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The response in floodplain respiration of an alpine river to experimental inundation under different temperature regimes

Tatjana Simčič,[1]* Nataša Mori,[1,2] Christian Hossli,[5] Christopher T. Robinson[2,3] and Michael Doering[2,4,5]

[1] *National Institute of Biology, Department of Freshwater and Terrestrial Ecosystems Research, Večna pot 111, 1000 Ljubljana, Slovenia*
[2] *Swiss Federal Institute of Aquatic Science and Technology (EAWAG), Überlandstrasse 133, 8600 Dübendorf, Switzerland*
[3] *ETH Zürich, Institute of Integrative Biology, Zürich, Switzerland*
[4] *Institute of Natural Resources Sciences, Zurich University of Applies Sciences (ZHAW), Grüental, 8820 Wädenswil, Switzerland*
[5] *eQcharta GmbH, Ecohydrology in application, Überlandstrasse 129, 8600 Dübendorf, Switzerland*

Abstract:

The respiratory potential [i.e. electron transport system activity (ETSA)] of soils and sediments from five floodplain habitats (channel, gravel, islands, riparian forest and grassland) of the Urbach River, Switzerland, and actual respiration rate (R) of the same samples exposed to experimental inundation were measured. Measurements were carried out at three incubation temperatures (4°C, 12°C and 20°C), and ETSA/R ratios (i.e. exploitation of the overall metabolic capacity) were investigated to better understand the effects of temperature and inundation on floodplain functional heterogeneity. Furthermore, ETSA/R ratios obtained during experimental inundation were compared with ETSA/R ratios from field measurements to investigate the exploitation in total metabolic potential at different conditions. Lowest ETSA and R were measured in samples from channel and gravel habitats, followed by those from islands. Substantially higher values were measured in soils from riparian forest and grassland. Both ETSA and R increased with increasing temperature in samples from all habitats, while the ETSA/R ratio decreased because of a rapid response in microbial community respiration to higher temperatures. The metabolic capacity exploitation (i.e. ETSA/R) during experimental inundation was lowest in predominantly terrestrial samples (riparian forest and grassland), indicating the weakest response to wetted conditions. Comparison of experimentally inundated and field conditions revealed that in rarely flooded soils, the metabolic capacity was less exploited during inundation than during non-flooded conditions. The results suggest high sensitivity in floodplain respiration to changes in temperature and hydrological regime. ETSA/R ratios are considered good indicators of changes in metabolic activity of floodplain soils and sediments, and thus useful to estimate the impact of changes in hydrological regime or to evaluate success of floodplain restoration actions. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS respiration; ETSA; alpine floodplains; inundation; temperature

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INTRODUCTION

Riverine floodplains are highly complex and dynamic ecosystems that are increasingly under threat by a range of local, regional and catchment wide stressors, including alterations of flow and thermal regimes, sediment loads, morphological features, and accumulation of organic and other contaminants (Kang and Stanley, 2005; Kang *et al*., 1998; Tockner *et al*., 2010). Moreover, climate change caused by global warming is expected to alter temperature regimes and water flow. Global average surface temperatures are expected to exceed 2°C from the present until the year 2100 according to scenarios of the Intergovernmental Panel on Climate Change (IPCC, 2013), and global average river water temperatures are estimated to increase on average by 0.8–1.6°C for the 2071–2100 period (van Vliet *et al*., 2013). These changes will have a major impact on the structure and functioning of floodplain habitats (Carpenter *et al*., 1992).

Alterations of different components of flow and thermal regimes can have various effects on ecosystem processes (Tockner *et al*., 2010). For instance, drying and rewetting events influence nutrient cycling and microbial respiration. As sediments dry out, bacterial biomass and activity decline, while rewetting flushes nutrients and enhancing bacterial activity (Baldwin and Mitchell, 2000; Fierer and Schimel, 2002). Although most floodplains are regularly and frequently flooded during the annual cycle for relatively short periods of time (days to weeks) (Baldwin

*Correspondence to: Department of Freshwater and Terrestrial Ecosystems Research, National Institute of Biology, Večna pot 111, 1000 Ljubljana, Slovenia.
E-mail: tatjana.simcic@nib.si

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and Mitchell, 2000; Doering *et al*., 2007), there have been few studies investigating floodplain soil and sediment response to short-term inundation. Immediately after inundation (within a day), carbon mineralization rates, amounts of labile carbon in soil and enzymatic activities all increased, indicating the importance of flooding for ecosystem processes (Wilson *et al*., 2011). Not only the flooding event but also its duration and frequency, control floodplain functioning. For instance, factors reducing the duration of inundation decelerate leaf breakdown rates, whereas a decrease in flow variation reduces leaf breakdown heterogeneity (Langhans and Tockner, 2006).

Generally, increased temperature accelerates chemical reactions and thus enhances biological activities (Davidson and Janssens, 2006). Consequently, warming directly affects ecosystem processes such as respiration and decomposition (Dang *et al*., 2009; Yvon-Durocher *et al*., 2012) and can affect organic matter cycling, the transfer of carbon to higher trophic levels (Ylla *et al*., 2014) as well as alter CO_2 concentrations in the atmosphere, which could have important feedbacks on climate (Davidson and Janssens, 2006). Short-term fluctuations in flow and temperature have greater consequences when they affect processes governed by microorganisms that respond quickly to environmental changes compared with higher organisms (Dang *et al*., 2009), as they have close relations with their surroundings due to their high surface to volume ratio. These microbes consist of bacteria, fungi and microalgae that drive a large portion of global biogeochemical cycles (Davidson and Janssens, 2006).

Respiration (R) is one of the most frequently measured functional parameters of ecosystems. It represents an important carbon flux; it is a well-studied process in both permanent aquatic and terrestrial ecosystems and is a sensitive indicator of ecosystem stress (del Giorgio and Williams, 2005; Doering *et al*., 2011; Feio *et al*., 2010; Hill *et al*., 2000; Luo and Zhou, 2006; Samaritani *et al*., 2011; Uehlinger *et al*., 2002). Mechanistically, respiration is the biotic conversion of organic carbon to carbon dioxide by all organisms in an ecosystem (Yvon-Durocher *et al*., 2012). In this paper, heterotrophic microbial respiration, excluding photoautotrophs, is quantified and can encompass up to 95% of total soil respiration (Ryan and Law, 2005). Because measurement of respiration is time-consuming and has low sensitivity in the case of low metabolic activity of organisms, other methods have been developed to estimate microbial respiration. Tetrazolium salts, 5-cyano-2,3-ditolyl tetrazolium chloride and 2-(4-iodophenyl)-3-(4-nitrophenyl)-5-phenyl tetrazolium chloride (INT) have been frequently used as electron acceptors to measure the respiratory potential [i.e. microbial electron transport system activity (ETSA)] of heterotrophic microorganisms in sediments and soils (Blenkinsopp and Lock, 1990; Blenkinsopp *et al*., 1991; García *et al*., 1997; Sabater and Romani, 1996; Subhani *et al*., 2000; Trevors, 1984). Because INT can be reduced by aerobes and anaerobes, the total microbial respiratory potential in the sediment is measured (Hunting and Van der Geest, 2011; Songster-Alpin and Klotz, 1995). Therefore, respiratory potential is a measure of biological oxidation capacity (Olanczuk-Neyman and Vosjan, 1977), which means that the overall activity (maximum reaction rate) of respiratory enzyme dehydrogenases is measured (Packard, 1985).

The respiratory potential and actual respiration rates in soils/sediments depend on biomass and activity of microorganisms involved in organic matter decomposition and further mineralization processes. The relationship between respiratory potential and actual respiration (ETSA/R ratio) provides important information on the metabolic response of different floodplain soils and sediments exposed to particular experimental factors (temperature and inundation) relative to the whole metabolic capacity. Extensive studies have been performed previously on ETSA/R ratios in freshwaters (Jones and Simon, 1979; Simčič and Brancelj, 2002a,b) and marine (Relexans, 1996a,1996b; Vosjan and Olanczuk-Neyman, 1977) sediments. In lake sediments, the ratio was higher in eutrophic than in oligotrophic lakes and at sediment surface than in deeper sediment layers, but our knowledge on ETSA/R ratios in floodplain soils and sediments is limited. Especially important is to know how the ratio changes during flooding that regularly occurs within floodplains and how changes in temperature due to climate change could affect the intensity of exploitation in metabolic activity.

In the present study, the respiration of inundated floodplain soils and sediments was experimentally measured across a mosaic of habitats differing in frequency and duration of inundation at different temperatures. Prior to experimental inundation, the respiratory potential (i.e. ETSA) of floodplain soils and sediments was measured. In order to better understand the patterns of response of soils and sediments from different habitats, the structural characteristics, that is, organic matter content, grain size composition and water-filled pore space (WFPS), were also determined prior to inundation. As an indicator of response intensity, the ratios between initial respiratory potential and actual respiration during inundation (ETSA/R) were used to understand how far actual respiration was from its maximum respiratory capacity in different habitats during experimental inundation and how temperature modulates this response. In addition, ETSA/R ratios from the inundation experiment were compared with those from the field during non-flood conditions to provide information on exploitation of metabolic potential in the field during non-flood conditions and immediately after inundation in different habitats. We expected that (1) experimental inundation

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will induce a decrease in the exploitation of the overall metabolic capacity (increase in ETSA/R ratio) in floodplain soils from predominantly terrestrial habitats compared with habitats permanently or frequently flooded because of suppressed respiration of the dominant microbial community; (2) an increase in temperature during experimental inundation will result in increased exploitation of respiratory potential (i.e. decrease in ETSA/R ratio) across all habitats because of a rapid response in microbial community respiration to higher temperatures; and (3) in comparison with non-inundated field conditions, the exploitation of metabolic potential during inundation will be lower in less frequently flooded soils (high ETSA/R ratio) because of suppressed actual respiration and higher (low ETSA/R ratio) in constantly or frequently flooded sediments because of enhanced respiration.

MATERIAL AND METHODS

Sites description and sampling protocol

Samples for laboratory measurements were collected in the floodplain of the Urbach River located in the Bernese Alps, Switzerland (46°40′N, 8°12′E) (Figure 1). Climate of the floodplain is characterized with precipitation of 1345 mm year^{-1} and mean annual temperature of 2.8°C. Floodplain vegetation is dominated by alder (*Alnus incana*) and willow (*Salix* spp.). The active tract of the floodplain is surrounded by grasslands that are grazed by livestock during the warm season (May to October). Part of the river water (approximately 30%) is abstracted for hydropower production, although with little effect on the flow regime. To encompass the functional heterogeneity of the floodplain, five habitats were sampled: aquatic sediments (river channel) and four mainly terrestrial habitats (grassland, riparian forest, islands and exposed gravel) (for details see Doering *et al*., 2012). Six sampling sites distributed evenly along the entire floodplain were chosen for each habitat. In total, 30 samples were collected (six sampling sites × five habitats) on 3 October 2011. At each sampling spot, the upper vegetation layer or larger stones were removed and a 10×10 cm^2 of soil/sediment was collected from a depth up to 5 cm in terrestrial habitats. In the river channel, the surface layer of sediments (~10 cm) was removed to avoid the presence of epilithic algae and to measure only the heterotrophic respiration. Samples were stored in polyvinyl chloride (PVC) bags and taken to the laboratory within a few hours.

Laboratory analyses

In the laboratory, soil and sediment samples were sieved (mesh size 8 mm) to exclude large stones representing metabolically inactive substrate. Plant debris and roots also were removed as much as possible. Due to high heterogeneity of the structural characteristics of floodplain soils and sediments that are the reflection of inundation patterns, we also considered the variability of main structural characteristics across habitat types to better understand the different responses of the microbial community from different habitats. A part of each sample was analysed for WFPS, organic matter content and grain-size distribution. WFPS (%) was calculated from the equation:

$$WFPS = \frac{SWC \times BD}{1 - \frac{BD}{PD}} \quad (1)$$

where SWC is the soil water content (g g^{-1}), BD is the bulk density (g cm^{-3}) and PD is the particle density (2.65 g g cm^{-3}) based on the average bulk density of rock with no pore space. Dried samples (24 h, 105°C) were ashed at 500°C for 3 h, and organic matter content was expressed as percentage of ash-free dry mass per dry mass of soil or sediment. The ashed samples were sieved to separate the grain size fractions of <0.063, 0.063−2, 2−4 and >4 mm. The grain-size distribution was expressed as percentage of the total sample weight. The remaining sample was used for ETSA and actual respiration rate measurements. For the former, samples were immediately frozen and kept at −80°C until analysis, and for the latter, samples were closed in PVC bags, stored at 4°C and used for measurements within 10 days. The freezing of samples prior to enzyme activity analysis has been frequently used (Freimann *et al*., 2013) and was shown to have only minor effects on enzyme activities or bacterial community profiling (Wallenius *et al*., 2010).

To examine the response of the microbial community in soils/sediments from different habitats to 'flooded' conditions, actual respiration rate (R) during experimental inundation was measured using a closed bottle method where oxygen concentration (in mg O_2 l^{-1}) was measured continuously (every 3 s) for 4 h at three temperatures (4°C, 12°C and 20°C). The chosen temperatures encompass the range and mean of the temperatures that occurred in the study area during the sampling campaign. Measurements were conducted using an optical fibre oxygen sensor apparatus (OXY-10, 10-Channel Fiber-Optic Oxygen Meter, PreSens, Precision Sensing GmbH, Germany) with 10 fibre optic oxygen probes. Six replicates (from six sampling sites) per each habitat and temperature were measured. The vessels (4 cm long, 3.6 cm in diameter) were filled with pre-sieved soils/sediments (up to 2 cm), filled to the top with re-aerated river water and closed by a plug incorporated with the sensor probes and stirrer to constantly ventilate the water. To avoid any photosynthetic activity, the sediment was taken 5 cm below the surface, where we do not expect photoautotrophs, and the bottles

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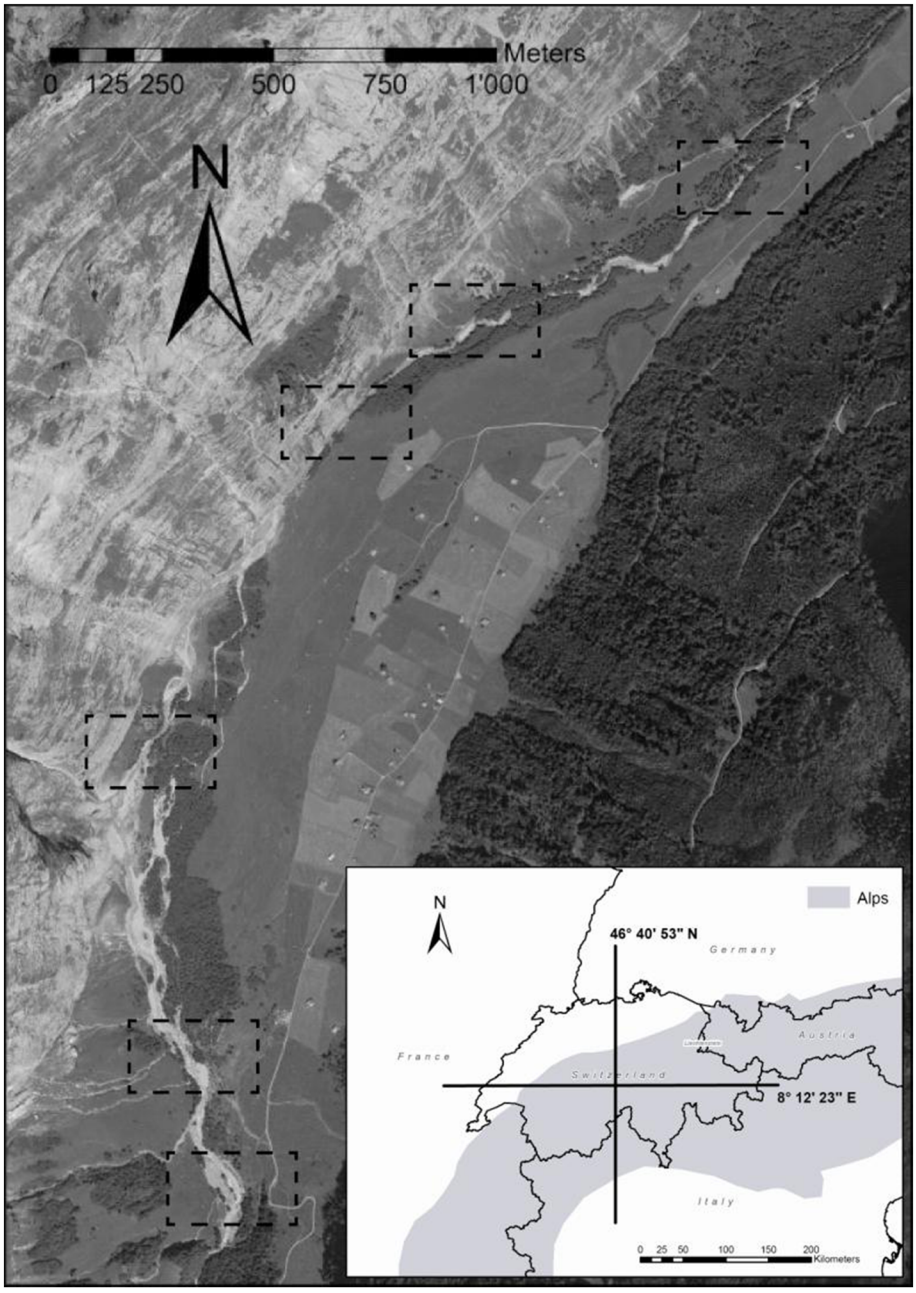

Figure 1. Aerial photograph of the Urbach River floodplain in 2007. The black dotted rectangles show the sampling sites. At each site, channel, gravel, island, forest and grassland habitat types were sampled. The inlet shows the location of the floodplain in the Canton Bern, Switzerland

were kept in the dark during the experiment. Temperature was maintained constant by an external cooling system. Respiration in each bottle was calculated as the difference between the oxygen concentration at the beginning and the end of incubation, multiplied by the volume of the bottle and a conversion factor 0.7 for converting mg O_2 into ml (Lampert, 1984) and divided by the incubation time and soil/sediment mass (ml O_2 gDW^{-1} h^{-1}).

Electron transport system activity was measured before inundation as an indicator of respiratory potential in soils/sediments from different habitats using the method originally proposed by Packard (1971) and modified by G.-Tóth (1999). Any toxic effect of INT is avoided in this assay, where ETSA is measured after incubation of a cell-free homogenate of organisms with substrates of the ETSA and INT in excess (Packard, 1971). One sample from each of six sampling replication sites per habitat and temperature were measured. Samples of soil/sediment (3–10 g wet weight) were placed on a pre-weighed aluminium foil and weighed on an electrobalance (Sartorius BP 210 S;

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Goettingen, Germany). Soils/sediments were immediately homogenized in 4 ml of ice-cold homogenization buffer (0.1 M sodium phosphate buffer pH = 8.4; 75 µM $MgSO_4$; 0.15% (w/v) polyvinyl pyrrolidone; 0.2% (v/v) Triton-X-100) using a mortar, followed by ultrasonic homogenization (4710; Cole-Parmer, Vernon Hills, IL, USA) for 3 min at 40 W. Samples were then centrifuged for 4 min at 0°C at 10 000 rpm (2K15, Sigma, St. Louis, MO, USA). A 0.5 ml aliquot of supernatant (in triplicate) was incubated with 1.5 ml substrate solution (0.1 M sodium phosphate buffer pH = 8.4; 1.7 mM NADH; 0.25 mM NADPH; 0.2% (v/v) Triton-X-100) and 0.5 ml reagent solution 2.5 mM 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyl tetrazolium chloride (INT) for 40 min at 4°C, 12°C and 20°C. The reaction was stopped by adding 0.5 ml stopping solution (formalin: H_3PO_4 conc = 1:1 (v/v)). Formazan production was determined spectrophotometrically (Lambda 12, Perkin-Elmer, Waltham, MA, USA) from the absorbance of the sample at 490 nm against the blank (0.5 ml of supernatant is added to incubated substrate and reagent solutions after stopping the reaction). ETSA was measured as the rate of tetrazolium dye reduction, which was converted to oxygen used per dry mass in a given time interval ($\mu l\, O_2\, gDW^{-1}\, h^{-1}$), as described by Kenner and Ahmed (1975).

The relationship between respiratory potential and actual respiration (i.e. ETSA/R ratio) was calculated to estimate the exploitation of overall metabolic potential for the actual intensity of metabolic processes. When actual respiration approaches the respiratory potential, the ratio comes close to 1, meaning that the system respires 'as much as possible'. Therefore, a high ETSA/R ratio indicates less efficient exploitation of respiratory potential.

To characterize the sensitivity of ETSA and actual respiration rate (R) to temperature changes, the temperature coefficient, Q_{10}, was calculated from the equation (Lampert, 1984):

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_2 - T_1}} \quad (2)$$

where R_1 and R_2 are the measured rates and T_1 and T_2 are the corresponding temperatures.

Field respiration measurements

For the calculations of ETSA/R ratios from the field during non-flood conditions, *in situ* respiration of aquatic river channel sediments was estimated as O_2 consumption over time in a closed bottle system (Uehlinger *et al.*, 2002), while respiration of terrestrial soils and sediments was measured as CO_2 efflux. For the former, the surface layer of the river sediments (~10 cm) was removed to avoid the presence of autotrophic organisms (periphyton), then the sediment was sieved (mesh size 8 mm) to avoid large stones representing a part of metabolic inactive substrate and placed into plexiglas tubes (32 cm long and 5.2 cm in diameter). Twenty plexiglas respiration tubes were placed in the river channel along the floodplain. The plexiglas respiration tubes half-filled with sediment were filled to the top with surface water from the sampling site and sealed with rubber stoppers. Subsequently, the tubes were incubated *in situ* by burying them into the surface sediment at the sampling site for 4–8 h. The tubes were buried in the dark to avoid artefacts during incubation. Temperature and oxygen concentration were measured by an HQ40d Dual-Input Multi-Parameter Digital Meter with a luminescent dissolved oxygen (LDO) temperature probe (Hach Company, Loveland, Colorado, USA) before and after incubation. For *in situ* respiration of terrestrial soils and sediments, 20 PVC collars (8 cm long and 10.5 cm in diameter) per habitat type were inserted into the soil and sediments to a depth of 5–7 cm at least 24 h prior to measurements to minimize the effect of disturbance because of the installation. Then, a soil respiration chamber (Li6400, LiCor, Lincoln, Nebraska, USA) attached to a portable Li-6400 infrared gas analyser was inserted on top of the collar, and measurements of CO_2 efflux ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$) were repeated four times for each site and values averaged. The *in situ* aquatic and terrestrial measurements were conducted a year before the inundation experiment but during the same season.

The *in situ* respiration measured in aquatic sediments and terrestrial habitats was corrected for temperature (12°C) using the following equation:

$$R_{12^oC} = e^{b^*(T - T_{12^oC})} \quad (3)$$

where T is the temperature measured at 5 cm depth (terrestrial habitat types) or the temperature of the chamber water (channel, at the end of the incubation). The parameter b was calculated using nonlinear regression applied to respiration and temperature data of each individual habitat type (detailed methods in Doering *et al.*, 2011). The correction to 12°C was applied because this value reflects the average of spatial and temporal temperature variation in the study floodplain.

The following procedure was applied to calculate the ETSA/R ratio from the field. Because ETSA measured in the samples collected for the inundation experiment and the one measured in the samples collected during the field measurements a year before did not differ significantly between each other at an incubation temperature of 20°C, the temperature conversion to 12°C and corresponding uncertainty was avoided by using the ETSA values for the former samples measured at an incubation temperature of 12°C. Further, the ETSA ($\mu l\, O_2\, gDW^{-1}\, h^{-1}$) was converted into the units used in terrestrial respiration

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($\mu mol\, CO_2\, m^{-2}\, s^{-1}$). A conversion factor of $1\, ml\, O_2 = 44.66\, \mu mol\, CO_2$ (Lampert, 1984) and a respiratory quotient of 0.85 (Dilly, 2001) was used in calculations:

$$ETSA\left(\ \mu mol\, CO_2\, m^{-2}\, s^{-1}\right) = ETSA\left(ml\, 0_2\, m^{-2}\, h^{-1}\right) \times \frac{1}{3600} \times 44.66\left(\ \mu mol\, O_2\, ml^{-1}\right) \times RQ \quad (4)$$

Statistical analyses

One-way analysis of variance (ANOVA) was applied to test for differences in Q_{10} over the whole temperature range (4–20°C) between habitats. Two-way ANOVA with replication was used to analyse differences in ETSA, actual respiration rate (R) and ETSA/R ratios from different habitat types and at different temperatures and to analyse differences in Q_{10} values between habitats and different temperature ranges (4–12°C and 12–20°C). A two-way ANOVA with replication was used to test for differences between the two ETSA/R ratios (laboratory *versus* field measurements) and between habitats. Tukey's honest significant difference test was performed after ANOVAs to determine which groups in the sample differ. The normal distribution of data was tested with the Shapiro–Wilk test and the equality of variances with Levene's test. The data were log-transformed or arcsin-transformed to achieve normal distributions and homogeneity of variances.

To examine the heterogeneity of soil/sediment structural characteristics and link them to ecosystem processes, one-way ANOVA was used to test for differences in temperature, WFPS, organic matter content and grain-size composition between habitats. The variation in soil/sediment physicochemical characteristics was investigated by applying a standardized principal component analysis (PCA) based on a correlation matrix where data were centred and standardized (ter Braak and Šmilauer, 2002). To search for patterns in the relationship between microbial activity and physicochemical characteristics of the samples, the scores of the first PCA axis were plotted against the ETSA, R and $ETSA/R_{lab}$ measured at 12°C. Further, the relationships between ETSA and soil/sediment characteristics (organic matter content, WFPS and soil/sediment grain-size composition) were explored by curve estimation, and the data for the best-fitted model (i.e. power regression) were given as results. Similarly, the relationships between ETSA and actual respiration rates were explored, and the best-fitted models selected for each temperature. All statistical analyses were performed using SPSS 13.0 (SPSS Inc. Chicago, IL, USA). The PCA analysis was run on the programme CANOCO 4.5 (ter Braak and Šmilauer, 2002).

RESULTS

Properties of soil/sediment samples

The mean temperature over spring, summer and autumn ranged from 9.2°C to 15.8°C across habitats and was highest in gravel sediments and lowest in the channel ($F_{4,29} = 17.56$, $p < 0.001$) (Table I). WFPS measured in soils/sediments from channel, grassland, riparian forest and island habitats was higher (mean 17.5–36.1%) than that in gravel samples ($4.5 \pm 2.5\%$) ($F_{4,29} = 17.56$, $p < 0.001$). The amount of organic matter was higher in grassland ($8.1 \pm 3.3\%$) and riparian forest soils ($3.7 \pm 2.3\%$) and lower (below 1%) in soils/sediments from gravel and channel habitats ($F_{4,29} = 39.42$, $p < 0.001$).

Particles of size range 2–0.063 mm dominated all samples (Table I). Comparison between habitats showed

Table I. Average temperature of spring, summer and autumn measurements, water-filled pore space (%), total organic matter content (%) and grain size composition of soils and sediments from different floodplain habitats

	Grassland	Forest	Islands	Gravel	Channel
Temperature (°C)	13.6 ± 6.2^{a}	$11.7 \pm 4.5^{a,b}$	12.4 ± 5.7^{a}	15.8 ± 8.8^{a}	9.2 ± 3.6^{b}
% Water-filled pore space	28.5 ± 2.7^{a}	17.5 ± 6.0^{a}	25.9 ± 19.2^{a}	4.5 ± 2.5^{b}	36.1 ± 14.7^{a}
% Organic matter content	8.1 ± 3.3^{a}	3.7 ± 2.3^{a}	0.9 ± 0.7^{b}	$0.5 \pm 0.3^{b,c}$	0.3 ± 0.1^{c}
Grain size distribution					
>4 mm (%)	3.8 ± 3.6^{a}	$12.4 \pm 16.6^{a,b,c}$	$6.1 \pm 7.1^{a,b}$	$24.0 \pm 8.3^{b,c}$	28.3 ± 10.9^{c}
4–2 mm (%)	4.9 ± 3.9^{a}	$13.1 \pm 9.2^{a,b}$	$6.7 \pm 5.7^{a,b}$	$18.5 \pm 4.0^{b,c}$	27.3 ± 8.3^{c}
2–0.063 mm (%)	83.2 ± 6.2^{a}	$67.6 \pm 20.4^{a,b}$	80.9 ± 12.6^{a}	55.1 ± 10.6^{b}	43.9 ± 18.1^{b}
<0.063 mm (%)	8.2 ± 2.1^{a}	$6.9 \pm 4.1^{a,b}$	$6.3 \pm 4.2^{a,b}$	$2.4 \pm 1.6^{b,c}$	0.5 ± 0.3^{c}

Mean ± standard deviation; $N = 6$.
[a,b] and [c] significant differences between habitats.
$p < 0.05$.

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the highest amount of particles >4 mm in gravel and channel sediments and the lowest in grassland soils ($F_{4,29}=5.81$, $p<0.01$). In contrast, the proportion of particles <0.063 mm was lowest in the former and highest in the latter samples ($F_{4,29}=10.77$, $p<0.001$). Samples from different habitats were distinct, mostly because of grain-size composition and organic matter content. PCA on soil and sediment physicochemical characteristics explained 52% of the variability in data on the first axis and 21% variability on the second axis. Grain-size differences between samples and organic matter content defined the first axis, and WFPS and temperature defined the second axis.

Respiratory potential – ETSA

Electron transport system activity measured prior to experimental inundation ranged between 0.22 µl O_2 $gDW^{-1}\,h^{-1}$ (channel sediment, 4°C) and 18.23 µl O_2 $gDW^{-1}\,h^{-1}$ (grassland soil, 20°C) (Figure 2a) and differed between habitats ($F_{4,90}=81.52$; $p<0.001$) and temperatures ($F_{2,90}=8.71$; $p<0.001$). A *post hoc* Tukey test showed significantly lower ETSA in sediments from channel and gravel habitats than in other habitats and significantly higher values in forest and grassland habitats. Respiratory potential increased with increasing temperature in soils/sediments of all habitat types and differed significantly between 4°C and 20°C.

Electron transport system activity increased with fine grain size and organic matter content as shown in Figure 3a. The relation between soil/sediment physicochemical characteristics and ETSA at all three temperatures was best explained by a power model, which was positive for organic matter content and the finest two grain sizes (2–0.063 mm, <0.063 mm), and negative for the largest two grain size classes (Table II).

Q_{10}-values for ETSA ranged between 1.21 (gravel) and 2.09 (grassland) and did not differ between habitats and between temperature ranges ((Figure 4a). Q_{10}-values for the whole temperature range (4–20°C) ranged from 1.37 in gravel to 1.80 in grassland, and did not differ between habitats ($p>0.05$).

Respiration rate – R

Respiration rate during experimental inundation ranged from 0.02 µl O_2 $gDW^{-1}\,h^{-1}$ in the sediments from gravel at 4°C to 3.46 µl O_2 $gDW^{-1}\,h^{-1}$ in grassland soil at 20°C (Figure 2b). Values were higher in grassland and riparian forest and lower in the gravel and channel ($F_{4,80}=21.05$; $p<0.001$; *post hoc* Tukey test) and increased with higher temperatures ($F_{2,80}=44.06$; $p<0.001$). The relationship between R and soil/sediment physicochemical characteristics was best

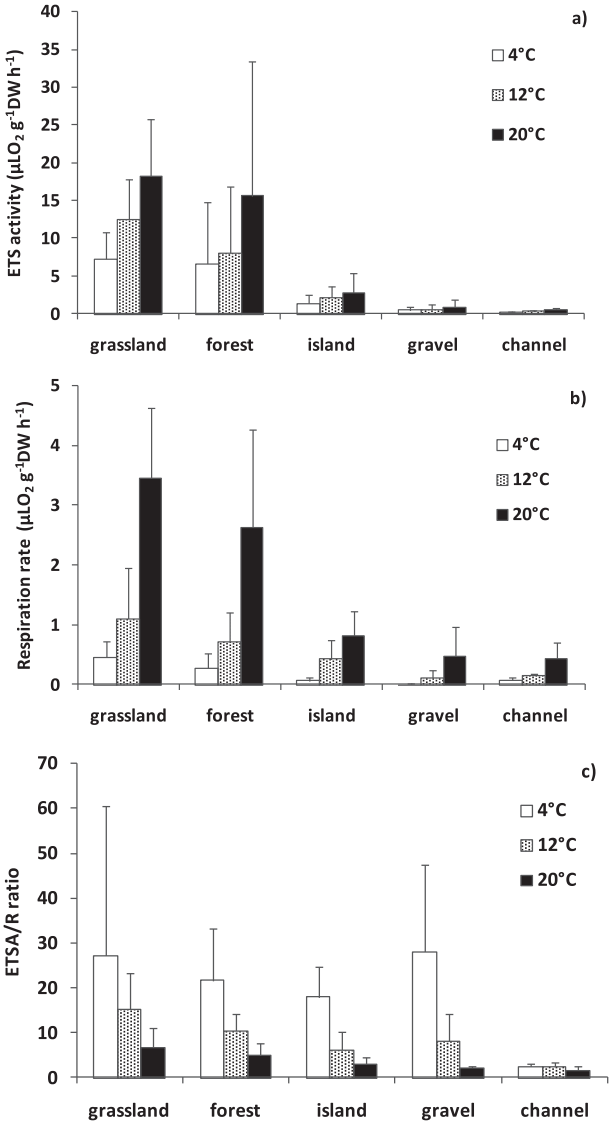

Figure 2. (a) Electron transport system activity (ETSA) prior to inundation (µl O_2 $gDW^{-1}\,h^{-1}$), (b) respiration rate during inundation (µl O_2 $gDW^{-1}\,h^{-1}$) and (c) ratios between ETSA and respiration rate (R) during inundation measured in soils/sediments from different floodplain habitats at three different temperatures. Bars represent mean + standard deviation; $N=6$

fit in the power regression model, with significant positive correlations with organic matter content, and significant positive correlations with WFPS at 4°C and 12°C (Figure 3b, Table II). Respiration rate correlated positively with the smallest two grain size classes (2–0.063 mm, <0.063 mm), but negatively with the largest ones (Table II).

In the temperature range 4–12°C, Q_{10}-values for respiration ranged from 1.97 in channel to 13.72 in island habitats (Figure 4b). Less variable Q_{10}-values were observed in the higher temperature range 12–20°C. Q_{10}-values did not differ between habitats and between both

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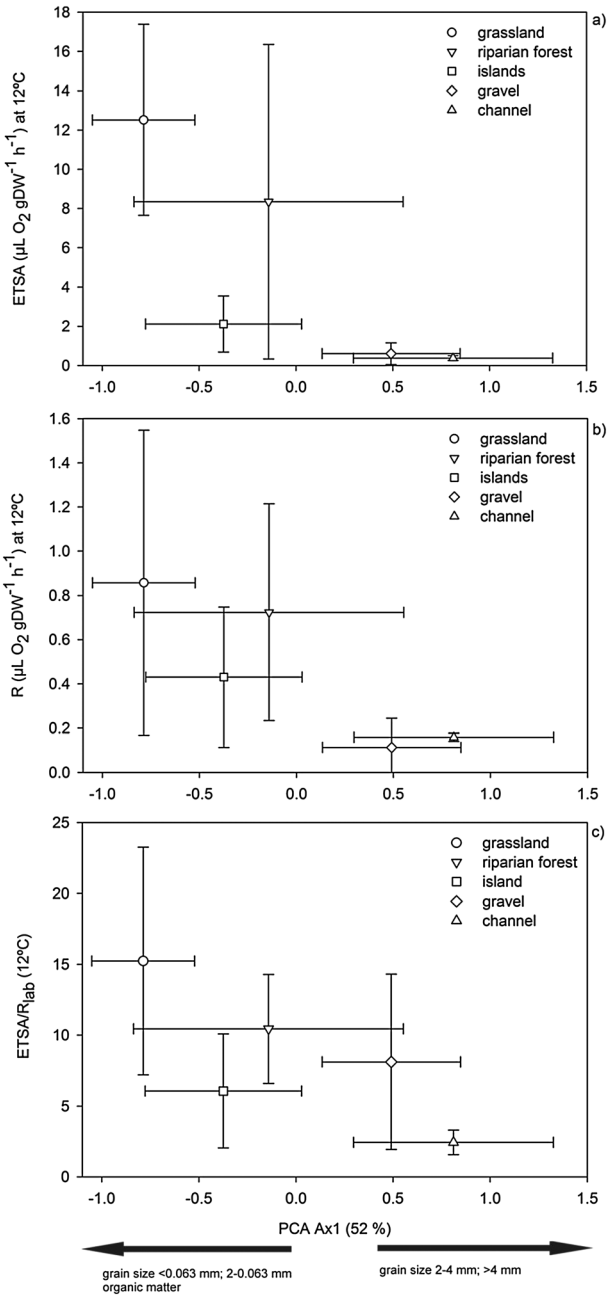

Figure 3. The relationship between scores of the first principal component analysis axis on soil/sediment properties (organic matter content and grain size distribution) and (a) electron transport system activity (ETSA) for non-flooded conditions, (b) R during experimental inundation and (c) $ETSA/R_{lab}$ ratio during experimental inundation at 12°C. Symbols are mean values of scores and error bars are standard deviations

temperature ranges ($p > 0.05$). Considering the whole temperature range (4–20°C), relatively high Q_{10}-value was measured in gravel, in comparison with all studied habitats, and it significantly differed from that measured in the channel habitat ($p < 0.05$).

The relationship between ETSA and respiration rate (ETSA/R)

The ETSA/R ratios during experimental inundation varied between 1.60 in channel sediments at 20°C and 28.06 in gravel sediments at 4°C (Figure 2c). Values differed between habitats ($F_{4,78} = 10.80$; $p < 0.001$) and temperatures ($F_{2,78} = 32.28$; $p < 0.001$). Considering habitat types, ETSA/R ratio was significantly lower in channel than in the other four habitats and significantly higher in grassland than in island, gravel and channel (*post hoc* Tukey test), indicating different responses in metabolic activity of microbial communities to inundation. Moreover, ETSA/R ratios differed significantly between all three experimental temperatures. Generally, the ratio increased with fine grain size and organic matter content (Figure 3c). Similar to ETSA and R, the best-fitted regression model for soil physicochemical characteristics of soils/sediments was a power model $y = ax^b$, with significant positive correlations between fine grains (<0.063 mm) and organic matter contents (Table II).

Comparison of ETSA/R during inundation experiment and ETSA/R from the field measurements

A two-way ANOVA was conducted, which examined the effect of measurement type and habitat on ETSA/R. There was a significant interaction between the habitat and field-lab effects ($F_{4,56} = 9.59$, $p < 0.001$). Simple main effects analysis showed that the ETSA/R was significantly higher during inundation in the laboratory than in the field in grassland ($p = 0.035$) and island ($p = 0.006$) habitats, but there were no differences in ETSA/R between field and experimental inundation in forest ($p = 0.067$), gravel ($p = 0.299$) and channel ($p = 0.662$) habitats. Yet, there was a tendency for higher ETSA/R values for the grassland, riparian forest and island soils measured in the laboratory experiment at 12°C (i.e. $ETSA/R_{lab}$) than those measured within the same habitats in the field (i.e. $ETSA/R_{field}$) during non-flood conditions, indicating more intensive exploitation of total metabolic capacity in field conditions (Figure 5). In contrast, a tendency for lower ETSA/R of gravel and channel sediments during experimental inundation was observed in comparison with those from the field measurements, suggesting more efficient exploitation in respiratory potential during experimental inundation.

DISCUSSION

Respiratory potential – ETSA in floodplain soils/sediments prior to experimental inundation

Floodplains are spatially heterogeneous systems in both structure and functioning. This is reflected in substantial spatial variability of respiratory potential

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Table II. Regression coefficients R^2 of the power model $y = ax^b$ for ETSA during pre-flooded conditions, and respiration rate (R) and ETSA/R ratio during experimental inundation as dependent variables and WFPS, organic matter or different grain-sized fractions as independent variables; calculated on the pooled data for five habitat types at experimental temperatures 4°C, 12°C and 20°C

				Grain size			
	N	WFPS	Organic matter	>4 mm	4–2 mm	2–0.063 mm	<0.063 mm
ETSA4	30	+0.070	+0.902***	−0.258**	−0.381***	+0.336***	+0.613***
ETSA12	30	+0.114	+0.916***	−0.249**	−0.403***	+0.313***	+0.543***
ETSA20	30	+0.098	+0.922***	−0.213*	−0.350***	+0.262**	+0.495***
R4	23	+0.360**	+0.638***	−0.100	−0.256***	+0.111	+0.267*
R12	29	+0.229**	+0.650***	−0.408***	−0.363***	+0.290**	+0.234**
R20	26	+0.122	+0.856***	−0.138	−0.249**	+0.131	+0.415***
ETSA/R4	23	-0.050	+0.173*	−0.050	−0.089	+0.131	+0.237*
ETSA/R12	29	-0.007	+0.357**	+0.018	−0.069	+0.039	+0.412***
ETSA/R20	26	+0.011	+0.665***	−0.085	−0.311**	+0.233*	+0.472***

ETSA, electron transport system activity; WFPS, water-filled pore space.
N = number of data; a sign in front of number indicating positive (+) or negative (−) relation.
*p < 0.05;
**$p < 0.01$;
***$p < 0.001$.

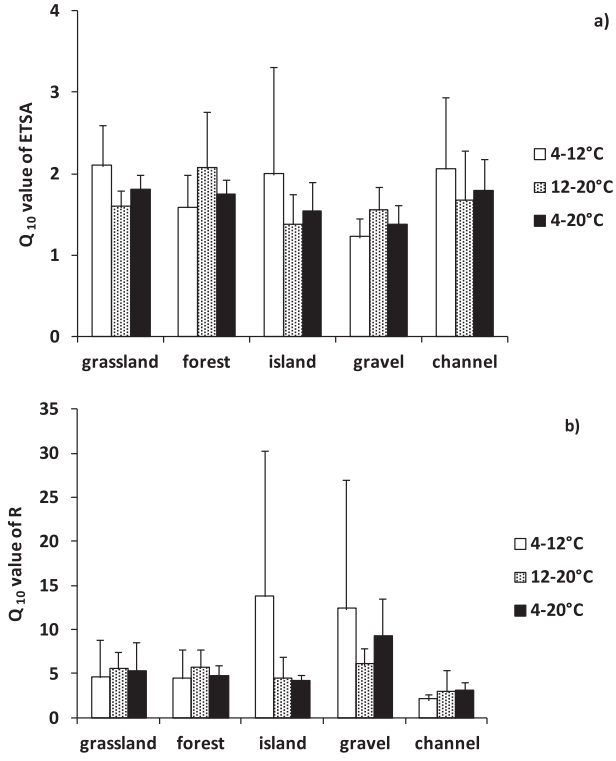

Figure 4. Q_{10} values of (a) electron transport system activity (ETSA) measured before inundation and of (b) respiration rate (R) measured during experimental inundation in soils/sediments from floodplain habitats for different temperature ranges. Bars represent mean + standard deviation; *N* = 6 for ETSA and *N* = 3–5 for R

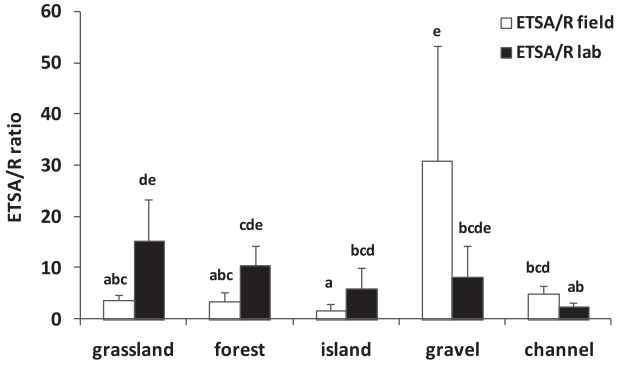

Figure 5. Ratios between electron transport system activity (ETSA) measured at 12°C before inundation (i.e. non-flood conditions) and respiration rate (R) measured in soils/sediments from different floodplain habitats during experimental inundation in the laboratory (ETSA/R lab) and ETSA/R ratios measured in the field in non-flood conditions (ETSA/R field). Data for R field were standardized to temperature of 12°C. Bar represents mean + standard deviation, *N* = 6, except for ETSA/R field in gravel *N* = 3. Bars labelled with different letters differ significantly; $p < 0.05$ (two-way analysis of variance, Tukey's honest significant difference test)

measured prior to experimental inundation. In general, respiratory potential of floodplain soils from riparian forest and grasslands was in the range of those previously reported for wetlands (Urbanc-Berčič and Gaberščik, 2003), and that from gravel and channel was similar to previous measurements in the same habitats from different rivers (Mori *et al*., 2011, 2012; Simčič and Mori, 2007). Yet, ETSA was substantially lower in comparison with freshwater lake sediments (de Vicente *et al*., 2010; Germ and Simčič, 2011; Muri and Simčič, 2004). Because autotrophs were excluded from the sampling by removing the surface layer, the overall respiratory potential was most likely underestimated. The highest ETSA observed in soils from riparian forest and grassland habitats is in accordance with the findings of Romaní *et al*. (1998) and Rulík and Spáčil (2004) who

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reported that higher extracellular enzymatic and ETSAs were related to higher quantity of organic matter. This was the case in our study, where the highest content of particulate organic matter was measured in grassland and riparian forest soils. Further, Rulík and Spáčil (2004) demonstrated that the presence of fine sand and silt grains, due to their high surface/volume ratio, contributes to high respiratory potential. Similarly, Simčič and Mori (2007) showed higher ETSA in river sediments when fine silt and sand particles were present in high amounts. The samples for respiratory potential measurements were taken from a range of floodplain habitats differing in inundation patterns, vegetation cover and main structural features, such as grain-size distribution, WFPS and organic matter content. Most likely, higher proportions of sand and silt together with higher organic matter content and lower hydrological stress (less frequent inundation) contributed to substantially higher ETSA in the grassland and forest soils in this study. However, additional analyses including the measurements of organic matter quality and nutrient availability, and data on previous on-site inundation patterns, are needed to better understand the patterns in respiratory potential across floodplain habitats.

The effect of inundation on floodplain respiration

Actual respiration rates (R) measured during experimental inundation were highest in grassland and forest soils, and lowest in gravel and channel sediments and were consistent with the pattern observed during measurements of respiratory potential (ETSA) prior to inundation. The higher respiration in predominantly terrestrial habitats is most probably because of higher organic matter content and fine grained soils. The soil texture has been shown as important determinant of microbial activity at global scale (Schimel *et al*., 1994) as well as within single floodplain (Samaritani *et al*., 2011). Similarly, organic matter contents underlaid the spatial variability of the respiration across heterogeneous floodplain habitats (Doering *et al*., 2011) and was shown to influence the microbial activity in river bed sediments (Fischer *et al*., 1996).

The exploitation of respiratory potential during inundation was lower in terrestrial habitats (i.e. high ETSA/R ratio) and higher in channel habitat (i.e. low ETSA/R ratio). Presently, it is known that high soil water content is connected with oxygen limitation, carbon excess conditions provoking excess metabolism and high microbial activity (Uhlířová *et al*., 2005). Fierer *et al*. (2003) found that drying–rewetting regimes can influence bacterial community composition in some soil types but not in others (oak *versus* grass soils). These two soils had different bacterial communities, and only the bacteria in the oak soil was significantly affected by drying–rewetting cycles because it was less frequently exposed to moisture stress in the natural environment (Fierer *et al*., 2003). It is well known that it takes some time to acquire optimal microbial growth under altered environmental conditions (Monod, 1949). Rinklebe and Langer (2006) have shown that frequently flooded soils, where the microbial community is under frequent stress, had a much higher respiration rate per unit microbial C indicating a stress response of aerobic soil microorganisms. Most probably, the soil microbes from terrestrial habitats that are rarely flooded are incapable to function optimally under flooded conditions, but this needs to be tested in further studies.

The exploitation of respiratory potential was less efficient (high ETSA/R ratio) during the inundation experiment than during field measurements for the predominantly terrestrial habitats (grassland, riparian forest and islands). Thus, the respiration rates of those samples were lower during experimental inundation than those measured in the field during non-flood conditions. Relexans (1996b) found that the ETSA/R ratio in marine sediments depends strongly on the availability of food. Generally, higher ratios occur in physiologically depressed organisms because of reduced respiration rates as a consequence of starvation (Christensen *et al*., 1980) or, in the case of this study, as a consequence of flooding. Yet, the measured ETSA/R ratios were much lower during inundation than in the field in the case of gravel sediments, indicating higher respiration rates during experimental inundation. Gravel sediments are frequently flooded and most probably contain a microbial community that can quickly respond to inundation. Wilson *et al*. (2011) showed for experimentally inundated floodplain soils, increases in 'labile' carbon fractions increase carbon mineralization and growth of opportunistic (*r*-selected) bacterial species, suggesting that immediate changes in carbon turnover and microbially driven processes can occur in soils adapted to frequent flooding.

The effect of temperature on floodplain soils/sediments during inundation

As expected, ETSA during pre-flooded conditions increased with increased incubation temperature. The measurements of ETSA in a gradient of temperatures can demonstrate the capability and strength of response of the respiratory system to changes in temperature (Martinez, 1992; Relexans, 1996b). ETSA of floodplain soils and sediments increased with higher rates than reported in a previous study of Trevors (1985) for freshwater sediments. The reason is probably the use of modified ETS-assay in this study, where cell-free supernatant with faster reaction rates was used in contrast to intact soils and sediments in the latter (G.-Tóth *et al*., 1994). Moreover, the acute response of soils and sediments

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to temperature was measured here, while Trevors (1985) incubated sediments for 24 h. In contrast, Simčič and Germ (2010) demonstrated a similar increase (up to 64%) in ETSA of lake sediments when incubated at different temperatures (2–24°C), which is comparable with this study (up to 66%).

In the present study, Q_{10} values of ETSA were relatively low and similar in all habitats and for all three temperature ranges, indicating similar rates of increase in respiratory potential after acute exposure to different temperatures. The mechanisms of temperature sensitivity on the respiratory potential in soils and sediments are not well understood because of a lack of relevant studies. Angilletta (2009) stated that, at the biochemical level, thermal sensitivity depends on the structural characteristics of the respiratory enzymes. Generally, it was shown that organisms that live in highly variable thermal environments have low temperature sensitivity (Simčič and Brancelj, 2004). This means that they are equipped with enzymes systems with extremely broad temperature optima (i.e. a temperature range where they function optimally), thereby preventing inactivation during sudden temperature changes. This may be the case for the study floodplain soils and sediment where the temperature gradient and its fluctuation across the floodplain were not distinct enough to cause differences in temperature sensitivity.

As expected, respiration rate also increased with temperature during inundation, but in contrast to ETSA, higher temperature sensitivity and higher variation in Q_{10} was observed within habitats. ETSA is an enzymatic process, depending on the concentration (Båmstedt, 1980) and characteristics (Packard, 1971) of the enzymes, whereas respiration is a complex physiological process, which can react immediately to altered environmental conditions, in contrast to ETSA where equilibrium ETSA is attained after a few days in the altered environment (Båmstedt, 1980). The temperature sensitivity of inundated soils and sediments was higher of that previously measured in non-flooded terrestrial and floodplain soils (Buchmann, 2000; Doering *et al*., 2011; Howard and Howard, 1993; Samaritani *et al*., 2011), indicating that the thermal sensitivity of soil respiration most likely increases during inundation. Further, Samaritani *et al*. (2011) observed the highest Q_{10} in non-flooded gravel sediments, which is in accordance with the inundated soils and sediments in this study. Howard and Howard (1993) suggested that organic matter quality is the main factor affecting the thermal sensitivity of soil respiration rates. Samaritani *et al*. (2011) showed that across the floodplain mosaic, gravel sediments contain the smallest amounts of water extractable organic matter, which is a proxy of available substrate for microorganism.

In general, the metabolic exploitation (ETSA/R ratio) was more efficient during exposure of inundated soils and sediments to higher temperatures. This is due to relatively more intense increase of respiration rates than respiratory potential for the reasons already discussed earlier. Stres *et al*. (2008) showed that environmental parameters such as temperature and water content act at the level of substrate availability and control the expression of specific enzymes involved in microbial processes, while the abundance and community structure of bacterial communities remain largely unaffected. Because heterotrophic metabolism in sediments follows the variation in environmental parameters, such as nutrients (Romaní *et al*., 1998), a reason for the relatively low differences in ETSA/R of channel sediments at different temperatures is likely nutrient limitation. The various qualities of organic matter and the physiological features of microorganisms are probably the main reason for the differences between habitats. It was observed by Wilson *et al*. (2011) that short-term inundations cause an almost immediate change in carbon turnover and microbial driven processes with a later change in microbial community structure. It seems that during inundation, respiration rates in some habitats increase more quickly than in others and are related to temperature. The exploitation of respiratory potential was lowest for the river channel, and it showed the most moderate temperature sensitivity as well.

CONCLUSIONS

The intensity of exploitation in respiratory potential was suppressed immediately after short-term inundation in soils from predominantly terrestrial habitats that are less frequently flooded, indicating that soil microbial activity needs some time to adapt to wetted conditions. Temperature during inundation plays an important role in the exploitation of respiratory potential, but with different extent across habitat types. For instance, an increase in temperature would cause a greater exploitation of metabolic potential in predominantly terrestrial habitats than aquatic habitats, suggesting the importance of future warming for enhancing carbon fluxes across floodplains. The results of the present study demonstrated that ETSA is sensitive to temperature variation, but to a lesser extent than actual respiration. Wetting–rewetting cycles in floodplain habitats and temperature variation alter the relationship between respiratory potential and actual respiration, and thus the ETSA/R ratio can be a good indicator of changes in metabolic activity of floodplain soils and sediments due to hydrological or temperature variation. The ETSA/R ratio is thus useful towards estimating the impact of changes in hydrological regime or to evaluate the success of restoration actions.

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CONFLICTS OF INTEREST

The authors declare that they have no conflict of interest.

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