**Hydrology and
Earth System
Sciences
Discussions**

Heterogeneity of soil carbon pools and fluxes in a channelized and a restored floodplain section (Thur River, Switzerland)

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and fluxes in Thur
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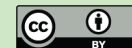Conclusions | References

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Abstract

Due to their spatial complexity and dynamic nature, floodplains provide a wide range of ecosystem functions. However, because of flow regulation, many riverine floodplains have lost their characteristic heterogeneity. Restoration of floodplain habitats and the rehabilitation of key ecosystem functions has therefore become a major goal of environmental policy. Many important ecosystem functions are linked to organic carbon (C) dynamics in riparian soils. The fundamental understanding of the factors that drive the processes involved in C cycling in heterogeneous and dynamic systems such as floodplains is however only fragmentary.

We quantified soil organic C pools (microbial C and water extractable organic C) and fluxes (soil respiration and net methane production) in functional process zones of adjacent channelized and widened sections of the Thur River, NE Switzerland, on a seasonal basis. The objective was to assess how spatial heterogeneity and temporal variability of these pools and fluxes relate to physicochemical soil properties on one hand, and to soil environmental conditions and flood disturbance on the other hand.

Overall, factors related to seasonality and flooding (temperature, water content, organic matter input) affected soil C dynamics more than soil properties did. Coarse-textured soils on gravel bars in the restored section were characterized by low base-levels of organic C pools due to low TOC contents. However, frequent disturbance by flood pulses led to high heterogeneity with temporarily and locally increased pools and soil respiration. By contrast, in stable riparian forests, the finer texture of the soils and corresponding higher TOC contents and water retention capacity led to high base-levels of C pools. Spatial heterogeneity was low, but major floods and seasonal differences in temperature had additional impacts on both pools and fluxes. Soil properties and base levels of C pools in the dam foreland of the channelized section were similar to the gravel bars of the restored section. By contrast, spatial heterogeneity, seasonal effects and flood disturbance were similar to the forests, except for indications of high CH_4 production that are explained by long travel times of infiltrating water favouring

reducing conditions. Overall, the restored section exhibited both a larger range and a higher heterogeneity of organic C pools and fluxes as well as a higher plant biodiversity than the channelized section. This suggests that restoration has indeed led to an increase in functional diversity.

1   Introduction

Embracing spatial heterogeneity is a major challenge in ecosystem ecology. The composition, spatial configuration and temporal dynamics of habitat patches determine biodiversity and ecosystem processes. Ecosystems therefore need to be considered as dynamically interacting mosaics rather than homogeneous entities. Floodplains are an ideal model to study spatial and temporal heterogeneity.

Floodplains are defined as low-relief areas that extend from the edge of permanent water bodies to the edge of uplands and are subject to flooding. In their natural state, the interaction between flood dynamics and geomorphic processes create a shifting mosaic of habitat patches (Naiman and Décamps, 1997; Stanford et al. 2005). These hydrogeomorphically distinct patches differ in age, inundation regime, and soil properties, thereby expressing a different productivity, system metabolism, organic matter dynamic, and biotic community composition. These patches can be referred to as "Functional Process Zones" (FPZs) (Thorp et al., 2006). In dynamic floodplains, and on a smaller than catchment scale, the various FPZs are arranged along distinct succession gradients (Naiman and Décamps, 1997), from recently deposited sand or gravel to mature alluvial forests.

Due to their spatial complexity and dynamic nature, floodplains provide a wide range of ecosystem functions and related services. Because flow alteration is one of the most serious threats to ecological integrity of river-floodplain systems (Tockner et al., 2008), the widespread regulation of the flow regime of large rivers, in particular in Europe and North America has led to the loss of characteristic environmental heterogeneity, biodiversity and associated ecosystem services in many floodplains (Tockner and Stanford,

2002). In the last decades, restoration of floodplain habitats and the rehabilitation of key ecosystem functions has become a major goal of environmental policy, and concurrently scientific approaches to evaluate its success have been put forward (Henry et al., 2002; Palmer et al., 2005; Woolsey et al. 2007). Motivated to a large extent by flood protection, restoration is achieved, e.g., by widening the main river channel through the removal of the embankments and by the setback of the flood levees (Rohde et al., 2005; van Stokkom et al., 2005).

Ecosystem services such as provision of plant and animal resources, removal and/or degradation of pollutants, nutrient retention, and carbon (C) storage are tightly linked to organic C dynamics in riparian soils. Although the need for a fundamental understanding of the factors that drive the processes involved in C cycling in heterogeneous and dynamic systems such as floodplains is recognized, knowledge is however still fragmentary (Pacific et al., 2008; Zehetner et al., 2009). There has been an increasing number of publications in recent years on abundance and community structure of microorganisms in riparian soils (e.g., Rinklebe and Langer, 2006; Unger et al., 2009), but still little information is available on bioavailable and mobile soil organic carbon (Bishop et al., 1994; Hill and Cardaci, 2004). The heterogeneity of soil-atmosphere exchange of CO_2 and methane has been addressed previously (e.g., Pulliam 1993; Gulledge and Schimel, 2000; Pacific et al. 2008). However, combined studies addressing both "active" carbon pools and gas exchange as proxies of different aspects of soil functionality have been rare.

In this study we quantify C dynamics in adjacent channelized and widened sections of the Thur River, NE Switzerland. This is the main test site of the interdisciplinary project RECORD (http://www.cces.ethz.ch/projects/nature/Record; Linde et al., 2011; Pasquale et al., 2011). The site is composed of three different types of FPZs: (i) frequently flooded, *dynamic* patches in the restored section, (ii) mature, *stable* alluvial forests that are flooded once or twice a year in the restored section, and (iii) geomorphologically homogeneous pasture in the channelized section. The objective was to assess spatial heterogeneity (among and within FPZs) and temporal variability of

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selected soil organic C pools (microbial C and water extractable organic C) and fluxes (soil respiration and methane fluxes) and how they relate to physicochemical soil properties on one hand, and to soil environmental conditions and flood disturbance on the other hand. Our motivation was to better understand C dynamics in the different types of floodplain FPZs, and, as a consequence, how differences in floodplain structure, in particular between regulated and restored river sections, may affect related ecosystem services.

2 Test site

The Thur River (catchment area: 1700 km^2) originates in the limestone formation of the Mount Säntis region (2500 m a.s.l.), crosses the Swiss Plateau, and enters the Rhine River at 345 m a.s.l. The river exhibits a flashy flow regime due to the absence of reservoirs and natural lakes. Maximum, mean, and minimum flow rates are 1130, 50, and 2 m^3 s^{-1}, respectively (recording period 1904–2005: http://www.hydrodaten.admin.ch/d/2044.htm). Flood events occur mainly during the snowmelt period in spring, and heavy rainfall events in summer and autumn. The formerly braided river was channelized in the 1890s to protect the river valley against flooding. In the 1970s, a plan to concurrently improve the flood protection and ameliorate the ecological state of the river corridor was elaborated. Since 1993, several 1–3 km long river sections were widened to allow the formation of alternating gravel bars and to increase hydrological connectivity between the main channel and its riparian zone. One of these sections is the test site. Basic data on the chemical quality of the Thur River and the adjacent alluvial aquifers can be found in Hoehn and Scholtis (2011).

The test site is located in the river corridor at Niederneunforn (Canton Thurgau, 8°77′12″ E; 47°59′10″ N), where a 2 km long section was restored in 2002. The main channel was widened from 50 m to 110 m by removing the foreland in front of the levees. In addition, the levees were lowered in some places to reconnect the old alluvial forest with the river during high floods. The newly exposed banks were partly enforced

by tree trunks, and additionally by planting a strip of willow saplings. In the widened river channel, discharge fluctuations and sedimentation have led to the evolution of a dynamic succession of gravel bars. At the test site, this morphodynamic has been monitored using innovative methodology (Pasquale et al., 2011), and the subsurface
5 structure of the gravel bars was characterized with the help of geophysical methods (Linde et al., 2011). The mean annual precipitation at the test site is 908 mm and the average monthly temperature ranges from 0.9 °C in January to 19.0 °C in July (study period; http://gate.meteoswiss.ch/idaweb).

Six FPZs were identified based on vegetation, distance to the river and topography
10 (Fig. 1): five in the restored section and one in an adjacent channelized section upstream. As a result of their topographic position, these FPZs are exposed to different flooding frequencies (Fig. 2). Starting from the riverbed, the first FPZ (GRAVEL) is a mosaic of bare gravel and patchy vegetation covering on average 33% of the ground. It is frequently inundated and has very little fine soil. The second FPZ (GRASS) is
15 gravel covered by up to 1 m of fine sediments that were trapped mainly by the dominant grass *Phalaris arundinacea*. The third FPZ (WILLOW BUSH) comprises the banks composed of older sediments with shrubby vegetation dominated by planted *Salix viminalis*. Other willow species were also present, and the relatively dense understory was dominated by *Rubus* sp. and various grass species. This strip varies in width from 5
20 to 10 m, and the study plots were selected in the middle of the bank slope. The fourth FPZ (MIXED FOREST) is the alluvial forest dominated by *Acer pseudoplatanus* and *Fraxinus excelsior*. The understory was dominated by *Allium ursinum* and *Ranunculus ficaria* in spring and *Carex pendula* and *Rubus* sp. later in the year. The North side of this FPZ is bordered by a side channel that drains the neighbouring agricultural hill
25 slope. The WILLOW FOREST FPZ at the downstream end of the restored section is an un-managed riparian forest dominated by mature *Salix alba* trees. The understory was dominated by *R. ficaria* in spring, and by very dense and monospecific patches of *Urtica dioica* later in the year. The northern border of this part of the forest is formed by an old side channel that has partly silted up, but still drains the hill slope and collects

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back flow water from River Thur. The PASTURE FPZ lies in the channelized section and is used by farmers for grazing and grass fodder production. The plant community was typical of managed grasslands and dominated by grass species (mainly *Elymus repens*, *Dactylis glomerata*, and *Arrhenatherum elatius*) and forbs such as *Taraxacum officinale* and *Trifolium repens*.

In this study, we have considered the first three FPZs in the restored section as "dynamic" FPZs, and the two forest FPZs as "stable" FPZs. In each FPZ, four plots of eight-meter diameter were selected. The upstream half-circle was used for vegetation mapping and gas sampling while the downstream half-circle was used for destructive soil sampling.

3 Methods

3.1 Vegetation

In each plot, all vascular plant species were recorded, and cover was estimated using Braun-Blanquet codes (Braun-Blanquet, 1964). Observations were repeated six times during the growing season 2008 and species richness was calculated from the combined data set.

3.2 Soil sampling

Topsoil samplings were carried out in April and October 2008, and in January, April and August 2009. The first sampling served to obtain basic background information on physicochemical soil properties, while the other four samplings were used for detailed measurements of C pools and fluxes. In each plot, three cores (6.5 cm diameter × 10 cm depth) were pooled. In GRAVEL plots, soil was collected in pits. One half of the field moist soil was sieved (2 mm) and stored at 4 °C while the other half was dried (40 °C, 48 h) and then sieved at 2 mm. In May 2008, two 1 m long soil cores were

taken with a drill corer from two plots of each FPZ except GRAVEL where coarse gravel prevented the use of the equipment. Each core was split into 20 cm long segments, and the samples were dried and sieved as described before.

3.3 Basic soil properties

Soil texture of dried samples was measured using the pipette method (Gee and Brauder, 1986) after removing organic matter with H_2O_2 and dispersing with sodium hexametaphosphate. Grain size classes were defined as clay ($<2\,\mu m$), silt (2–$63\,\mu m$) and sand ($63\,\mu m$–$2\,mm$). Soil pH was measured in a 1:2 slurry of dried soil in 0.01 M $CaCl_2$ after 30 min equilibration. Total N and organic and inorganic C contents of finely ground, dried soils were determined as described by Walthert et al. (2010). For Olsen P as a proxy of available P, dried soil was extracted for 30 min at 25 °C with 0.5 M sodium hydrogen carbonate at pH 8.5 with a soil to extractant ratio of 1:20. The extracts were filtered through Schleicher & Schuell 0790½ and the extracted phosphate measured colorimetrically using the molybdenum blue method (Kuo, 1996).

3.4 Soil environmental conditions

Soil temperature (T) at 5 cm depth was measured in the centre of each plot during the entire observation period (30 min resolution; TidBit v2 temperature loggers, onset, Bourne, MA, USA). The temperatures recorded at the time of the soil samplings were used in this study. Gravimetric Water Content (WC) was determined as weight loss upon drying 20 g of fresh soil at 105 °C for 24 h. Days since last inundation (LI) was estimated using elevation and position of the FPZ and the river discharge (Fig. 2).

3.5 Carbon pools

Water extractable organic carbon (WEOC) was extracted from dried soils with 10 mM $CaCl_2$ at a soil:extractant ratio of 1:2 for 10 min on an end-over-end shaker (Embacher

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et al., 2007). The soil slurries were then centrifuged for 10 min at 1335 g and filtered through a 0.45 µm membrane filter. The filtered extracts were measured for non-purgeable organic C (NPOC) using a TOC analyzer (Formacs HT, Skalar Analytical, Breda, The Netherlands). Water extractable organic matter of soils, measured
5 as WEOC, is an operationally defined proxy of dissolved organic matter in the soil solution, playing important roles as substrate of microorganisms and as transport agent (Embacher et al., 2007). Although WEOC also represents part of the microbial biomass when extracted from dried soils as in the present study (Embacher et al., 2007), we consider this pool mainly as proxy of available substrate.
10 Microbial biomass C (MC) was determined by the chloroform fumigation extraction method (Beck et al., 1997). Fresh soil samples corresponding to 10 g dry mass were placed in a desiccator containing chloroform. The desiccator was evacuated and left in the dark for 24 h. These fumigated soil samples and another set of fresh soil samples were extracted for one hour with 0.5 M K_2SO_4 at a 1:5 soil to extractant ratio. The
15 extracts were filtered (0.45 µm) and frozen. The NPOC in these samples was measured using a TOC analyzer (TOC-V CPH/CPN, Shimadzu, Kyoto, Japan). Microbial C was calculated as

$$MC = \frac{(C_{fumigated} - C_{unfumigated})}{k_{EC}} \tag{1}$$

where $C_{fumigated}$ and $C_{unfumigated}$ are the NPOC contents of $CHCl_3$-fumigated and unfu-
20 migated samples, and $k_{EC} = 0.45$ corrects for extraction efficiency (Beck et al., 1997).

3.6 Carbon fluxes

For soil respiration (SR) and methane flux (MF) measurements, PVC rings with 30 cm diameter and 30 cm height (20 cm below and 10 cm above surface) were installed in each plot. Immediately before sampling, vegetation within the rings was clipped and
25 the chamber closed with an air-tight lid. Headspace air samples were collected after 5, 25 and 45 min, injected into a pre-evacuated exetainers, and analyzed for CH_4 and CO_2

using a gas chromatograph with a flame ionization detector (Agilent 6890, Santa Clara, USA). Soil-atmosphere CH_4 and CO_2 exchange were calculated by linear regression of concentration against sampling time. Temperature dependence of SR was modeled for each FPZ using an exponential equation (Buchmann, 2000)

$$y = a \cdot e^{(b \cdot T)} \tag{2}$$

where a and b are regression coefficients, and T is the temperature at the time of gas sampling. Q_{10} values were calculated as

$$Q_{10} = e^{(10 \cdot b)} \tag{3}$$

Soil respiration normalised to a reference temperature of 10 °C (SR_T10) was calculated according to Döring (2007) as

$$SR\_T10 = SR \cdot e^{(b(10-T))} \tag{4}$$

Soil respiration is an indicator of the actual biological activity at the sampling site including both microbial and root respiration. Positive methane flux indicates net methane production while negative flux indicates net methane consumption in the soil.

3.7 Statistical analyses

Differences in the soil physicochemical properties among the sites were tested using one–way analysis of variance (ANOVA, SPSS 17, SPSS Inc.). Interactive effects of time and FPZ were tested by one-way repeated measures ANOVA. Post hoc tests were carried out using Tukey HSD if homogeneity of variance could be assumed or else using Games Howell (Field, 2005). Principal component analysis (PCA) was carried out for soil physicochemical properties measured in the soil profile samples. Redundancy analyses (RDA) were carried out for C pools and fluxes as multivariate response to soil properties and environmental conditions. The RDA triplot was projected using scaling method 2 (Kindt and Coe, 2006). The program R (R Development Core Team, 2010) with package vegan (Oksanen et al., 2010) was used for PCA and RDA.

4 Results

4.1 Vegetation

Mean plant species richness was lowest in GRASS and WILLOW FOREST, and highest in WILLOW BUSH (Table 1). Spatial variability was higher in GRAVEL and GRASS than in the other FPZs (Table 2). A principal component analysis of plant species composition and cover revealed that the vegetation in PASTURE and in both forested FPZs was rather similar, while it exhibited completely different characteristics in the three dynamic FPZs (data not shown).

4.2 Basic soil properties

All soils were rich in carbonates and, accordingly, had a pH of about 7.5 (Table 1). In the restored section, soils became more finely textured along a gradient from GRAVEL to WILLOW FOREST. Total organic carbon (TOC) and total nitrogen (TN) contents increased along the same gradient, while the C/N was around 15 in all FPZs. Available P was significantly higher in GRASS than in WILLOW BUSH and MIXED FOREST. Soil properties of PASTURE were similar to GRASS except for a significantly lower available P content. Spatial variability of texture and TOC content were highest in GRAVEL and GRASS, and lowest in the two forest FPZs (Table 2).

Soil texture did not vary much with depth in any of the FPZs (data not shown). TOC and TN contents were also homogenously distributed within the soil profiles except for WILLOW FOREST. There, TOC and TN decreased with depth to $15\,\mathrm{g\,C\,kg^{-1}}$ and $1.1\,\mathrm{g\,N\,kg^{-1}}$ respectively. Available P decreased gradually with depth to $7\,\mathrm{mg\,kg^{-1}}$ in WILLOW FOREST, and to about $5\,\mathrm{mg\,kg^{-1}}$ in mixed forest and WILLOW BUSH. In GRASS available P did not vary with depth and in PASTURE it first decreased to less than $5\,\mathrm{mg\,kg^{-1}}$ at 20–40 cm depth and then increased to $12\,\mathrm{mg\,kg^{-1}}$ at 80–100 cm depth. The PCA (Fig. 3) showed soil texture as the main factor separating the different FPZs, and demonstrated a generally larger lateral than vertical variation of the soil

properties. It also showed PASTURE soils were relatively homogeneous and overall most similar to the soil in WILLOW BUSH.

According to the world reference base for soil resources (IUSS Working Group WRB, 2006) the soils in GRASS, WILLOW BUSH, mixed forest, and PASTURE can be classi-
5 fied as haplic Fluvisols (calcaric, humic), those in WILLOW FOREST as haplic or gleyic Fluvisols (calcaric, humic, siltic).

4.3 Soil environmental conditions

Temperature measured in GRAVEL was significantly different from all other FPZs at all seasons (Table 3). At each sampling date, either the lowest or highest temper-
10 atures were measured there, including the extremes ($-0.7\,^\circ$C, and $20.2\,^\circ$C). Overall, there was no significant difference in T among the FPZ, but in August all non-forested FPZs exhibited distinctly higher temperatures than the forested FPZs. Willow forest and GRAVEL represented the wettest and driest conditions, respectively. The spatial variability of soil moisture was highest in GRAVEL and GRASS (Table 2). Particularly
15 high WCs were measured in August sampling, which was carried out two weeks after a major flood (see LI in Table 3), and in January when the soils were covered by snow and partially frozen.

4.4 Carbon pools

On average, the WEOC contents increased from GRAVEL to willow forest, and PAS-
20 TURE exhibited low WEOC contents (Table 3). WEOC was significantly higher ($P < 0.05$) in August, and lower in April, compared to other samplings. Spatial variability of WEOC was largest in GRAVEL and GRASS (Table 2), with particularly high variability in GRASS in April and August.

Microbial C was higher in WILLOW FOREST than in other FPZs (Table 3). In Oc-
25 tober, MC contents were significantly lower than at the other samplings ($P < 0.05$) and
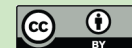
highly variable. With the exception of PASTURE, spatial variability of MC was large (Table 2).

4.5 Carbon fluxes

Soil respiration (SR and SR_T10) was lowest in GRAVEL and highest in GRASS and WILLOW BUSH at most of the samplings, however differences were statistically not significant (Table 3). Within-patch variability of SR was generally high in all dynamic FPZs (Table 2) with hot spots in GRASS in April and August and in WILLOW BUSH in October and August. While SR values were lowest in January and highest in August, SR_T10 values varied only little with time. The Q_{10} value was highest for GRAVEL, while it was similar for all other FPZs (Table 4).

All FPZs took up methane except for August. Then uptake was observed only for WILLOW BUSH and mixed forest, while the other FPZs emitted methane into the atmosphere. At all samplings, plots in GRAVEL showed very low uptake or even low emissions, while mixed forest exhibited the highest uptake rates of all FPZs.

4.6 Carbon pools and fluxes as multivariate proxy of soil C dynamics

Carbon dynamics are presented as multivariate response comprising C pools (WEOC, MC) and fluxes (SR MF), explained by soil properties and environmental conditions (LI, T, WC, TOC, clay). Data were clearly distributed according to sampling date (Fig. 4). The model explained 38.0% (adjusted R^2) of the variance of the response dataset and the two first canonical axes were significant ($P = 0.001$, 1000 permutations). Overall, WC and T explained the main gradient of C pools and fluxes along axis 1, which separates samples of August from all others. Soil respiration was positively correlated with T and negatively correlated with the number of days since the last inundation. WEOC correlated mainly with WC, whereas MC was strongly linked with clay and TOC content.

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Our data allow (i) to relate differences between soil C dynamics in different functional process zones (FPZs) of the Thur River floodplain to differences in physicochemical soil properties on one hand, and to effects of flood disturbance on the other hand, (ii) to evaluate the relative magnitude of temporal variability as well as among and within-FPZ spatial heterogeneity of C dynamics. Based on this, conclusions about the effects of river restoration on C dynamics can be drawn.

5.1 Soil properties, environmental conditions and degree of disturbance in different FPZs

With their high carbonate content the soils at our test site are representative of young, weakly developed alluvial soils (Guenat et al., 1999). The mostly homogeneous distribution of soil properties with depth and the strong correlation between TOC and TN contents and soil texture indicates soil formation by fluvial sedimentation of homogeneous source material (Cabezas and Comin, 2010). Further homogenization can be attributed to bioturbation by earthworms. This was especially clear in the forested FPZs where earthworm biomass was maximum (Fournier et al., unpublished data), most likely because of the lower frequency of inundation and fluvial dynamics (Guenat et al., 1999). On the other hand, the depth gradient of TOC and TN in WILLOW FOREST, representing an advanced stable FPZ, indicates in-situ pedogenesis. Soil texture, the main factor differentiating the FPZs according to the PCA (Fig. 3), reflects the average sedimentation conditions with texture becoming finer with decreasing stream energy (Nanson and Croke, 1992). The TOC contents are within the range found in floodplain sediments of other large rivers in Europe (Graf et al., 2007; Pies et al., 2007). The low C/N ratios and high available P contents (Morel et al., 1992) indicate high nutrient availability in all FPZs, which is characteristic of many river floodplains (Tockner and Stanford, 2002). The particularly high P availability in GRASS can be explained by high sedimentation rates (Steiger and Gurnell, 2003). Low C/N values also indicate

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favourable conditions for organic matter degradation, which is confirmed by the observation of fast mineralisation of leaf litter in most FPZs and by the humus morphology (carbonate-rich Mull; data not shown).

The high variability and extreme values of T measured in GRAVEL are consistent with the general finding of bare gravel bars as extreme environments. The absence of stable vegetation cover to buffer temperature variations accompanied by high thermal conductivity due to low water contents explain this harshness (Tonolla et al., 2010). The differences in WC among FPZs can be explained mainly by a combined effect of precipitation, inundation frequency and water retention capacity of the soils. In particular, the maximum WC in WILLOW FOREST can be attributed largely to the finely textured soil that retains water efficiently. The additional effects of shading and water uptake by the plants on WC via evapotranspiration are not obvious from the data.

Considering the days after the last inundation (LI), the samplings carried out over the course of this study represent conditions that are typical for this site (Fig. 2), i.e. inundation of the low-lying dynamic FPZs on a regular basis, and flooding of the entire floodplain once or twice a year. The high spatial heterogeneity of physicochemical soil properties, environmental conditions, and plant species richness in GRAVEL and GRASS (Table 2) reflects the patchy and dynamic geomorphology due to the frequent disturbance by flooding, while the low variability in the forested FPZs can be related to stable conditions leading to homogenization of properties, conditions and communities. The low variability in PASTURE can in addition be explained by its particularly homogeneous geomorphology strongly reducing erosion and sediment deposition. In agreement with the hypothesis of maximum biodiversity at intermediate levels of disturbance or connectivity (Ward et al., 1999), the pattern of plant species richness in the restored section FPZs reflects the degree of disturbance. This hypothesis predicts highest species richness in habitats characterised by intermediate inundation frequency (i.e. WILLOW BUSH), and lower diversity under high and low degrees of disturbance (i.e., GRASS and the two forested FPZs, respectively) where competitive species dominate (in particular *Phalaris arundinacea* as flood tolerant species in

GRASS, Foster and Wetzel, 2005). Considering the low inundation frequency, the relatively high species richness observed in PASTURE can be explained mainly by the regular harvesting, that reduces the effect of competition.

5.2 Carbon pools and fluxes as related to soil properties, environmental conditions and disturbance in different FPZs

The strong correlation between MC and TOC suggests C-limitation of microbes, which is especially common in nutrient rich soils (Wardle, 1992). The pattern of WEOC suggests an influence of both TOC and WC. The correlation with TOC indicates similar solubility of soil organic matter across FPZs. The influence of WC is mainly a flooding effect as demonstrated by the highest WEOC contents in August after the major flood. On one hand, this pattern suggests temporally increased soluble C pools due to input of non-structured fine soil and fresh litter along with the decreased aeration in the waterlogged soils. During soil saturation, dissolved organic matter production is expected to increase (Kalbitz, 2000). On the other hand, flooding has also been shown to increase the rates of enzymatic soil organic matter degradation (Wilson et al., 2010). The flood-related increase in available C is also reflected by increased MC, except in WILLOW FOREST where the almost completely saturated soil suggests longer unfavourable conditions for microbial growth (Rinklebe and Langer, 2006; Unger et al., 2009).

The measured range of SR, which includes root and microbial respiration, was similar to results from other floodplains (Pulliam, 1993; Gulledge and Schimel, 2000; Döring, 2007; Pacific et al., 2008). The strong correlation of SR with T has been commonly observed (Lloyd and Taylor, 1994; Buchmann, 2000) and explains the differences between the samplings to a large extent. The temperature dependence in terms of Q_{10} values in most FPZs is similar to riparian and uphill forests (Buchmann, 2000; Döring, 2007), while the Q_{10} value of GRAVEL is much higher than in similar systems (Döring, 2007). According to Pacific et al. (2008) soil CO_2 efflux is determined

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both by CO_2 production and diffusive transport in the entire soil, and soil moisture levels observed in our study would support high respiration in all FPZs most of the time. Considering this, the often highest CO_2 efflux in GRASS and WILLOW BUSH can be explained on one hand by the coarse soil texture allowing optimal gas diffusion,

5   on the other hand by the frequent and large input of available organic C during flooding (Döring, 2007). In addition, the sediment translocations during high floods may increase the content of available organic C also at greater depths. Together with the high spatial variability in sedimentation, this can explain the hot spots of SR observed in these two FPZs. The low SR in GRAVEL is likely due to the low content of fine soil.

10   Consumption of atmospheric methane is largely determined by CH_4 diffusion in the soil (Dörr et al., 1993), and CH_4 produced in water saturated soil layers can be consumed in upper aerated soil layers (Boon and Lee, 1997). Net CH_4 production can therefore be considered as an indicator of the balance between overall soil aeration and underlying CH_4 production. The observed decrease of net CH_4 production along

15   the elevation gradient from GRAVEL to mixed forest is in line with increasing aeration with increasing average thickness of unsaturated soil, and confirms earlier studies showing a strong influence of landscape position on CH_4 consumption (Burke et al., 1999; Gulledge and Schimel, 2000). This interpretation is supported by an increase in earthworm diversity (Fournier et al., unpublished data). In WILLOW FOREST, net

20   CH_4 production was higher than expected at that elevation, which suggests a relatively weak aeration, confirmed by hydromorphic features in upper soil layers (data not shown) and/or high CH_4 production. These evidences are both congruent with the maximum WC and finest soil texture found in this FPZ (Dörr et al., 1993). The high net CH_4 production in the relatively high laying PASTURE, characterized by a sandy

25   soil texture, suggests generally high CH_4 production in the water-saturated layers of this FPZ. This can be explained by the relatively long travel time of infiltrating water in the channelized section of the river (Vogt et al., 2010), favouring reducing conditions in deeper soil layers.

In summary, microbial and available C pools are determined mainly by physicochemical soil properties with some additional effects of flooding via WC. By contrast, C fluxes are strongly influenced by flood disturbance, and either T (SR) or geomorphology (net CH_4 consumption).

5.3 Temporal variability and within-FPZ heterogeneity of soil C pools and fluxes

Carbon pools and fluxes as multivariate proxy of soil C dynamics differed more among sampling dates than among FPZs. This indicates that overall factors related to seasonality and flooding (T, WC, and organic matter input) influence soil C dynamics more than differences in soil physicochemical properties in the test site.

The high spatial heterogeneity of all C pools and fluxes within GRAVEL and GRASS can be related to the variability in both soil properties and environmental conditions caused by frequent flooding disturbance. The high variability of MC in all FPZs of the restored section cannot be explained exclusively by the large-scale variability between replicate plots but might in addition be due to small-scale variability at the soil aggregate level as well as to additional heterogeneity brought by the rooting pattern and related exudation of plants. Similarly, it can be speculated that hot spots of CO_2 and CH_4 emissions in otherwise homogeneous FPZs (WILLOW BUSH, PASTURE) are due to small-scale heterogeneities in substrate availability and water saturation in the subsoil (Ramakrishnan et al., 2000; Sey et al., 2008).

6 Conclusions

A study of organic C dynamics in the Thur River floodplain revealed that in the dynamic FPZs of the restored section characterised by low TOC contents and coarse-textured soils, frequent disturbance by flood pulses temporarily and locally increased SR and the otherwise low base-levels of organic C pools. By contrast, in the stable forested FPZs, the finer texture of the soils was responsible for higher TOC contents and water

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retention capacity both leading to high base-levels of C pools. Spatial heterogeneity was smaller than the effects of major floods and seasonal T differences on C pools and fluxes. The PASTURE FPZ stood out by (i) low C pools due to coarse-textured soils low in TOC, as in the dynamic FPZs, (ii) spatial heterogeneity, seasonal effects and flood disturbance, similar to the forest FPZs, and (iii) high CH_4 production that can be explained by slow travel times favouring reducing conditions.

Our results show that (i) the large range of soil properties and flooding frequencies from GRAVEL to WILLOW FOREST, and (ii) the high spatial heterogeneity of soil properties and environmental conditions in the dynamic FPZs, increased the spatial and temporal variability of organic C pool and fluxes in the restored section of the Thur River floodplain as compared to the channelized section. Together with the much higher plant biodiversity in the restored section, this suggests that restoration has led to a strong increase in functional diversity. Our results therefore support recent findings that short-term inundations are important drivers of microbial habitat structure and function in floodplains (Wilson et al., 2010). Further comprehensive studies in similar as well as contrasted sites are required for generalisation of the results. In particular, studies in sites with carbonate-free fluvial source material would be interesting, because soil organic matter turnover differs between acidic and carbonate-containing soils (Walse et al., 1998).

Based on our results, we recommend that river restoration, in order to achieve maximum recovery of ecosystem functions, should aim at creating near-natural floodplains comprising both dynamic gravel bars and stable alluvial systems.

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Table 1. Mean ± standard deviation of vegetation characteristics and physicochemical soil properties in the six functional process zones ($n = 4$) of the test site in the Thur River floodplain, Switzerland. Soil properties are for the top 10 cm of soil. Values with different superscript letters in the same row are significantly different ($P < 0.05$; Tukey post-hoc test).

	Units	GRAVEL	GRASS	WILLOW BUSH	MIXED forest	WILLOW FOREST	PASTURE
Species richness		55.0 ± 13.6^{bc}	41.5 ± 11.2^{c}	79.8 ± 8.8^{a}	50.8 ± 4.5^{bc}	41.5 ± 3.1^{c}	67.7 ± 3.5^{ab}
pH		7.6 ± 0.1^{a}	7.4 ± 0.1^{a}	7.5 ± 0.0^{a}	7.5 ± 0.0^{a}	7.4 ± 0.0^{a}	7.5 ± 0.0^{a}
Sand	$g\,kg^{-1}$	806 ± 52^{a}	660 ± 17^{abc}	442 ± 90^{bc}	378 ± 57^{c}	245 ± 40^{c}	651 ± 69^{ab}
Clay	$g\,kg^{-1}$	53 ± 13^{d}	83 ± 36^{bcd}	117 ± 18^{abc}	148 ± 18^{ab}	177 ± 24^{a}	78 ± 16^{cd}
Inorganic C	$g\,CaCO_3\,kg^{-1}$	355 ± 25^{b}	385 ± 18^{ab}	408 ± 5^{a}	390 ± 6^{a}	390 ± 3^{a}	382 ± 7^{ab}
Organic C	$g\,kg^{-1}$	10.1 ± 3.7^{c}	16.3 ± 5.8^{bc}	17.1 ± 3.2^{abc}	21.4 ± 3.6^{ab}	24.8 ± 1.5^{a}	12.9 ± 2.9^{bc}
Total N	$g\,kg^{-1}$	0.7 ± 0.2^{c}	1.0 ± 0.4^{bc}	1.1 ± 0.3^{bc}	1.6 ± 0.3^{ab}	1.8 ± 0.1^{a}	0.9 ± 0.2^{c}
C:N	$g\,g^{-1}$	15.2 ± 0.5^{ab}	16.2 ± 1.6^{a}	15.2 ± 0.7^{ab}	13.4 ± 0.6^{b}	14.0 ± 0.2^{b}	14.0 ± 0.4^{b}
Available P	$mg\,kg^{-1}$	24.6 ± 11.1^{ab}	35.9 ± 10.1^{a}	16.7 ± 5.5^{b}	14.2 ± 4.5^{b}	22.3 ± 7.6^{ab}	8.3 ± 4.5^{b}

Table 2. Coefficients of variation (CV) for species richness and soil properties (clay content Clay, total organic carbon TOC) within different functional process zones (FPZs) of the test site in the Thur River floodplain, Switzerland ($n = 4$); mean CV for soil environmental conditions (temperature T, gravimetric water content WC), carbon pools (water extractable organic carbon WEOC, microbial carbon MC) and soil respiration (SR as measured, SR_T10 normalised to reference T of 10 °C) within different FPZs ($n = 4$) at the different sampling times ($n = 4$).

	GRAVEL	GRASS	WILLOW BUSH	MIXED FOREST	WILLOW FOREST	PASTURE
Species richness	0.25	0.27	0.11	0.09	0.07	0.05
Clay	0.23	0.43	0.16	0.12	0.14	0.20
TOC	0.37	0.35	0.19	0.17	0.06	0.22
WC	0.36	0.20	0.11	0.09	0.08	0.08
T	0.005	0.004	0.002	0.001	0.002	0.001
WEOC	0.33	0.38	0.19	0.17	0.22	0.18
MC	0.41	0.42	0.31	0.24	0.31	0.16
SR	0.50	0.42	0.49	0.17	0.30	0.37
SR_T10	0.49	0.47	0.49	0.17	0.33	0.38

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Table 3. Mean ± standard deviation of soil environmental conditions (days since last inundation LI, temperature T, gravimetric water content WC), carbon pools (water extractable organic carbon WEOC and microbial carbon MC), and fluxes (soil respiration SR as measured, SR_T10 normalised to reference T of 10 °C, and methane flux MF) in the six FPZs ($n = 4$ of the test site in the Thur River floodplain, Switzerland. Samplings were repeated four times from autumn 2008 to summer 2009. Also shown are results of repeated measures ANOVA over all samplings; different lower case letters in the same row indicate significant differences ($P < 0.05$; Tukey or Games-Howell post-hoc test).

			GRAVEL	GRASS	WILLOW BUSH	MIXED FOREST	WILLOW FOREST	PASTURE
Oct 2008	LI	days	21	21	21	49	49	49
	T	°C	16.0 ± 1.9	14.5 ± 2.9	13.7 ± 0.4	13.4 ± 0.3	13.0 ± 0.6	13.5 ± 0.2
	WC	g kg^{-1}	171 ± 48	268 ± 37	220 ± 34	251 ± 19	302 ± 17	210 ± 11
	WEOC	mg kg^{-1}	127 ± 37	141 ± 24	82 ± 15	160 ± 27	164 ± 37	80 ± 18
	MC	mg kg^{-1}	132 ± 92	168 ± 131	158 ± 119	132 ± 100	227 ± 161	73 ± 12
	SR	mmol m^{-2} day^{-1}	43 ± 22	327 ± 39	322 ± 117	194 ± 22	214 ± 47	228 ± 86
	SR_T10	mmol m^{-2} day^{-1}	17 ± 3	224 ± 24	203 ± 74	144 ± 16	150 ± 26	144 ± 55
	MF	μmol m^{-2} day^{-1}	−2 ± 1	−15 ± 3	−25 ± 9	−58 ± 11	−22 ± 9	−6 ± 6
Jan 2009	LI	days	14	14	14	140	140	140
	T	°C	−0.1 ± 0.4	0.5 ± 0.3	0.3 ± 0.4	0.0 ± 0.2	0.2 ± 0.3	0.5 ± 0.1
	WC	g kg^{-1}	325 ± 57	296 ± 50	255 ± 33	257 ± 26	347 ± 35	252 ± 29
	WEOC	mg kg^{-1}	85 ± 29	143 ± 22	123 ± 19	155 ± 38	147 ± 50	116 ± 11
	MC	mg kg^{-1}	208 ± 99	178 ± 71	297 ± 56	231 ± 42	471 ± 58	331 ± 49
	SR	mmol m^{-2} day^{-1}	8 ± 5	50 ± 28	58 ± 37	41 ± 9	55 ± 36	37 ± 14
	SR_T10	mmol m^{-2} day^{-1}	52 ± 34	172 ± 98	251 ± 169	128 ± 30	170 ± 111	120 ± 44
	MF	μmol m^{-2} day^{-1}	−1 ± 3	−6 ± 7	−18 ± 13	−35 ± 19	−17 ± 9	−6 ± 5
Apr 2009	LI	days	5	21	112	240	240	240
	T	°C	15.2 ± 2.8	11.4 ± 0.7	11.0 ± 0.7	10.3 ± 0.5	11.7 ± 0.5	10.7 ± 0.8
	WC	g kg^{-1}	169 ± 99	204 ± 43	248 ± 7	219 ± 26	276 ± 23	152 ± 13
	WEOC	mg kg^{-1}	84 ± 28	96 ± 67	117 ± 20	98 ± 16	139 ± 15	94 ± 28
	MC	mg kg^{-1}	148 ± 30	135 ± 49	210 ± 28	223 ± 29	445 ± 72	208 ± 15
	SR	mmol m^{-2} day^{-1}	91 ± 40	304 ± 143	134 ± 47	130 ± 10	178 ± 25	139 ± 43
	SR_T10	mmol m^{-2} day^{-1}	72 ± 46	303 ± 193	147 ± 49	135 ± 8	144 ± 42	118 ± 46
	MF	μmol m^{-2} day^{-1}	7 ± 23	−9 ± 2	−15 ± 5	−55 ± 5	−21 ± 5	−18 ± 3
Aug 2009	LI	days	2	7	14	14	14	14
	T	°C	19.3 ± 1	18.4 ± 0.8	16.6 ± 0.2	16.3 ± 0.1	16.6 ± 0.6	18.8 ± 0.2
	WC	g kg^{-1}	181 ± 70	388 ± 117	348 ± 41	365 ± 30	493 ± 44	276 ± 15
	WEOC	mg kg^{-1}	155 ± 60	324 ± 168	418 ± 103	480 ± 44	608 ± 131	297 ± 34
	MC	mg kg^{-1}	334 ± 90	351 ± 48	306 ± 46	361 ± 36	263 ± 66	190 ± 47
	SR	mmol m^{-2} day^{-1}	283 ± 127	432 ± 237	654 ± 390	260 ± 67	315 ± 48	345 ± 145
	SR_T10	mmol m^{-2} day^{-1}	50 ± 18	152 ± 90	246 ± 148	124 ± 31	147 ± 29	115 ± 46
	MF	μmol m^{-2} day^{-1}	8 ± 8	17 ± 43	−23 ± 10	−27 ± 9	52 ± 79	151 ± 236
ANOVA results	T			a	b	b	b	b
	WC			c	ab	bc	b	a	bc
	WEOC			c	bc	bc	ab	a	bc
	MC			b	b	b	b	a	b
	SR			b	a	a	ab	a	ab
	SR_T10			a	a	a	a	a	a
	MF			b	b	b	a	b	b

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Table 4. Modeled relationship between soil respiration (y, $\mathrm{mmol\,CO_2\,m^{-2}\,day^{-1}}$) and soil temperature ($T$, °C) in different FPZs of the test site in the Thur River floodplain, Switzerland.

FPZ	$y = a\,e^{(bT)}$	SE_a	SE_b	Q_{10}	n	F	R^2	P
GRAVEL	$y = 6.85\,e^{(0.179T)}$	0.02	2.1	6.0	13	54.7	0.83	<0.0001
GRASS	$y = 51.09\,e^{(0.128T)}$	0.02	15.1	3.6	16	28.6	0.67	<0.0001
WILLOW BUSH	$y = 43.02\,e^{(0.148T)}$	0.02	9.86	4.4	16	55.8	0.80	<0.0001
MIXED FOREST	$y = 40.84\,e^{(0.117T)}$	0.01	3.53	3.2	16	235.7	0.94	<0.0001
WILLOW FOREST	$y = 44.83\,e^{(0.116T)}$	0.02	8.46	3.2	16	56.1	0.80	<0.0001
PASTURE	$y = 33.96\,e^{(0.124T)}$	0.01	6.18	3.4	16	77.9	0.85	<0.0001

a and b: regression coefficients.
SE_a and SE_b standard errors of a and b.
Q_{10}: relative increase in soil respiration upon a T increase of 10 °C.
n: number of individual measurements. F, R, P: F-value, coefficient of determination, and level of significance of the regression, respectively.

- GRAVEL
- GRASS
- WILLOW BUSH
- MIXED FOREST
- WILLOW FOREST
- PASTURE
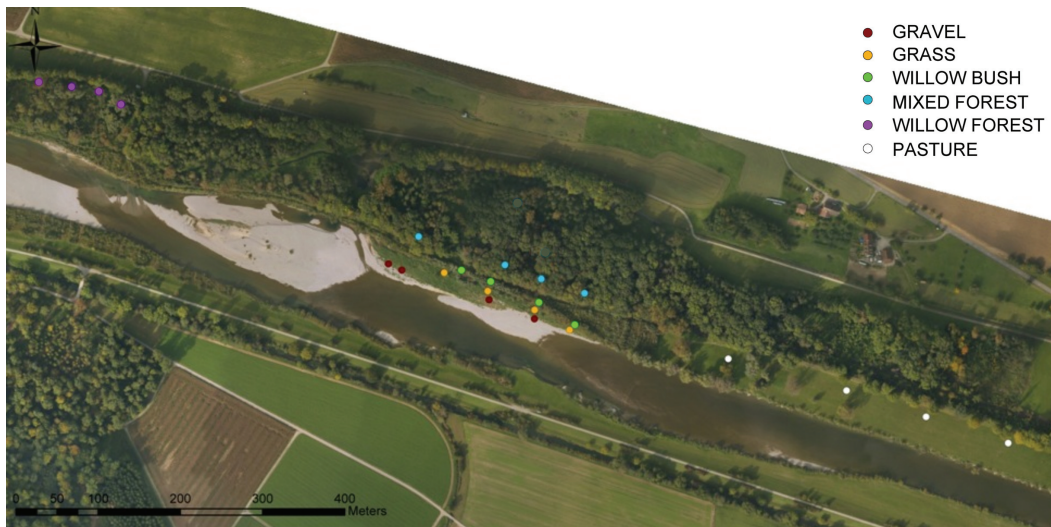
Fig. 1. Aerial view of the Thur River test site near Niderneunforn (North-Eastern Switzerland) showing the different plots for each of the six functional process zones.
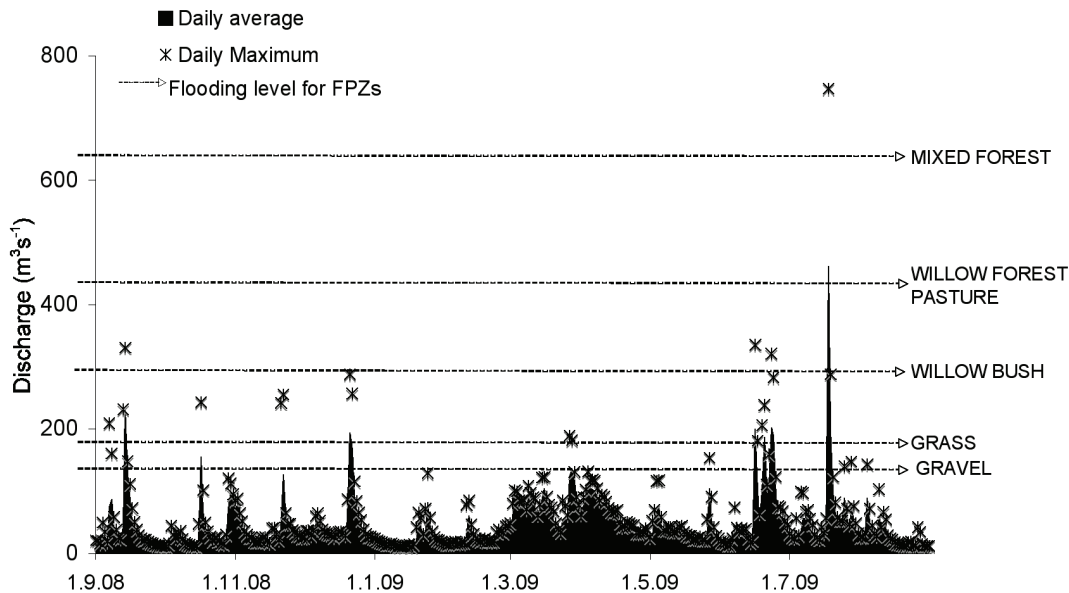
Fig. 2. Daily average and maximum discharge of the Thur River at the test site. Minimum discharge required for inundation is different for each functional process zone (FPZ) and the flooding level shown here is the average elevation of the four plots for each FPZ.
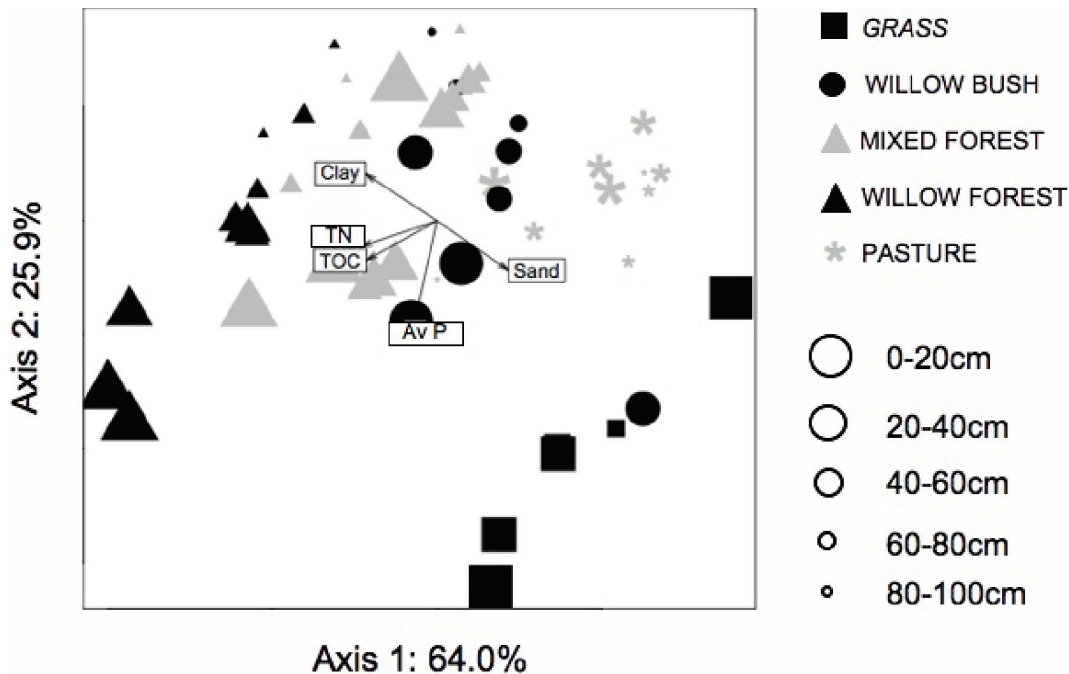
Fig. 3. Five functional process zones at the test site in the Thur River floodplain, Switzerland, with two replicates each are represented on the two first axes of a PCA performed on soil physicochemical properties (total organic carbon TOC, total nitrogen TN, available phosphorus Av P, sand and clay content) measured in the soil profiles. The decreasing size of the symbols represents increasing soil depth.
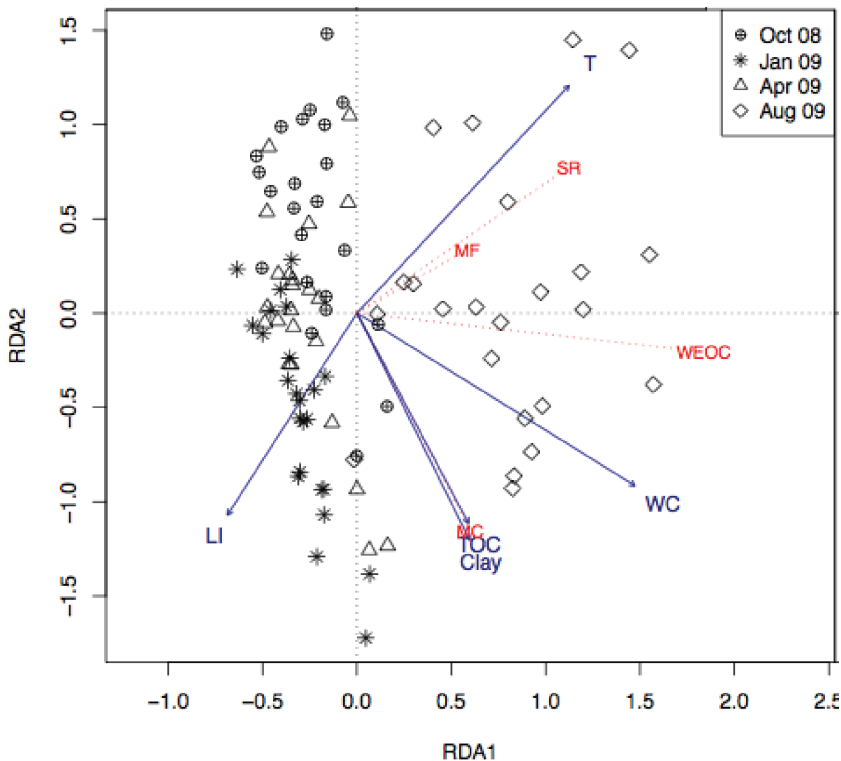
Fig. 4. RDA triplot for carbon pools and fluxes in the six functional process zones at the test site in the Thur River floodplain, Switzerland (water extractable organic carbon WEOC, microbial carbon MC, soil respiration SR, methane flux MF) as multivariate response variables, constrained by soil properties and environmental conditions (days since last inundation LI, soil temperature T, gravimetric water content WC, clay content Clay and total organic carbon TOC) as explanatory variables. Four soil sampling dates are represented with different symbols. Axis 1 explains 35.4% and axis 2 11.3% of the variance. Data were projected using scaling method 2.