fixation in the other systems; Fig. 2a).

After 7 days, the systems still kept almost 60% of net fixation, with $35 \pm 7\%$ of the fixed ^{13}C in the AG biomass, $15 \pm 5\%$ in the BG biomass and $8 \pm 2\%$ in the soil on average. Only the portion of soil ^{13}C differed among the treatments, being lower in F than UF systems ($F = 6.3, P < 0.05$, Fig. 2b). When expressed in total ^{13}C amounts, the F systems kept more ^{13}C than UF ones in all compartments: in the AG ($F = 66.5, P < 0.001$) and BG ($F = 25.8, P < 0.001$) plant biomass as well as in the soils ($F = 6.8, P = 0.022$). Additionally, the BG biomass (but not the AG biomass) of fertilized plants immobilized more ^{13}C per unit of root-C, indicating higher specific root growth compared to unfertilized systems. Despite the differences in root growth rates, the specific rhizodeposition per unit of root-C was comparable among treatments (Table 2) showing that the amounts of ^{13}C deposited in the soil were mainly driven by root biomass.

3.5. ^{13}C incorporation in microbial PLFAs

In 4 h of ^{13}C fixation by plants, the ^{13}C amount bound in PLFA was already 270–500 ng $^{13}\text{C} \text{ kg}^{-1}$ soil, with significantly higher amounts in the UF than F systems (Table 3, Fig. S2). The ^{13}C formed on average 0.06‰ of PLFA-C in all treatments (Table 3). During the following 7 days, the ^{13}C amount in PLFA increased to 770–1120 ng $^{13}\text{C} \text{ kg}^{-1}$ soil. The ^{13}C contributed to PLFA-C by 0.12‰ in UF systems, but significantly more in F systems, where the ^{13}C enrichment reached 0.18‰ ($F = 18.0, P < 0.01$, Table 3, Fig. S2). PLFA- ^{13}C represented 0.3–0.7% of total soil ^{13}C at the beginning but later pronouncedly decreased to 0.2–0.4% in all treatments, indicating that ^{13}C labelled compounds other than microbial PLFAs increased in the soil.

The variable labelling intensity of specific PLFA markers among the four treatments implied unique patterns in microbial processing of ^{13}C rhizodeposits at both sampling times. At T0, most bacterial PLFAs were comparably or more intensively labelled compared to fungal marker 18:2 ω 6,9 (Fig. 3), this being the most evident in the HW-UF treatment with the largest proportion of microbial ^{13}C found in bacterial PLFAs (Fig. 4). The most labelled bacterial markers were the G+ PLFAs i16:0 and a17:0 in HW-UF systems (Fig. 3), but the majority of bacterial PLFA ^{13}C was found in G- markers (Fig. 4). Nevertheless, fungi importantly contributed to processing of ^{13}C exudates in all treatments (Fig. 4).

Table 1

The total microbial, fungal and bacterial PLFA contents, and F/B ratios in mesocosms with different fertilization (F – fertilized, UF – unfertilized) and water level (HW – high water, LW – low water) treatments. Mean values \pm SDs from both sampling times are given in the upper part of the table. Results of two-way ANOVA (F values) of the effects of fertilization (F), water level (W) and their interaction (W x F) are presented in the lower part of the table.

Treatment		n	PLFA _{tot} mol/g soil DW	Fungi mol/g soil DW	Bacteria mol/g soil DW	F/B
Water	Fertilization					
HW	UF	4	36.3 \pm 7.8 ^a	10.9 \pm 2.9 ^a	9.68 \pm 2.5 ^a	1.16 \pm 0.26 ^{ab}
HW	F	4	20.5 \pm 5.5 ^b	6.20 \pm 2.3 ^{ab}	4.6 \pm 1.4 ^b	1.3 \pm 0.18 ^a
LW	UF	4	36.6 \pm 7.9 ^a	9.26 \pm 2.1 ^{ab}	10.66 \pm 2.7 ^a	0.88 \pm 0.08 ^b
LW	F	4	20.4 \pm 7.8 ^b	5.81 \pm 2.7 ^b	4.76 \pm 2.3 ^b	1.24 \pm 0.10 ^a
UF		8	36.4 \pm 7.9 ^a	10.1 \pm 2.7 ^a	10.2 \pm 2.6 ^a	1.02 \pm 0.24 ^b
F		8	20.5 \pm 6.9 ^b	6.0 \pm 2.5 ^b	4.70 \pm 1.9 ^b	1.27 \pm 0.15 ^a
HW		8	28.4 \pm 10.5 ^a	8.6 \pm 3.5 ^a	7.15 \pm 3.2 ^a	1.23 \pm 0.24 ^a
LW		8	28.5 \pm 11.3 ^a	7.5 \pm 2.9 ^a	7.71 \pm 3.9 ^a	1.06 \pm 0.20 ^a
		df				
F		1	12.05 **	12.92 **	7.98 *	6.69 *
W		1	0.10	0.47	0.51	3.18
F x W		3	0.11	0.37	0.37	1.09

Different superscript letters indicate significant differences between particular treatments ($P < 0.05$; results of Tukey post-hoc test; upper part of the table). Statistically significant differences are indicated by * $P < 0.05$ and ** $P < 0.01$ (lower part of the table).

Table 2

The immobilization of ¹³C in roots, specific root growth, rhizodeposition flux, and partitioning between rhizodeposition and root growth in mesocosms with different fertilization (F – fertilized, UF – unfertilized) and water level (HW – high water, LW – low water) treatments. Mean values \pm SDs are given in the upper part of the table. Results of two-way ANOVAs (F-values) of the effects of fertilization (F), water level (W) and their interactions (F x W) are presented in the lower part of the table.

Treatment		n	root ¹³ C		specific root growth	rhizodeposition		rhizodeposition versus root growth
Water	Fertilization		mg root ¹³ C/g root		mg root ¹³ C/g root C	μg soil ¹³ C/g root C		μg soil ¹³ C/μg root ¹³ C
			T0	T7	T7	T0	T7	T7
HW	UF	4	0.013 \pm 0.005 ^a	0.11 \pm 0.03 ^{ab}	0.29 \pm 0.08 ^{ab}	87.8 \pm 11.5 ^a	181 \pm 17.3 ^a	0.71 \pm 0.12 ^a
HW	F	4	0.017 \pm 0.005 ^a	0.19 \pm 0.06 ^{ab}	0.51 \pm 0.15 ^a	31.2 \pm 11.3 ^b	221 \pm 61.1 ^a	0.54 \pm 0.18 ^{ab}
LW	UF	4	0.014 \pm 0.005 ^a	0.10 \pm 0.02 ^b	0.26 \pm 0.05 ^b	39.4 \pm 7.1 ^b	169 \pm 42.8 ^a	0.71 \pm 0.19 ^a
LW	F	4	0.012 \pm 0.002 ^a	0.19 \pm 0.05 ^a	0.50 \pm 0.10 ^a	32.1 \pm 14.6 ^b	136 \pm 13.8 ^a	0.31 \pm 0.05 ^b
UF		8	0.014 \pm 0.005 ^a	0.11 \pm 0.03 ^b	0.28 \pm 0.07 ^b	63.6 \pm 26.0 ^a	175 \pm 33.2 ^a	0.71 \pm 0.16 ^a
F		8	0.015 \pm 0.004 ^a	0.19 \pm 0.05 ^a	0.50 \pm 0.13 ^a	31.7 \pm 13.1 ^b	179 \pm 61.3 ^a	0.42 \pm 0.18 ^b
HW		8	0.015 \pm 0.005 ^a	0.15 \pm 0.06 ^a	0.40 \pm 0.16 ^a	59.5 \pm 30.5 ^a	201 \pm 49.0 ^a	0.62 \pm 0.18 ^a
LW		8	0.013 \pm 0.004 ^a	0.15 \pm 0.06 ^a	0.38 \pm 0.14 ^a	35.8 \pm 12.0 ^b	153 \pm 35.8 ^a	0.51 \pm 0.24 ^a
		df						
W		1	0.4	0.02	0.12	12.96 *	4.68	1.72
F		1	0.24	12.38 *	15.39 *	23.41 **	0.02	11.74 *
W x F		3	1.78	0.11	0.01	13.91 *	2.6	3.39

Different superscript letters indicate significant differences between particular treatments ($P < 0.05$; results of Tukey post-hoc test; upper part of the table). Statistically significant differences are indicated by * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ (lower part of the table).

The ¹³C enrichment of the fungal PLFA 18:2ω6.9 increased 5-to-20 times during the week ($P < 0.0001$, $F = 97.4$) and became the most enriched marker of all (Fig. 3). The G- PLFAs as well as non-specific PLFAs also became increasingly enriched in ¹³C over time ($P < 0.0001$ and 0.003, $F = 39.0$ and 10.9, respectively), while the labelling of G+ markers remained stable or even decreased in HW-UF soils (Fig. 3). As a result, the fungal PLFA contained 41–52% of ¹³C bound in total PLFA, the contribution of non-specific markers decreased to ca 38% of the total PLFA ¹³C content compared to $\geq 50\%$ contribution at T0, and bacterial PLFA incorporated 8.5–18% of PLFA-¹³C (Fig. 4). The relative importance of fungi over bacteria in ¹³C immobilization was 4–7 times higher in F treatments compared to the UF systems, where fungi immobilized only 2–3.5 times more ¹³C than bacteria (significant F effect; Table 3) and the bacterial (mainly G-) markers contributed significantly more to ¹³C immobilization compared to F ones (Fig. 4).

3.6. Effects of fertilization and water regime on ¹³C partitioning and processing in the plant-soil system

Fertilization and water level interacted in their effects on ¹³C distribution in the plant-microbe-soil system at both sampling times (both pseudo- $F = 5.4$, $P = 0.002$ and 0.001, respectively; the treatments explained 47 and 51% of variation in the data, respectively). In the beginning, the HW-UF pots functioned differently from all other systems mainly due to the largest total as well as relative release of fresh ¹³C assimilates to the soil and fast ¹³C incorporation into bacterial PLFAs compared to the other systems (Fig. 5a, Table 3).

After 7 days, the UF and F systems separated along the first principal component. The UF pots had a larger amount of ¹³C immobilized in microbial PLFA and a higher PLFA-¹³C contribution to the total soil ¹³C content. On the contrary, the F systems were characterized by a higher absolute soil ¹³C content, higher root ¹³C content and concentration,

Table 3

The incorporation of ¹³C into microbial PLFA in mesocosms with different fertilization (F – fertilized, UF – unfertilized) and water level (HW – high water, LW – low water) treatments. Mean values ± SDs of soil PLFA ¹³C contents, enrichment of microbial PLFA, contribution of PLFA ¹³C content to soil ¹³C content, F/B ¹³C ratios and soil ¹³C content specific to soil PLFA content are given in the upper part of the table. Results of two-way ANOVA (F values) of the effects of fertilization (F), water level (W) and their interaction (W x F) are presented in the lower part of the table.

Treatment		n	¹³ C PLFA		PLFA ¹³ C on PLFA C		PLFA ¹³ C on soil ¹³ C		F/B ¹³ C PLFA		soil ¹³ C per PLFA C
Water	Fertilization		ng ¹³ C/kg soil		‰		%		T0	T7	ng ¹³ C/μg PLFA C
			T0	T7	T0	T7	T0	T7			T7
HW	UF	4	506 ± 137 ^a	887 ± 186 ^a	0.06 ± 0.01 ^a	0.11 ± 0.02 ^b	0.35 ± 0.11 ^a	0.30 ± 0.07 ^a	0.55 ± 0.15 ^b	2.26 ± 0.2 ^b	30.4 ± 5.9 ^b
HW	F	4	270 ± 119 ^a	854 ± 202 ^a	0.06 ± 0.02 ^a	0.19 ± 0.02 ^a	0.43 ± 0.20 ^a	0.20 ± 0.09 ^a	1.03 ± 0.51 ^{ab}	6.67 ± 2.2 ^a	72.2 ± 18.5 ^a
LW	UF	4	426 ± 141 ^a	1122 ± 348 ^a	0.06 ± 0.02 ^a	0.14 ± 0.02 ^{ab}	0.67 ± 0.31 ^a	0.39 ± 0.12 ^a	1.58 ± 0.24 ^a	3.07 ± 0.8 ^b	26.4 ± 6.2 ^b
LW	F	4	288 ± 112 ^a	768 ± 217 ^a	0.06 ± 0.01 ^a	0.17 ± 0.03 ^a	0.39 ± 0.16 ^a	0.21 ± 0.08 ^a	1.14 ± 0.24 ^{ab}	4.60 ± 0.9 ^{ab}	72.2 ± 21.6 ^a
UF		8	483 ± 144 ^a	1005 ± 303 ^a	0.06 ± 0.01 ^a	0.12 ± 0.02 ^b	0.51 ± 0.28 ^a	0.34 ± 0.11 ^a	1.07 ± 0.55 ^a	2.67 ± 0.7 ^b	28.4 ± 6.4 ^b
F		8	279 ± 116 ^b	811 ± 214 ^a	0.06 ± 0.01 ^a	0.18 ± 0.03 ^a	0.41 ± 0.18 ^a	0.21 ± 0.08 ^a	1.09 ± 0.40 ^a	5.63 ± 2.0 ^a	72.2 ± 20.1 ^a
HW		8	388 ± 174 ^a	871 ± 195 ^a	0.06 ± 0.02 ^a	0.15 ± 0.04 ^a	0.39 ± 0.16 ^a	0.25 ± 0.09 ^a	0.79 ± 0.44 ^b	4.46 ± 2.7 ^a	51.3 ± 25.0 ^a
LW		8	356 ± 145 ^a	945 ± 340 ^a	0.06 ± 0.01 ^a	0.15 ± 0.03 ^a	0.53 ± 0.29 ^a	0.30 ± 0.13 ^a	1.36 ± 0.33 ^a	3.84 ± 1.1 ^a	49.3 ± 27.9 ^a
F		1	8.98 *	2.41	0.02	18.00 **	0.71	6.34 *	0.11	16.67 **	26.05 ***
W		1	0.00	0.58	0.01	0.32	1.29	0.85	9.93 **	0.75	0.05
F x W		3	0.07	1.81	0.31	2.01	2.11	0.55	6.65 *	3.96	0.05

Different superscript letters indicate significant differences between particular treatments ($P < 0.05$; results of Tukey post-hoc test; upper part of the table). Statistically significant differences are indicated by * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ (lower part of the table).

more important role of fungi over bacteria in ¹³C immobilization, more ¹³C enriched PLFAs and a lower proportion of PLFA-¹³C in total soil ¹³C (Fig. 5b). The second principal component separated the F systems according to their water level mainly due to having larger specific ¹³C rhizodeposition and soil ¹³C content under the high-water level, even though the differences were not statistically significant. Fig. 5b further demonstrates that the total amount of soil ¹³C correlates with the fungal-to-bacterial ¹³C PLFA ratio ($r = 0.675$, $P = 0.004$, $n = 16$) but not with microbial biomass (fungal, bacterial, total PLFA) or with PLFA-¹³C.

4. Discussion

4.1. Plant performance and ¹³C allocation to the soil

The final ¹³C allocation to soil was significantly influenced by fertilization but not by the water level treatments. In relative numbers, plants in the UF systems, which were more strongly limited by nutrient availability, deposited to the soil a larger proportion of net ¹³C fixation (9–10%) compared to fertilized plants (6–7%) during 7 days. The larger relative loss of assimilates from roots is often attributed to support of microbial growth and enzymatic activities connected with nutrient mining from SOM, which then facilitates plant nutrient uptake in nutrient poor environments (Kuzyakov, 2010; Poorter et al., 2012; Kaštovská et al., 2018). The observed values are similar to results reported by Tian et al. (2013) for a rice system 14 days after fixation (ca

Label in individual PLFA (‰ ¹³ C in PLFA C)	T0				T7			
	HW-UF	HW-F	LW-UF	LW-F	HW-UF	HW-F	LW-UF	LW-F
G+ markers								
i16:0	0.16	0.10	0.03	0.00	0.03	0.04	0.01	0.07
i17:0	0.05	0.09	0.05	0.05	0.04	0.07	0.06	0.10
a17:0	0.14	0.08	0.07	0.07	0.08	0.07	0.09	0.07
G- markers								
16:1ω7c	0.12	0.12	0.06	0.10	0.11	0.14	0.07	0.11
16:1ω5	0.07	0.07	0.09	0.09	0.10	0.07	0.11	0.11
cy17:0	0.04	0.06	0.05	0.06	0.07	0.08	0.07	0.06
18:1ω7	0.08	0.00	0.03	0.05	0.08	0.07	0.10	0.11
General bact. markers								
17:0	0.02	0.00	0.07	0.12	0.13	0.04	0.11	0.14
18:1ω5	0.09	0.08	0.06		0.14	0.09	0.10	
Fungal marker								
18:2ω6	0.03	0.02	0.05	0.05	0.16	0.37	0.26	0.37
Non-specific markers								
18:1ω9c	0.08	0.04	0.07	0.08	0.11	0.15	0.13	0.16
16:0	0.04	0.23	0.04	0.09	0.13	0.21	0.11	0.21
18:0	0.11	0.10	0.08	0.10	0.10	0.10	0.10	0.14
19:1ω8	0.08	0.13	0.09	0.09	0.10	0.17	0.09	0.11
20:0	0.12	0.06	0.04	0.06	0.05	0.08	0.07	0.03

Fig. 3. ¹³C enrichment of individual microbial PLFAs (in ‰ ¹³C in PLFA-C) in systems facing different fertilization (UF– unfertilized, F – fertilized) and water level (HW – high water, LW – low water) treatments (mean, n = 4). Situations shortly after ¹³C fixation (T0) and after 7 days (T7) are compared. An increasing ¹³C enrichment in PLFAs is graphically presented by darker colors.

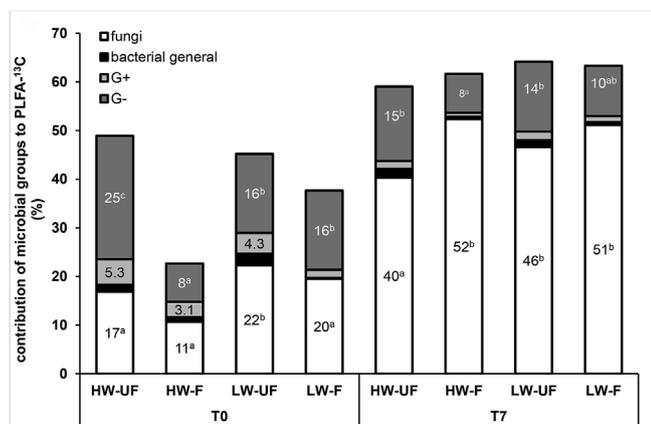


Fig. 4. Relative contribution of grouped microbial PLFAs to the total ¹³C in PLFAs in systems facing different fertilization (UF – unfertilized, F – fertilized) and water level (HW – high water, LW – low water) treatments (means, n = 4). Situations shortly after ¹³C fixation (T0) and after 7 days (T7) are shown. Only values larger than 2% are shown. Superscripts indicate significant differences in contribution of particular PLFA groups among treatments at particular times T0 and T7 revealed by Tukey-HSD test (*P* < 0.05).

4–10% of fixation) or by [Kuzuyakov and Domanski \(2000\)](#). However, the absolute amounts of root-released ¹³C kept in the soils were larger in the F than in the UF systems, being a consequence of enhanced above- and belowground plant productivity in the F systems. Larger fertilized plants fixed ca two times more ¹³C than the UF ones, which was followed by the larger ¹³C flux to the roots. Although they invested relatively more assimilates into root growth than UF plants, which was evident from the higher specific root growth (higher enrichment of root C by ¹³C), the amount of ¹³C deposited to the soil during 7 days was still higher than in the UF systems.

4.2. Effects of fertilization and soil water status on temporal dynamics of ¹³C allocation to the soil

The fertilization treatment in interaction with soil water level significantly influenced the temporal dynamics of ¹³C release from plants to the soil within 7 days. We expect that the ¹³C compounds released to the soil within several hours after fixation (in our case the T0 sampling), will be predominantly simple, low-molecular weight compounds such as primary metabolites with fast turnover ([Jones et al., 2004](#)). Differently, the compounds released later will be importantly contributed by more complex compounds like root lysates, secondary metabolites, mucilage, enzymes, sloughed-off cells and others ([Kuzuyakov and Domanski, 2000](#); [Jones et al., 2004, 2009](#)), and will be less degradable ([Edwards et al., 2018](#)). The observed differences in temporal rhizodeposition dynamics thus indicate treatment-related differences in the quality of the released compounds.

In our experiment, the allocation velocity of the recently fixed ¹³C below ground was the most rapid, and the short-term ¹³C exudation flux to the soil at T0 was the most massive, in the HW-UF systems ([Fig. 2a](#), [Table 2](#)). Our results agree with the observations of [Henry et al. \(2007\)](#) who found a 45% increase in exudation in a flooded system with crested wheatgrass compared to a non-flooded control, but contradict those of [Tian et al. \(2013\)](#) and [Atere et al. \(2017\)](#) who reported decreasing ¹³C exudation in flooded compared to non-flooded rice systems. We suggest that larger exudation flux of recent assimilates in HW-UF than other systems could be explained as a plant response to the lowest soil fertility in this treatment, documented by the lowest concentrations of dissolved N in the soils from all the mesocosms ([Table S1](#)). The high root exudation flux in response to nutrient deprivation ([Kuzuyakov, 2010](#), [Poorter et al., 2012](#)) likely overruled the potentially negative effect of soil water saturation on root exudation.

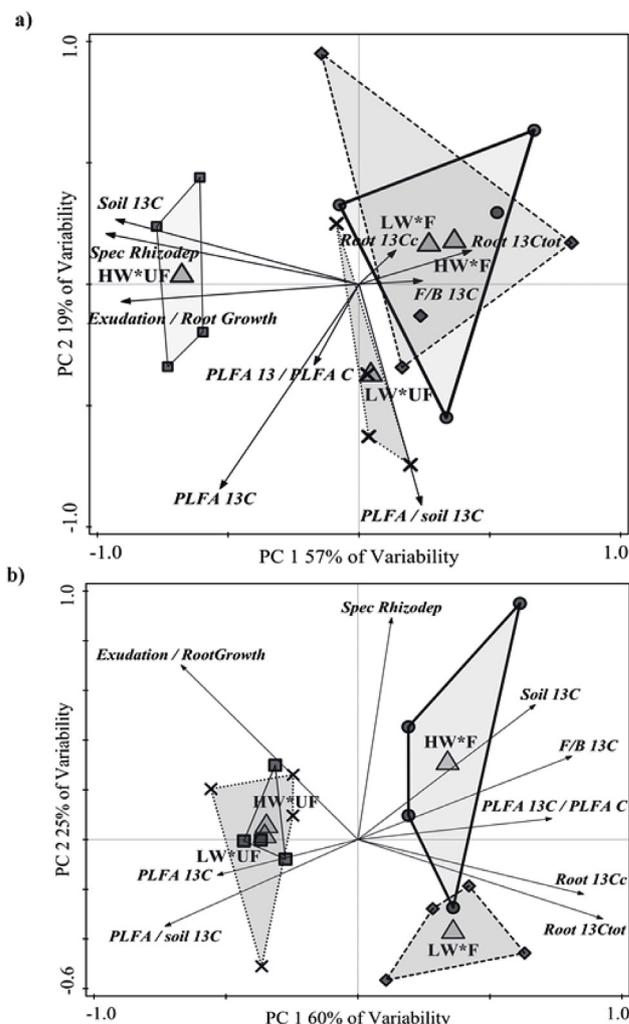


Fig. 5. PCA ordination diagrams depict differences in partitioning of fixed ¹³C in the plant-microbial-soil systems facing different fertilization (UF – unfertilized, F – fertilized) and water level (HW – high water, LW – low water) treatments. Situation (a) shortly after plant ¹³C fixation (T0) and (b) after 7 days (T7). The thin solid (squares) and bold solid (circles) lines represent high water unfertilized and fertilized systems, the dotted (X mark) and dashed (diamonds) lines represent low water unfertilized and fertilized systems, respectively (n = 4). Arrows indicate direction in which the respective parameter value increases. The treatments were used as supplementary variables. The portion of variability explained by each axis is given in the axis title. Labels used in the figure: Soil ¹³C – total soil ¹³C content, Spec Rhizodep – ¹³C released per root mass, Exudation/RootGrowth – ratio between deposited ¹³C and ¹³C immobilized in the root biomass, PLFA ¹³C – total PLFA ¹³C content, PLFA ¹³C/PLFA C – ¹³C enrichment of total microbial PLFA C, PLFA/soil ¹³C – ratio between ¹³C amounts in microbial PLFA and in the bulk soil, Root ¹³Cc – ¹³C concentration in the root mass, Root ¹³Ctot – total ¹³C immobilized in the roots, F/B ¹³C – ratio between ¹³C incorporated into fungal and bacterial PLFA.

The amount of soil ¹³C increased several-fold in all treatments during the one-week period, showing an ongoing release of fixed ¹³C to the soil and its slower mineralization. However, the ¹³C accumulation dynamics in the soils differed among treatments. While the amount of soil ¹³C only doubled in the HW-UF pots despite the previous largest exudation, it increased ca 4 times in both LW treatments and even ca 7-times in HW-F systems ([Table 2](#)). We suggest that the lowest increase of soil ¹³C in the HW-UF systems, resulting also in the lowest final soil ¹³C amounts, was related to it having the lowest root biomass among the treatments (although not significantly different from that in LW-UF systems). In the fertilized systems, plants fixed more ¹³C and had larger

and more enriched root biomass, which can largely contribute to the ^{13}C flux by the release of more complex compounds originating from root turnover later after labelling (Kaštovská et al., 2017). The largest temporal increase in soil ^{13}C in the HW-F systems may be further supported by retarded decomposition of root-released compounds due to low oxygen availability in the water-saturated soils. Since the later released compounds are commonly of lower biodegradability (Edwards et al., 2018), they could importantly contribute to the dissolved organic C pool in soils and partly explain the highest DOC contents in the HW-F systems.

In summary, plants in differently treated systems varied in C fixation and resource allocation between root growth and exudation, which resulted in unique patterns of root ^{13}C deposition dynamics and shifted the quality of ^{13}C substrates entering the rhizosphere, which might have implications for soil C sequestration and DOC availability.

4.3. Effects of fertilization and soil water status on ^{13}C incorporation and channelling in microbial PLFA

The significant ^{13}C enrichment of microbial PLFA occurred rapidly after plant fixation, similarly as has been observed in other wetland and grassland ecosystems (Lu et al., 2004; Deneff et al., 2007; Balasooriya et al., 2014; Kaiser et al., 2015). At T0, the ^{13}C content in PLFA was ca 50% higher in the UF than F soils, corresponding to larger and faster ^{13}C exudation by unfertilized plants and the larger PLFA content in the UF soils. The comparable ^{13}C enrichment of G-, G+ and fungal markers indicate that all these microbial groups were active in the utilization of simple ^{13}C exudates in the *C. acuta* rhizosphere (Fig. 3). The G+ markers were some of the most enriched in both HW treatments, which is in agreement with another study of wetland systems (Tian et al., 2013), but contradict the results of many studies from other ecosystems (Treonis et al., 2004; Deneff et al., 2007; De Deyn et al., 2011; Balasooriya et al., 2014; Yuan et al., 2016). This discrepancy might be ascribed to the higher tolerance of G+ bacteria than G- bacteria to anaerobic conditions (Bossio and Scow, 1998) and thus their greater importance in the utilization of root-derived C in wetland soils. Both bacterial groups were especially important in exudate utilization in the HW-UF mesocosms (Fig. 4), characterized by having the largest initial ^{13}C flux into the soil among all treatments (Table 3), which differentiated the behaviour of this system from the others (Fig. 5a).

However, the situation changed during the week, when more complex ^{13}C compounds increasingly contributed to the root ^{13}C efflux. Independent of treatment combination, fungal PLFA became the most enriched among the specific markers, as also observed by Treonis et al. (2004) and Yuan et al. (2016). After a week, fungal PLFA highly exceeded the bacterial contribution to total PLFA ^{13}C incorporation in all treatments (Fig. 4). This revealed that fungi dominated the processing of ^{13}C root products deposited to the soil later during the week. During the 7 day period, the ^{13}C enrichment of fungal as well as total PLFA became higher in the F versus the UF treatments. The F systems thus differed from the UF systems by having a smaller microbial community, which was more active in processing root-released ^{13}C mainly due to fungal ^{13}C utilization. The role of fungi in the processing of root-released ^{13}C in F systems was even more important than in the UF systems. This was likely related to the larger and faster growing root biomass in the F vs UF systems, resulting in a different quality of root-derived compounds entering the soils and also with the proposed higher ability of fungi compared to bacteria in utilizing more complex C substrates (Strickland and Rousk, 2010). Likewise, we found that fungal ^{13}C enrichment was closely related with the inputs of root-derived ^{13}C to the soil between days 1 and 7. Therefore, the fungal role in processing of root derived ^{13}C was most important in HW-F systems while it was least important in HW-UF systems, where the largest portion of root ^{13}C was deposited as exudates and the lowest as later root-released ^{13}C (Table 3). This favoured bacteria and resulted in low F/B ratios (Table 1). The relative proliferation of bacteria compared to fungi in

HW-UF systems together with their low efficiency in nutrient mining from SOM (Strickland and Rousk, 2010) thus may explain the lowest N availability in the HW-UF systems compared to other treatments (Table S1).

As the fungal contribution to the processing of root-derived ^{13}C increased, the final amount of ^{13}C found in the soil was greater while a smaller proportion of soil ^{13}C was finally found in microbial PLFAs (Table 3, Fig. 5). This showed that other forms of ^{13}C compounds than phospholipids accumulated in the soil. This might indicate that i) fungi and bacteria allocated the acquired ^{13}C during biomass synthesis differently and/or ii) that a fungal-dominated pathway of rhizodeposition processing mediated incorporation of root-derived C into SOM (Simpson et al., 2004; Six et al., 2006; Fontaine et al., 2011; Kögel-Knabner, 2017).

Contrary to our hypotheses, we did not find any negative effects of long-term soil water saturation either on microbial biomass or microbial and, specifically, fungal ^{13}C processing. Likely explanations for this lack of an effect is the well-developed ability of *C. acuta* to transport oxygen to its rhizosphere (Visser et al., 2000; Colmer, 2003) and adaptation of the microbial community including fungi to these conditions. Similarly, although fertilization reduced microbial biomass, we did not observe any negative effect of fertilization on fungal ^{13}C processing but rather increased fungal activity. We can demonstrate this in the HW-F mesocosms, characterized by a large input of ^{13}C rhizodeposits, which were efficiently processed by the small but active fungal-dominated community and accumulated in the soil in larger amounts in comparison to other systems.

5. Conclusions

Fertilization and soil water regime interacted in their effects on the performance of the plant-soil system, controlling productivity of the system, the input and quality of rhizodeposits and their processing by various groups within the microbial community. We found differences in the dynamics of ^{13}C rhizodeposition and its processing by fungi and bacteria between fertilized and unfertilized systems. The fertilized plants deposited to the soil relatively less exudates, but larger amounts of more complex rhizodeposits, than unfertilized plants with these being mainly processed by fungi. The differences in system functioning were most pronounced in fertilized vs unfertilized systems under high water level. Together, these results showed complex environmental control over C inputs and sequestration processes in the experimental mesocosms. In this regard, our study points to the weaknesses of studies examining the effects of single environmental variables. In summary, we demonstrated that fungi play a crucial role in the processing of rhizodeposited C in wetland systems dominated by a common sedge *C. acuta* independent of soil water level and that the fungal importance in C transformation increases in fertilized systems in relation with increasing root biomass and input of more complex rhizodeposits. The enhanced fungal activity might increase the potential for stabilization of recently assimilated C in the soils of fertilized oligotrophic sedge grasslands with *C. acuta*.

Conflicts of interest

None.

Acknowledgements

This study was supported by the Czech Science Foundation (GACR, project 16-21743S) and by the Ministry of Education, Youth and Sports of the Czech Republic (MEYS; projects LM2015075, EF16_013/0001782 – SoWa Ecosystems Research). The analytical instrumentation used for stable isotope determination was purchased from the Operational Programme Prague - Competitiveness (Project CZ.2.16/3.1.00/21516). Institutional funding for K.J. was provided by the Center for Geosphere

Dynamics (UNCE/SCI/006).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.03.031>.

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