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Environmental heterogeneity and respiration in a dynamic river corridor: Structural properties and functional performance

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Summary

Riverine floodplains are complex ecosystems that undergo cycles of expansion, contraction, and fragmentation along the longitudinal, lateral, and vertical dimensions. They can be conceptualized as a three dimensional shifting habitat mosaic. Thus, they can serve as model ecosystems to investigate the linkage between environmental heterogeneity and ecosystem functioning.

The primary goal of the study was to assess environmental heterogeneity at the habitat and landscape level in a floodplain ecosystem and to link this environmental heterogeneity with ecosystem processes. The focus was on respiration as a key process in the carbon cycle that integrates the energy flow through the biotic compartments of aquatic and terrestrial ecosystems.

The study was conducted in the Tagliamento River, a 7th order Alpine river in northeastern Italy. The river is morphologically intact over most of its course. The lack of high dams, a minimally altered geomorphic setting that includes a complex and extensive floodplain, and a highly dynamic flow regime, contribute to the relatively pristine character of this river that Alpine Rivers must have had before human alteration.

The first chapter of the thesis documents the highly dynamic expansion and contraction of the river ecosystem. We identified two river reaches along a 41.5 km long braided section within the Tagliamento river. In the upper 29 km (losing zone), surface flow decreased on average by 2.5 $m^3 s^{-1}$ per river-km and in the downstream 12.5 km (gaining zone), surface flow increased on average by 0.3 $m^3 s^{-1}$ per river-km. Up to 23 km of the losing zone can lack surface flow during dry periods. Frequent and irregular flow pulses result in rapid expansion and contraction of the wetted channel. Timing, frequency, magnitude (spatial extent), and duration of expansion- contraction cycles reflected the flashy flow regime of the Tagliamento River. Even small changes in flow translate into substantial changes in ecosystem size.

Chapter 2 examines the effect of vertical hydraulic exchange at two different scales (reach and pool-riffle) on hyporheic respiration and periphyton biomass. At the reach scale vertical hydraulic exchange enhances respiration in the losing reach and periphyton abundance in the gaining zone. Local hydrologic exhange at the pool riffle scale had no significant effect on both parameters.

In chapter 3 we studied the effect of habitat heterogeneity on the function of aquatic and terrestrial soil and sediment respiration over an annual cycle in a complex island-braided reach. The investigated habitats (riparian forest, vegetated islands, large wood accumulations, exposed gravel sediments, river-channels and floodplain ponds) exhibited high variability in their structural properties; e.g., organic matter and water content was lowest in the exposed gravel sediment and highest in the vegetated islands. This variability was reflected in the intensity of soil and sediment respiration that averaged 0.54 μmol $CO_2\,m^{-2}$ in the exposed gravel sediments and 3.89 μmol $CO_2\,m^{-2}\,s^{-1}$ in the vegetated islands. Soil and sediment respiration followed a distinct seasonal trend and inundation led to a decline in respiration rates of 69 to 91 % within 6 hours. The data were used to develop an empirical model for soil and sediment respiration using temperature and inundation as key variables.

In chapter 4 this empirical model was applied into a three dimensional GIS based application to simulate the effect of temperature, inundation and changes in habitat composition on soil and sediment respiration at the landscape level. The model predicted total annual respiration rates ranging from 144 g C $m^{-2}\,yr^{-1}$ (exposed gravel sediments) to 1149 g C $m^{-2}\,yr^{-1}$ (vegetated islands), thereby spanning the whole range of global aquatic and terrestrial soil and sediment environments. Respiration was extremely sensitive to temperature; e.g., an increase in air temperature of 4 °C was predicted to increase annual respiration of the total floodplain by 33 %. Although inundation had a strong impact on soil and sediment respiration at the habitat level, the impact at the landscape level was relatively low. A change in habitat composition severely affected soil and sediment respiration; e.g., the elimination of islands covering only 9 % of the total floodplain area resulted in a decrease of 18 % in total floodplain soil and sediment respiration.

The results of this thesis demonstrated the pivotal role of heterogeneity for ecosystem functioning in particular for respiration and underline the importance of viewing linkages of environmental heterogeneity and ecosystem processes at different spatial scales.

Zusammenfassung

Schwemmebenen sind komplexe Ökosysteme, die einem Kreislauf von Expansion, Kontraktion und Fragmentierung entlang der longitudinalen, vertikalen und lateralen Dimension unterlegen sind und können somit als dreidimensionale, sich verändernde Habitatmosaike betrachtend werden. Aus diesem Grund stellen sie Modellökosyteme zur Untersuchung der Wechselwirkungen zwischen der Heterogenität und dem Funktionieren von Ökosystemen dar.

Das Hauptziel dieser Arbeit war, die Heterogenität einer Schwemmebene sowohl auf Habitat als auch auf Landschaftsebene zu untersuchen und den Zusammenhang zwischen Heterogenität und Ökosystemprozessen aufzuzeigen. Insbesondere wurde die Respiration untersucht, ein Schlüsselprozess im Kohlenstoffkreislauf aquatischer und terrestrischer Ökosysteme.

Diese Studie wurde am Tagliamento, einem alpinen Fluss siebter Ordnung in Nordost Italien durchgeführt. Der Fluss zeichnet sich durch eine intakte Morphologie entlang dem Grossteil seiner Fliessstrecke aus. Das Fehlen von hohen Dämmen, eine minimal veränderte Morphologie, die eine komplexe und ausgedehnten Schwemmebene beinhaltet und ein hoch dynamisches Abflussverhalten tragen zu einem natürlichen Charakter bei, den die meisten alpinen Flüsse gehabt haben müssen bevor sie verbaut wurden.

Das erste Kapitel dieser Arbeit dokumentiert die hoch dynamische Expansion und Kontraktion dieses Flussökosystems. Entlang eines 41.5 km langen Flussabschnitts konnten zwei Teilbereiche unterschieden werden: Ein 29 km langer Abschnitt, der durch einen durchschnittlichen Wasserverlust von 2.5 $m^3 s^{-1}$ geprägt war (Verlustzone) und ein 12.5 km langer Abschnitt, in dem der oberirdische Abfluss um durchschnittlich 0.3 $m^{-3} s^{-1}$ zunahm (Gewinnzone). Während Trockenperioden können bis zu 23 km in der Verlustzone trocken fallen. Häufige und unregelmässige Wasserstandsänderungen führen zu einer schnellen Expansion und Kontraktion des Flusses. Der Zeitpunkt, die Häufigkeit,

die räumliche Ausdehnung und die Dauer dieser Expansion und Kontraktion spiegeln das dynamische Abflussregime des Tagliamento wieder. Selbst geringe Wasserstandsänderungen haben eine starke Auswirkung auf die Grösse des Ökosystems.

Kapitel 2 beschäftigt sich mit dem Effekt des vertikalen Wasseraustausches auf die hyporheische Respiration und die Periphyton Biomasse in dem oben beschriebenen grossräumigen Flussabschnitt und entlang von kleinräumigen morphologischen Gegebenheiten (Pool-Riffle Sequenzen). Entlang des Flussabschnitts begünstigte der vertikale Wasseraustausch die Respiration in der Verlustzone und die Periphytonabundanz in der Gewinnzone. Im Gegensatz dazu hatte der kleinräumige Wasseraustausch entlang der Pool Riffle Sequenzen keinen signifikanten Einfluss auf beide Parameter.

In Kapitel 3 wurde über ein Jahr der Einfluss von Habitatheterogenität auf Boden- und Sedimentrespiration in einem stark strukturierten Teil der Schwemmebene untersucht. Die untersuchten Habitattypen (Auenwald, bewachsene Inseln, Totholzhaufen, Schotterflächen, Flusskanäle und stehende Kleingewässer) zeichneten sich durch eine hohe Variabilität in ihren Struktureigenschaften aus, z. B. war der Wassergehalt und der Gehalt an organischem Material am geringsten in den Schotterflächen und am höchsten auf den bewachsenen Inseln. Diese ausgeprägte Variabilität spiegelte sich in der Intensität der Boden- und Sedimentrespiration wieder. Geringste durchschnittliche Respirationsraten mit 0.54 μmol CO_2 m^{-2} s^{-1} wurden in den Schotterflächen und höchste durchschnittliche Raten mit 3.89 μmol CO^2 m^{-2} s^{-1} auf den Inseln gemessen. Die Boden- und Sedimentrespiration folgte einem ausgeprägten jahreszeitlichen Trend. Überflutung führte zu einer Abnahme der Respiration zwischen 69 und 91 % innerhalb von 6 Stunden. Unter Verwendung der beiden Schlüsselvariablen Temperatur und Überflutung wurde ein empirisches Modell zur Beschreibung der Boden- und Sedimentrespiration erstellt.

In Kapitel 4 wurde dieses empirische Modell in eine drei dimensionale GIS Anwendung implementiert, um den Effekt der Temperatur, der Überflutung und des Wechsels der Habitatzusammensetzung auf die Boden und Sedimentrespiration auf Landschaftsebene zu simulieren. Das Modell berechnete jährliche Respirationsraten, die von 144 g C m^{-2} a^{-1} (Schotterflächen) bis 1149 g C m^{-2} a^{-1} (Inseln) reichten. Diese Raten umfassen die gesamte Reichweite der Respiration in terrestrischen und aquatischen Boden- und Sedimentökosystemen weltweit. Die Respiration war äusserst empfindlich bezüglich der Temperatur, z. B. hatte ein simulierter Anstieg der Lufttemperatur um 4 °C zur Folge, dass die jährliche Respiration der gesamten untersuchten Schwemmebene um 33 % anstieg. Obwohl die Überflutung einen starken Einfluss auf Habitatebene hatte, war deren Auswirkung, betrachtet auf Landschaftsebene, relativ gering. Ein Wechsel in der Habitatzusammensetzung hatte massgebliche Auswirkungen auf die Boden- und Sedimentrespiration, z. B. führte der Verlust der Inseln, die nur 9 % der Fläche der Schwemmebene repräsentieren, zu einer Abnahme der Boden- und Sedimentrespiration der Schwemmebene um 18 %.

Die Ergebnisse dieser Arbeit demonstrieren deutlich die ausserordentliche Rolle der Habitatheterogenität für das Funktionieren von Ökosystemen, insbesondere für die Respiration. Ferner unterstreicht diese Studie die Wichtigkeit, die Zusammenhänge zwischen der Heterogenität der Umwelt und dem Funktionieren von Ökosystemprozessen auf verschiedenen räumlichen Ebenen zu betrachten.

Introduction

Freshwater ecosystem services

Freshwater ecosystems, including rivers, lakes, marshes, and costal areas, provide many services that contribute to human well-being and poverty alleviation. These services include, for example, food and freshwater supply, flood control, groundwater recharge, water purification, recreation or storage, recycling, and processing of nutrients.

Two of the most important freshwater ecosystem services affecting human well-being are food supply and water availability. Inland fisheries are of particular importance in developing countries to assure their needs for animal protein. For example people in Malawi obtain about 70-75 % of their total animal protein from inland fishery (Millennium Ecosystem Assessment 2005b). Groundwater often recharged through rivers, plays an important role in water supply. It is estimated that 1.5-3 billion people depend on it as a source of drinking water (Millennium Ecosystem Assessment 2005b).

In order to exploit these benefits provided by freshwater ecosystems, humans have modified these systems dramatically. Modifications include: canalization and modification for navigation, construction of dams built for flood protection and electricity generation, water withdrawal for irrigation and drinking water, and alterations in water quality. Worldwide more than 500,000 km of waterways have been altered for navigation and more than 63,000 km of canals have been constructed (Abramovitz 1996, Tockner and Stanford 2002, Revenga and Kura 2003). There are now more than 45000 large dams (>15 m), and more than 2800 large reservoirs (>0.1 km^3) store more than 6300 km^3 of freshwater (Revenga and Kura 2003). Water withdrawals comprise more than 3800 km^3 per year, and contamination with pathogens, decomposable organic matter and organic micro pollutants severely affect inland water systems at the global scale (Meybeck 2003). In developing countries, an estimated 90 % of waste water is discharged directly to rivers and streams without any previous treatment.

Other threats to inland water systems are invasive species that contribute to species extinction in some freshwater systems, or climate change that will directly or indirectly affect the biota, processes and services in a largely unknown way (Millennium Ecosystem Assessment 2005a).

In other words, human domination affects almost all aspects of freshwater ecosystems but, in particular, the flow regime, water quality, biodiversity and biogeochemical cycles. Therefore, the need for managing this natural capital in a sustainable way has highest priority. However, to develop sustainable ecosystem management and ecosystem services, it is critical to understand ecosystem structure and function (Norberg 1999, Ward et al. 2002).

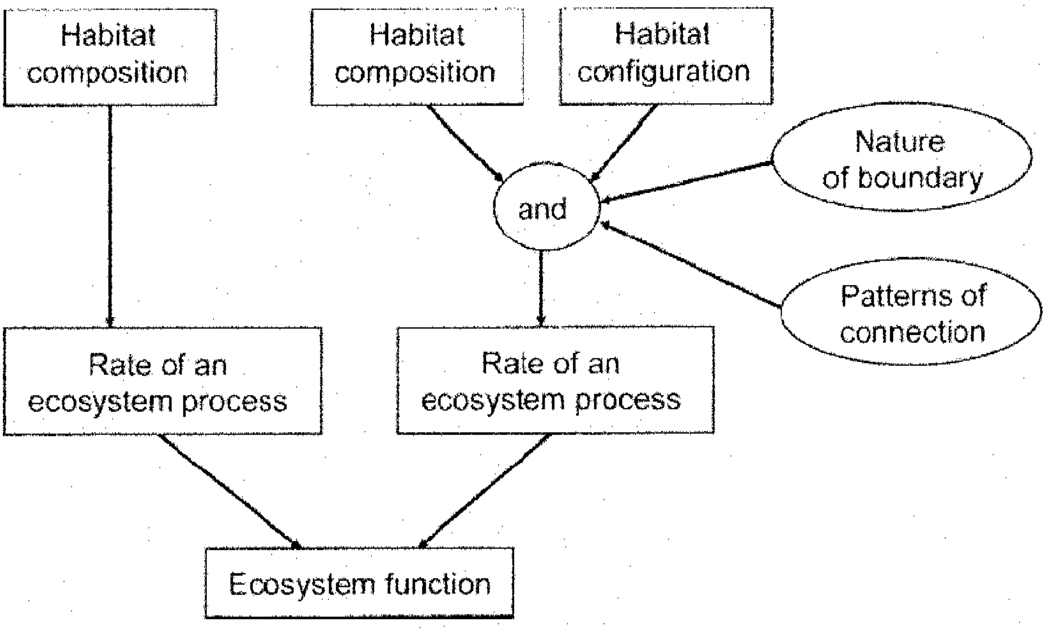

Figure 1: Illustration how landscape composition and configuration control ecosystem function. Influence is indicated by arrows, and ellipses enclose aspects of configuration that influence process rates (Meyer 2005).

Habitat heterogeneity and ecosystem function

Environmental heterogeneity is considered as the variance of pattern and processes over space and time (Kolasa and Rolle 1991, Langhans et al. 2006). The key components of heterogeneity are the composition, configuration and connection of habitats determining ecosystem functioning. When process rates vary little between landscape patches or where there is little exchange between patches, ecosystem function reflects landscape composition. Both, composition and configuration will play a role in determining the rate of an ecosystem process, depending on the nature of boundary between landscape components with different process rates and on the patterns of connection between components (Meyer 2005; Figure 1).

Natural rivers

Natural river corridors can function as model ecosystems to investigate the linkage between environmental heterogeneity and ecosystem functioning. They are highly diverse, dynamic, and complex ecosystems that undergo cycles of expansion, contraction, and fragmentation along the longitudinal, lateral, and vertical dimensions (Stanley et al. 1997, Norberg 1999, Ward et al. 2002). They can be conceptualized as a three dimensional dynamic mosaic of different landscape elements and hydrological exchange patches (Malard et al. 2002, Stanford et al. 2005). These landscape elements differ widely in their structural properties und functional performance and hydrology is one of the most important variables for creating and maintaining habitat heterogeneity and influencing various ecosystem processes (Benke et al. 2000, Tockner et al. 2000, Van der Nat et al. 2002).

Research gaps

Understanding causes and consequences of spatial heterogeneity in ecosystem functioning has been considered as the "final frontier" in ecology.

We need a detailed documentation of how environmental heterogeneity affects ecosystem function to provide a more complete understanding of landscape function and to enhance our ability to scale up and down (Turner and Chapin III 2005). Further, we need to incorporate spatial heterogeneity into spatially explicit models that which allow us to make predictions about the future behaviour of highly complex and dynamic ecosystems (Canham et al. 2003, Dole and Niemi 2004), which is useful for the development of management strategies.

The Tagliamento River study system

The study was conducted in the Tagliamento river in northeastern Italy. Detailed descriptions of the system are given in the various chapters of this thesis or elsewhere (e.g., Ward et al. 1999, Arscott et al. 2002, Van der Nat et al. 2002, Tockner et al. 2003). Important system characteristics in the context of this thesis are:

(1) Moderate human impact: Despite some constraints and water abstraction, the upper and middle sections of the Tagliamento River are still in a near natural state. Only in the lowermost 30 km is the river constrained by artificial embankments.

(2) A near natural flow regime: The Tagliamento River is characterized by a flashy discharge regime with peaks in spring and autumn and frequent water level variations (flow pulses).

(3) Strong vertical hydrologic exchange: In the mid section of the Tagliamento River a large losing and gaining zone extend downstream. Between these zones the river lacks surface flow.

(3) Landscape diversity: Within the mid-section of the Tagliamento River different aquatic (e.g., channels, ponds) and terrestrial (e.g., riparian forest, vegetated islands, exposed gravel sediments, large wood accumulations) habitat types can be found, which are all affected by variable flow regimes.

Goal and organisation of the study

The thesis is part of a holistic ecosystem study integrating investigations of hydrological and morphological dynamics, biodiversity patters, foodweb structures, ecosystem processes and surface-subsurface exchange patterns along the longitudinal, lateral, vertical and temporal dimensions (Arscott 2001, Van der Nat 2002, Karaus 2004, Pätzold 2004, Langhans 2006). It was further incorporated into the EU project "TempQsim" (www.tempqsim.net) that was aimed to improve the understanding of water quality dynamics in temporary waters and to develop and extend environmental models.

The primary goal of this study was to assess environmental heterogeneity at the habitat and landscape level in a floodplain ecosystem and to link this heterogeneity with ecosystem processes. The focus was on respiration as a key process in the carbon cycle that integrates the energy flow through the biotic compartments of aquatic and terrestrial ecosystems. Therefore, respiration is a suitable parameter to characterize the functional integrity of ecosystems (Van Voris et al. 1980, Uehlinger and Naegli 1998, Euskirchen et al. 2003).

The thesis encompasses four chapters addressing different aspects of environmental heterogeneity and ecosystem function:

In chapter 1 we investigated the dynamic nature of floodplain ecosystems by quantifying expansion and contraction dynamics (longitudinal, lateral and vertical) along the floodplain. This included channel mapping, discharge and vertical hydraulic gradient measurements using Doppler and piezometer techniques and the simulation of expansion and contraction dynamics using simple empirically derived models.

In chapter 2 the influence of vertical hydraulic exchange on the habitat template, hyporheic respiration and periphyton dynamics was investigated at the reach scale and the scale of bedform units, i. e. pool riffle sequences.

In chapter 3 of the thesis, soil and sediment respiration in different aquatic and terrestrial floodplain habitats such as gravel bars, vegetated islands, riparian forest and channels across gradients in organic matter content, temperature, moisture, and grain size was studied as well as the effect of inundation using a combined approach of *in situ* and laboratory measurements. The results were used to develop a one-dimensional empirical model to predict soil and sediment respiration

In chapter 4, we implemented this one-dimensional empirical model into a spatially explicit GIS based model to upscale sediment respiration in the dynamic and heterogeneous floodplain. The model was used to investigate and predict the effect of changes in habitat heterogeneity on soil and sediment respiration at the landscape scale.

The research of this thesis is a contribution toward the understanding of the linkage between environmental heterogeneity and ecosystem functioning in complex and dynamic floodplain systems at different spatial scales. The results can contribute to develop a sustainable management strategy of riverine ecosystems and related ecosystem services.

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1. ECOSYSTEM EXPANSION AND CONTRACTION DYNAMICS ALONG A LARGE ALPINE ALLUVIAL CORRIDOR (TAGLIAMENTO RIVER, NORTHEAST ITALY)

M. Doering, Uehlinger, U., Rotach, A., Schlaepfer, D. R., and Tockner, K. (2007): Ecosystem expansion and contraction dynamics along a large alpine alluvial corridor (Tagliamento River; Northeast Italy). Earth Surface Processes and Landforms. In press

Abstract

Riverine floodplains are pulsing ecosystems that expand and contract with changing flow. In this study we quantified large-scale expansion and contraction dynamics of surface waters along a 41.5 km braided section of the last remaining semi-natural large Alpine gravel-bed river (Tagliamento River; NE Italy). To assess surface-subsurface exchange patterns we measured discharge and vertical hydraulic gradients at multiple locations along the corridor. We identified two river sections delineated by distinct geomorphic knickpoints. In the upper 29 km, Section I (losing zone), surface flow decreased on average by $2.5 \pm 0.8\ m^3\ s^{-1}$ *per river-km. In the downstream 12.5 km, Section II (gaining zone), surface flow increased on average by* $0.3 \pm 0.1\ m^3\ s^{-1}$ *per river-km. The losing zone experienced frequent and extensive drying and rewetting cycles. The length of the dry river section was measured over a 1.5 year period using differential GPS. Up to 23 km of Section I fell dry at the surface. Frequent and irregular flow pulses led to rapid expansions of the wetted channel at velocities of up to 3* $km\ h^{-1}$*, while the subsequent contraction velocities were less than 0.5* $km\ h^{-1}$*. Water level was linearly regressed against the total length of the dry river section (*$R^2=0.74$*;* $p < 0.0001$*). This relationship, in combination with a continuous stage record, was used to evaluate expansion and contraction dynamics over a 4 year period. Timing, frequency, magnitude (spatial extent), and duration of expansion and contraction dynamics reflected* *the flashy flow regime of the Tagliamento River including a high intra- and inter-annual variability of surface drying and rewetting. Our study emphasizes that even small changes in flow can cause major increases or decreases of ecosystem size, thereby creating a highly dynamic and harsh environment for both terrestrial and aquatic organisms.*

Introduction

Riverine floodplains are defined as the entire channel network and valley-bottom area that is capable of flooding (Stanford et al., 2005). As such they are highly complex and dynamic ecosystems that undergo distinct cycles of expansion, contraction, and fragmentation along longitudinal, lateral, and vertical dimensions (Stanley et al. 1997, Ward 2002, Malard et al. 2006). Flood pulses exceeding bankfull level and droughts represent two extremes of the flow regime (Lytle and Poff 2004). Between these extremes rivers experience frequent instream water level fluctuations ('flow pulses' *sensu* Tockner et al. 2000), which lead to expansion and contraction of the channel network. The magnitude, frequency, duration, and timing of the expansion and contraction are important variables influencing the size, spatial configuration, and connectivity of aquatic and terrestrial habitats of floodplain ecosystems (Junk 1989, Sparks et al. 1990, Ward 2002). These dynamic processes shape floodplain communities and ecosystem functioning (e.g., Jones 1995, Robertson et al. 1999, Lake 2000, Humphries and Baldwin 2003, Langhans and Tockner 2006).

The lateral expansion and contraction of floodplain ecosystems has been studied extensively; examples include the subtropical Ogeechee River in southeastern USA (Benke et al. 2000), the Amazon River (Sippel et al. 1998), and the Alpine Tagliamento River in northeastern Italy (Van der Nat et al. 2002). However, only few studies focused on large-scale longitudinal expansion and contraction in combination with vertical exchange processes. Notable examples are studies in the proglacial Val Roseg River floodplain in Switzerland (Malard et al. 2002, Malard et al. 2006) and the semi-arid catchment of Sycamore Creek in Arizona, USA (Stanley et al. 1997).

Apart from these studies, information on longitudinal expansion and contraction dynamics is widely lacking. However, such information is essential to understand the effect of changing flow conditions on biogeochemical processes and nutrient transformations, especially in temporary streams (Baldwin and Mitchel 2000, Jakobson et al. 2000, Dahm et al. 2003, Humphries and Baldwin 2003). Worldwide 30 % of all rivers are temporary, but our knowledge about their functioning is still in its infancy (Poff 1992).

The goal of this study was to investigate expansion and contraction dynamics along a large braided corridor and to discuss their potential significance for terrestrial and aquatic communities as well as for ecosystem processes. To achieve this goal we quantified (i) vertical exchange processes and (ii) large-scale expansion and contraction dynamics at different time scales along one of the last remaining semi-natural river corridors in Central Europe, the Tagliamento River in northeastern Italy. Two key questions were asked: First, what is the magnitude of surface – subsurface water exchange along the gravel-bed corridor? Second, what are the magnitude (spatial extent), duration (number of days), frequency (number of drying and rewetting cycles), and timing (season) of surface expansion and contraction along the gravel-bed corridor? To answer these questions we quantified surface discharge and vertical hydraulic gradient at multiple locations along the corridor. Further, we developed a simple model to predict surface drying and rewetting at average daily intervals along the entire study reach. This model is based on the relationship between water level and the spatial extent of ecosystem expansion and contraction. Finally we discuss potential ecological implications of these large-scale expansion and contraction dynamics that were historically a common feature of braided gravel-bed rivers, particularly in Mediterranean and semi-arid regions (Tockner et al. 2006).

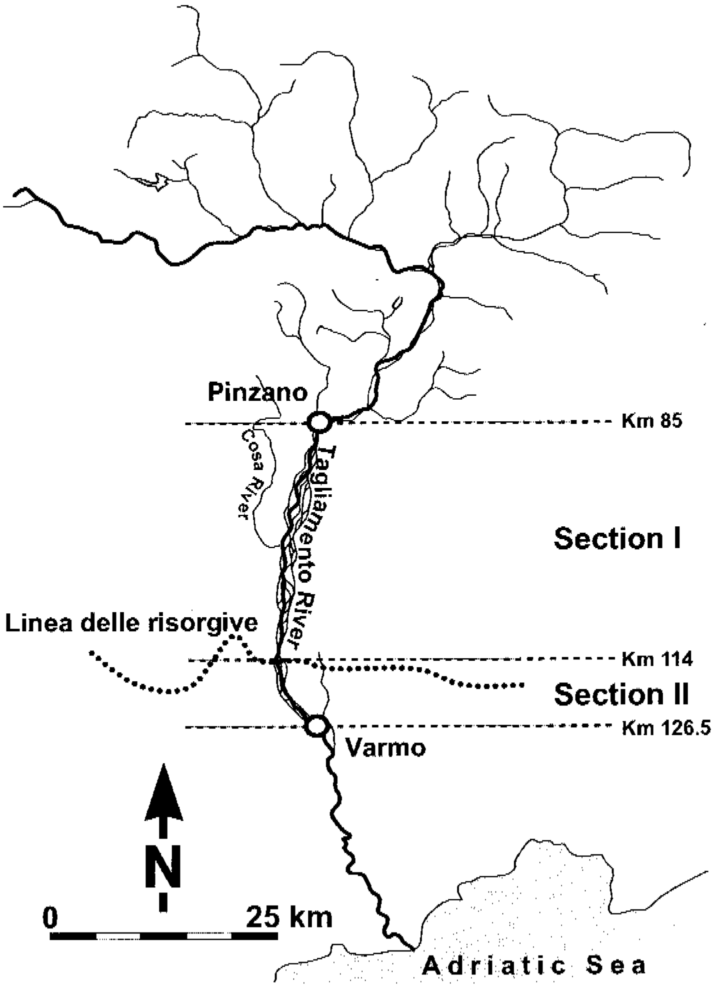

Figure 1: Map of the Tagliamento catchment indicating the location of the main study area delineated by distinct geomorphic knickpoints (modified after Ward et al. 1999). Section I extends from the bed-rock constrained knickpoint at Pinzano (river-km 85-114) to the knickpoint of the "linea delle risorgive". Section II (river-km 114-126.5) extends to the transition between the braiding and meandering section.

Study area

The Tagliamento River in northeastern Italy (46° N, 12°30' E; Figure 1) is a 7th order river, that flows unimpeded by high dams for 172 km to the Adriatic Sea and drains an area of approximately 2580 km^2. It is a mountainous catchment over 70 % of which is located in the Alps. The highest peak in the catchment is Mt. Coglians (2781 m a.s.l.). The mean altitude is 987 m a.s.l. The Alpine and prealpine areas consist mainly of limestone and flysch, occasionally intermixed with layers of gypsum (Tockner et al. 2003). The lowland section is part of the Venetian - Friulian Plain forming a highly permeable aquifer, several hundred meters deep (Fontana et al. in press; Figure 3).

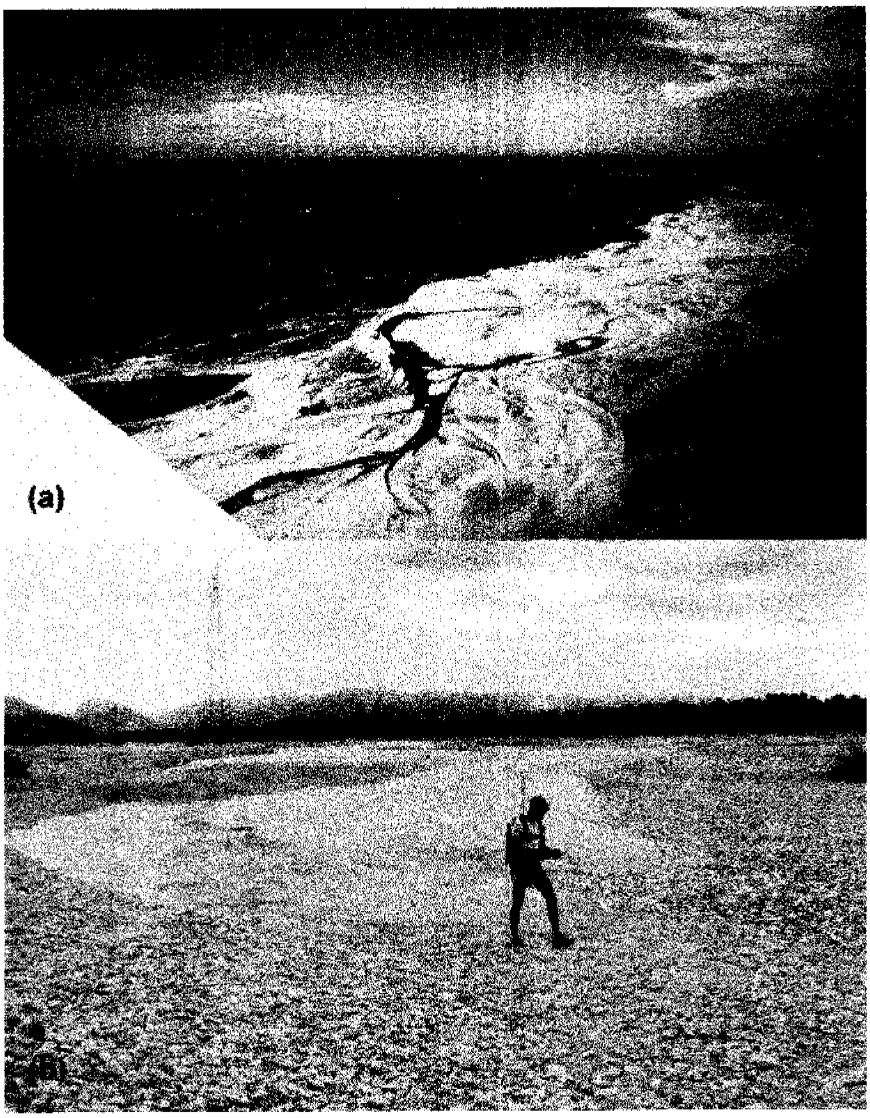

Figure 2: (a) Aerial photograph of Section I showing the downstream end of the wetted channel and the dry river corridor. (Photo: D. Van der Nat). (b) Flow front of the expanding channel after a headwater storm event (Photo: A. Rotach).

Average annual precipitation is 2150 mm, but precipitation increases from W to E and S to N from 1000 mm to ~3000 mm. The Tagliamento River is influenced by both Alpine and Mediterranean snowmelt and precipitation regimes (Q_{80} = 72 m^3 s^{-1}; Ward et al. 1999). As a result, it exhibits a flashy discharge regime with peaks in spring and autumn. However, flow and flood pulses (≥ bankful discharge) can occur at any time of the year (Arscott et al. 2002). Despite local human impacts, the Tagliamento River is considered to be the last remaining large semi-natural river corridor in Central Europe.

Our main study area (Figure 1) is an unconstrained 41.5 km river segment downstream of the bedrock constrained knickpoint at Pinzano (river-km 85) to the bridge at Varmo (river-km 126.5) situated in the lowland section. Downstream of Pinzano (Section I) the river loses surface water into the highly permeable alluvial aquifer (Figure 2 and 3). A portion of the river in this segment lacks surface flow (maximum dry length: 23 km) under low flow conditions. At river-km 114 the "linea delle risorgive" (Figure 1) consisting of silt and clay sediments acts as an aquiclude and forces the groundwater to the surface (Fontana et al. in press; Figure 3).

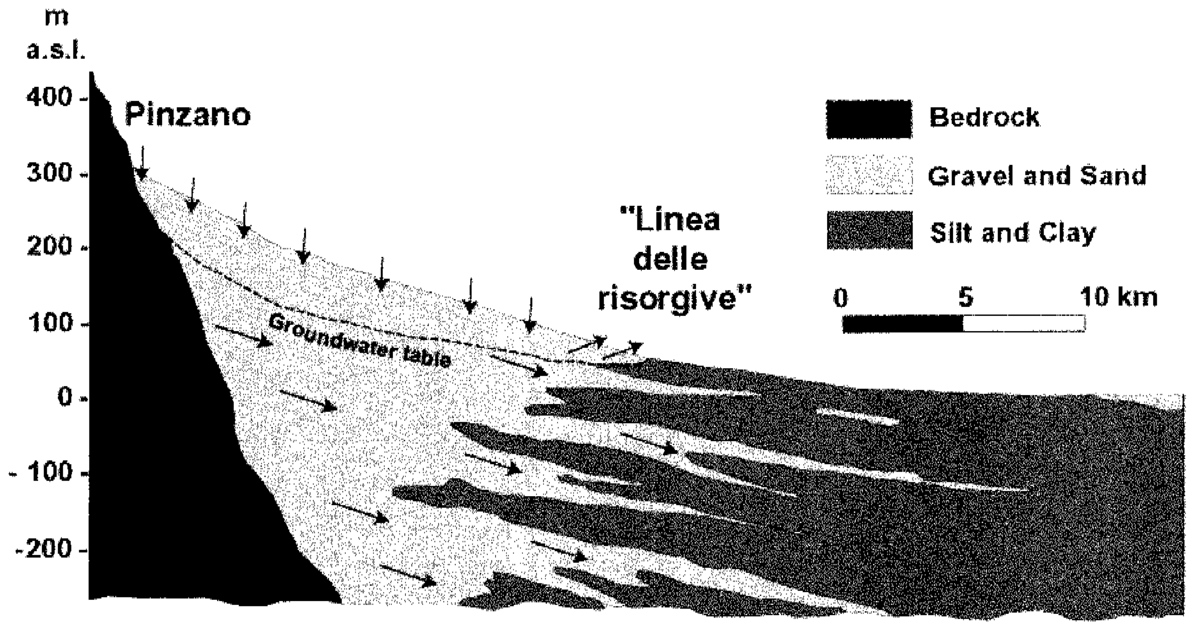

Figure 3: Longitudinal - vertical profile of the Venetian - Friulian Plain (modified after Fontana et al. 2004). Arrows mark the direction of the surface- and subsurface flow.

This results in massive upwelling of Tagliamento River water (Section II) (Figs. 1). Only a small fraction of this water returns to the Tagliamento Riverbed itself since it also feeds adjacent rivers (Fontana et al. in press), as for example, the Stella River located to the east of the Tagliamento River. Downstream of the bridge at Varmo the braiding river transforms into a meandering river (geomorphic knickpoint at the downstream end of Section II).

The fluvial corridor of the main study reach is up to 2 km wide and contains exposed gravel (32 km^2), surface water ($\leq$ 5 km^2), vegetated islands (6 km^2), riparian forest (20 km^2), and developed land (21 km^2). At river-km 88.5 water is abstracted for fish farming and irrigation (3.3 ± 0.1 m^3 s^{-1}; n = 3). The Cosa River, the only natural although temporary tributary along the study reach, enters the Tagliamento River at river-km 98.8 (see Figure 1). Surface flow was observed only twice during the study period (20 January 2004: 1.89 m^3 s^{-1}; 22 October 2004: 2.31 m^3 s^{-1}).

For a complete description of the catchment and longitudinal geomorphic features see Ward et al. (1999), Arscott et al. (2000), Gurnell et al. (2001), Arscott et al. (2002), and Tockner et al. (2003).

Methods

Vertical hydraulic gradient and surface discharge

We determined the direction and intensity of groundwater - stream water exchange by measuring the vertical hydraulic gradient (VHG). VHG is defined as:

$$VHG = \frac{\Delta h}{\Delta l}$$

where Δh is the difference in hydraulic head between the water level in the piezometer and the level of the stream surface (cm), and Δl is the depth from the surface of the streambed to the first opening in the piezometer sidewall (Baxter et al. 2003). Therefore, VHG is a unitless metric. It is positive under upwelling conditions and negative under downwelling conditions.

VHG was measured in five mini-piezometers installed across each of 8 to 10 transects equally spaced along Sections I and II (six different dates, July 2003 to April 2004). The number of transects differed with the wetted length of

Section I. Differences in VHG among transects were evaluated using Kruskal-Wallis ANOVA.

We calculated infiltration- and exfiltration rates (m^3 sec^{-1} km^{-1}) along the entire study area by measuring surface discharge across 7 to 13 transects (nine dates between July 2003 and October 2004). In shallow channels we used a Mini-air flow meter (Schildknecht Messtechnik AG, Gossau, CH) and an Acoustic Doppler Velocity Meter (ADV; Flowtracker, SonTek, San Diego, CA, USA). Discharge was calculated using the area-velocity method (Gore 1996). In channels deeper than ~1m, we applied an Acoustic Doppler Profiler (ADP; SonTek, CA, USA) mounted to an inflatable raft. Detailed information on ADP and ADV applications are provided by Lorang et al. (2005).

Expansion and contraction dynamics

Between April 2003 and October 2004, we monitored expansion and contraction dynamics along the main study area by determining the beginning and end of the wetted river section with a differential global positioning system (dGPS; TCS1, Trimble, Sunnyvale, California, USA). In total, we measured the downstream end of the wetted channel (Section I) 200 times and the emergence of channels in Section II 22 times. In addition, the expansion and contraction dynamic of a major flow pulse was monitored between 2 and 14 July 2003 (total: 536 measurements). The length of the wetted channel (Section I) was regressed against water level in a linear model (Statistica 5.1; Statsoft Inc., Tulsa, Oklahoma, USA).

Duration, frequency, extent and timing of dry and wet cycles

Duration, frequency, magnitude, and timing are important components of the drying and rewetting cycle. We used the calculated relationship between the length of the wetted channel and water level to convert 4 years of daily water level values (from Pinzano station) to daily dry length of Section I. Then we calculated duration of surface drying and wetting distribution, number (frequency) of shifts between surface drying and wetting, and magnitude of dry-wet cycles at 1 km distance intervals along the entire 41.5 km study reach.

We limited the application of our predictive regression to four years (2001 - 2004) for the following reasons: First, the analyses of the hydrograph from 1982 to 2004 indicated that the yearly average stage height declined by 2 cm per year. We could not attribute this decline to changes in morphology (deepening of channels) or hydrology (increased abstraction). Second, the period of 2001 to 2004 covers a representative range of the hydrologic conditions of the Tagliamento River and includes an extremely dry (2003) and a wet (2002) year.

Results

Vertical hydraulic gradient (VHG) and surface discharge

Average VHG was significantly different between Section I and Section II (Kruskal Wallis ANOVA, $\chi^2 = 129.79$, df = 1, $p < 0.001$). Average VHG was negative along Section I (-0.67 ± 0.55) and positive along Section II (0.03 ± 0.23). However, local down- and upwelling conditions were measured along both sections (Figure 4a). Spatio-temporal variation, expressed as the maximum range of VHG across individual transects, was higher in Section I (range: -2.07 to + 0.55) than in Section II (range: -0.59 to + 0.70) (Figure 4a).

Discharge decreased (Section I) and increased (Section II) linearly along the study reach. In Section I discharge decreased on average 2.5 ± 0.8 $m^3 s^{-1}$ (n = 9) per river-km. In Section II discharge increased on average 0.3 ± 0.1 $m^3 s^{-1}$ (n = 9) per river-km (Figure 4b). Along Section I up to 60 $m^3 s^{-1}$ downwelled into the expansive aquifer. However, along the 12.5 km long Section II less than 13 $m^3 s^{-1}$ re-emerged to the surface of the Tagliamento River bed. There was no significant correlation between total discharge, measured at the knickpoint in Pinzano, and the relative rate of infiltration and exfiltration.

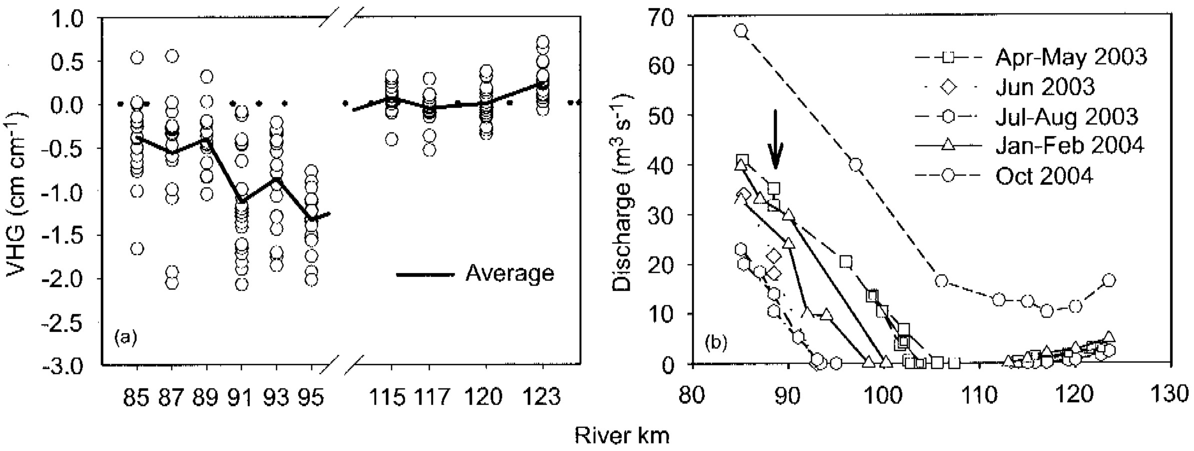

Figure 4: (a) Vertical Hydraulic Gradient (VHG; cm cm^{-1}) along Section I (n=183) and Section II (n=129) (July 2003 to April 2004). (b) Surface discharge (m^3 s^{-1}) along Section I and Section II (April 2003 to October 2004). Arrow marks the location of water abstraction.

Expansion and contraction dynamics

Between 2001 and 2004 average daily water level at the knickpoint at Pinzano (river-km 85) ranged from 73 cm to 361 cm. The corresponding calculated discharge ranged from 20 to > 200 m^3 s^{-1}. Average annual water level ranged from 121 cm (2004) to 167 cm (2002) (Table 1).

Table 1: Average, minimum and maximum water level (cm) at the knickpoint Pinzano (river-km 85). Percentage and days of disconnection between Sections I and II, and average length (km) and relative proportion (%) of Section I that falls dry at the surface (2001 to 2004; based on average daily water level records provided by the Direzione Centrale dell'Ambiente).

Year	Average stage (cm)	Minimum stage (cm)	Maximum stage (cm)	Disconnection (% of year)	Average length (km) and proportion (%) that falls dry
2001	157	90	286	59 (215 days)	6.1 km (21%)
2002	167	100	361	49 (179 days)	4.9 km (17%)
2003	121	73	279	96 (350 days)	13.1 km (45%)
2004	142	85	307	85 (310 days)	8.1 km (28%)
Average	**147**	**87**	**308**	**73 (266 days)**	**(8.1 km) (28%)**

Sections I and II became surficially connected when river discharge at the knickpoint at Pinzano reached 60 m^3 s^{-1} (water level: 165 cm). Below this threshold, water level at the downstream end of Section II (river-km 126.5) remained very constant despite a pulsed hydrograph at the upstream end of Section I (Figure 5a).

During dry summer conditions the upstream end of the wetted channel in Section II moved from river-km 113.6 slowly downstream to river-km 114.5 before it moved 1.5 km upstream again with the onset of autumnal rain events. In Section I, the uppermost 6 km (river-km 85 to 91) carried surface flow during the entire study period. However, downstream of river-km 91 the dry channel rapidly expanded and contracted with changing water levels. During the main investigation period (April until August 2003) we calculated a maximum expansion velocity of 2.9 km h^{-1} and a contraction velocity of up to 0.5 km h^{-1} (Figure 5b).

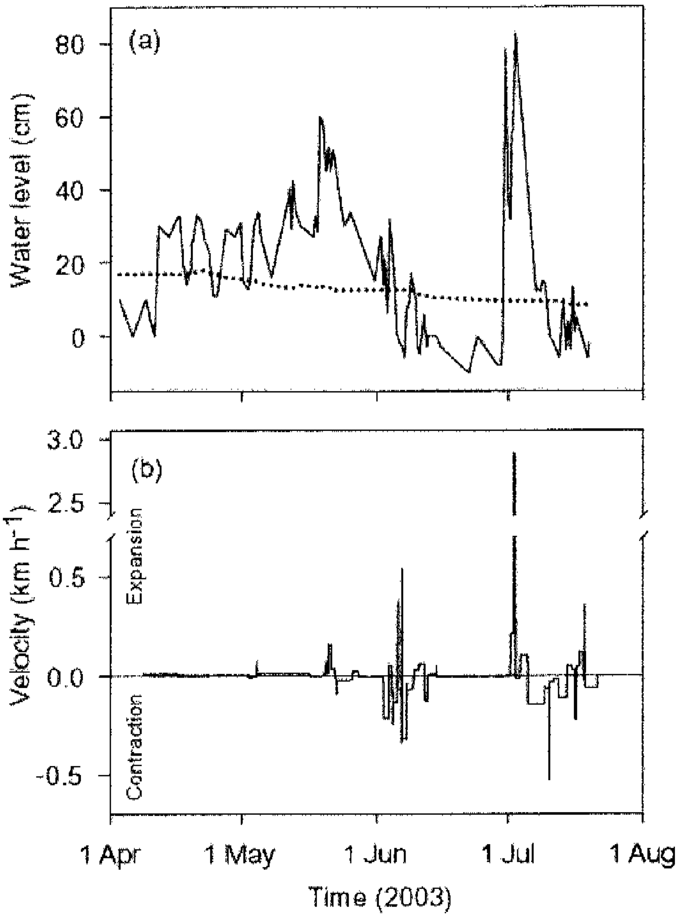

Figure 5: (a) Average daily water level (cm) records at Pinzano (river-km 85; solid line) and at the bridge at Varmo (river-km 126.5; dotted line) from April to August 2003. (b) Expansion and contraction velocity (km h^{-1}) of the wetted channel in Section I from April to August 2003.

The length of the dry riverbed was significantly related to the water level (and discharge) at the knickpoint at Pinzano (Figure 6a). The maximum length of the dry riverbed was 23.5 km. During a single flow pulse, beginning on 2nd

July 2003, the wetted channel expanded by 19.9 km within 4 days and contracted by 21.7 km during the subsequent 9 days (Figure 6b). This flow pulse exhibited a distinct hysteresis effect with fast expansion and delayed contraction of the wetted channel. For example, at a water level of 140 cm the length of the dry river bed was 20 km during the expansion phase but 5 km during the contraction phase (Figure 6b).

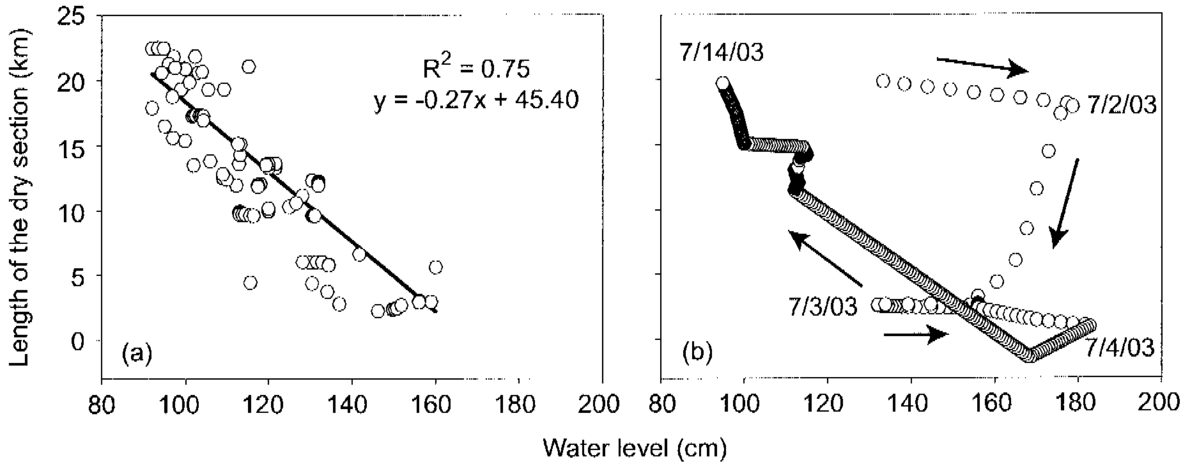

Figure 6: (a) Relationship between water level (cm) at Pinzano (river-km 85) and length of the dry channel in Section I (April 2003 to October 2004; n = 200). (b) Relationship between water level (cm) at Pinzano (river-km 85) and length of the dry channel in Section I during a single flow pulse from 2 July to 14 July 2003. Data points represent a linear interpolation (hourly interval) of the length of the dry river corridor and the stage at Pinzano.

Duration, frequency, and timing of dry and wet cycles

We used the relationship between water level and length of the dry channel to model expansion and contraction dynamics over a four year period (2001 to 2004; average daily values). This simple model was based solely on the average length of the dry channel. It did not take into account potential hysteresis effects (Figure 6b) and the area of wetted surface. The output of the model suggested a substantial inter-annual variability in duration, frequency, and timing of surface drying and rewetting (Figure 7). The average annual length of the dry reach varied from 5 km (2002) to 13 km (2003) (Table 1). Maximum contraction was calculated either in late summer (2001, 2003) or in early spring (2002, 2004); with frequent and often rapid expansion and contraction cycles at any given time of the year (Figure 7).

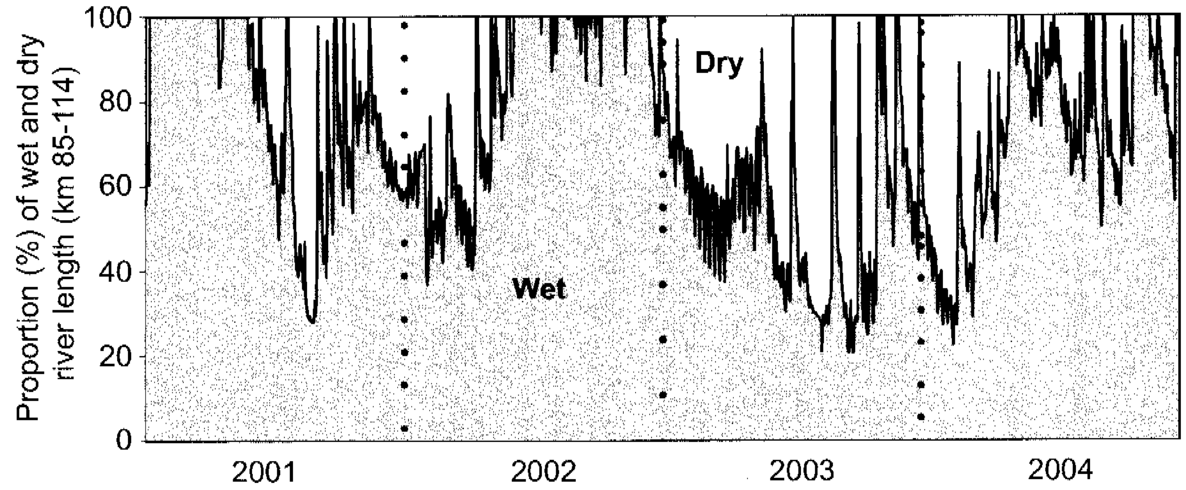

Figure 7: Relative proportion (%) of wet (gray area) and dry (white area) channel length along Section I from 2001 to 2004 (daily averages).

Along Section I, the relative duration (% of time) of surface flow decreased continuously downstream of river-km 91. At the downstream end of the temporary section (river-km 114) the number of days with surface flow ranged from 16 (2003) to 185 (2002) (Figure 8a). Frequency of dry and wet cycles exhibited a unimodal distribution. The maximum number of drying and rewetting cycles ranged from 33 (2002) to 53 cycles per year (2003), and the location with highest frequency differed among years (Figure 8b).

Discussion

Rapid changes in ecosystem size are a well-known phenomenon in Mediterranean and semiarid rivers although quantitative data are very scarce (Stanley et al. 1997, Gasith and Resh 1999, Tockner et al. 2000). In this study we quantified longitudinal expansion and contraction dynamics of surface water and vertical hydraulic exchange (infiltration and exfiltration rates) along the 41.5 km braided river corridor of the Tagliamento River, NE Italy. The Tagliamento River offers the rare opportunity to study large-scale hydrologic, geomorphic, and ecological processes under near-natural conditions; therefore it serves as a model ecosystem of European importance (Tockner et al. 2003). It still contains the complexity and dynamics that most Alpine rivers had prior to river regulation and dam construction.

Underlying mechanisms of large-scale expansion and contraction dynamics

The rapid expansion and contraction dynamics along the Tagliamento River corridor is primarily a function of high infiltration rates and distinct flow variations. The average infiltration rate of 2.5 m^3s^{-1} was much higher than in the Middle Fork of the Flathead River (USA, NW Montana) (~1.3 m^3s^{-1} per river km; Stanford et al. 2005) or the semi-arid Homestead Creek (Australia) (~1.1 m^3s^{-1}; Dunkerley and Brown 1999). High negative vertical hydraulic gradients in Section I exceeded reported maximum negative values of up to -0.37 cm cm^{-1} (Vallet et al. 1994, Baxter et al. 2000). Infiltration rates are expected to be influenced by water temperature, which affects viscosity, sediment permeability affected by grain size distribution and porosity, and wetted channel area (Brunke and Gonser 1997, Constantz 1998). Temperature is subject to seasonal and diel variation but also changes along the river continuum. For a losing reach in the Ohio River, Constantz (1998) reported a doubling of the infiltration rate for a temperature increase from 0 to 25 °C. For the Tagliamento River we found no seasonal variation of the infiltration rate, an indication that other factors mask potential temperature effects. During flow or flood pulses deposition or removal of fine sediments affects the permeability of surface bed sediments (Dunkerley and Brown 1999, Gasith and Resh 1999). For example, we observed temporary clogging of the bed sediments in the Tagliamento River after an extremely flashy flood event in August 2003. A subsequent flood restored high permeability. Although not measured, we assume that the wetted area increases linearly with flow as shown by Van der Nat et al. (2002), for two floodplain segments located upstream of our study reach. In our main study reach the number of wetted channels across a transect ranged from 1 to a maximum of 11 channels at mean flow conditions (Ward et al. 1999). However, we did not find a relationship between discharge, which reflects channel area, and specific infiltration rate.

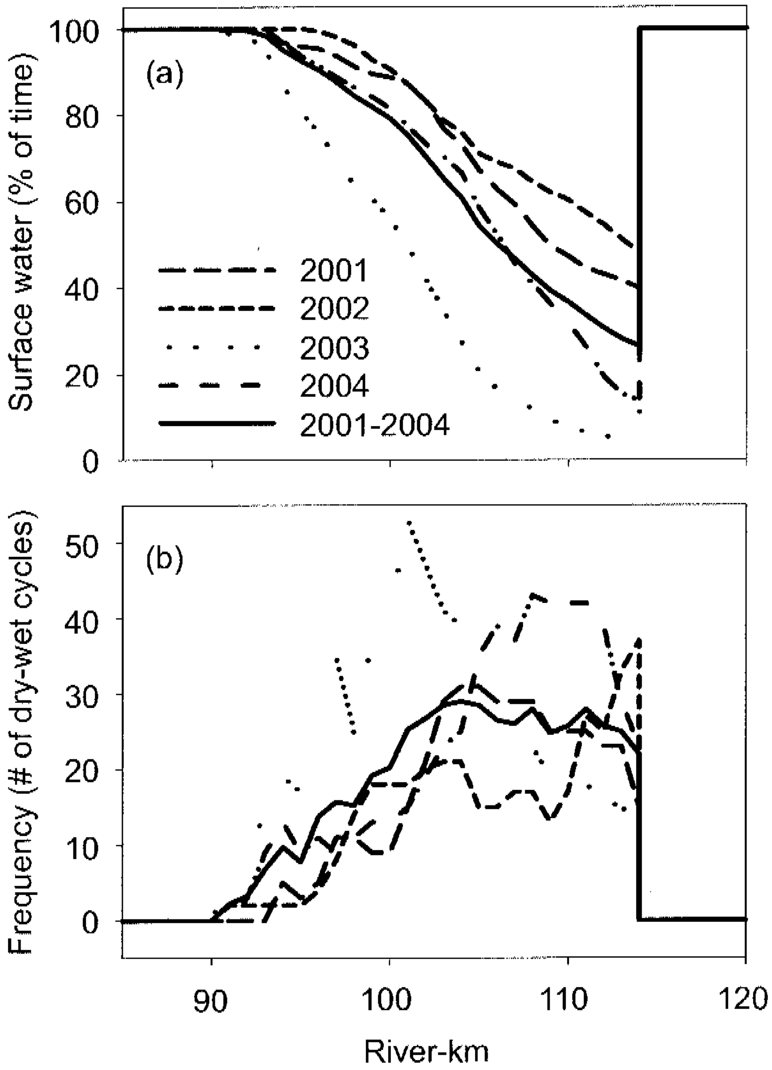

Figure 8: (a) Spatiotemporal distribution of surface flow duration (% of time) along Section I and the upper part of Section II (average of 2001 to 2004 and average of all individual years). (b) Number of dry-wet cycles (frequency) along Section I and the upper part of Section II (average of 2001 to 2004 and average of all individual years).

We observed an abrupt transition from the losing section (Section I) to the permanent gaining section (Section II). A layer of impermeable fine sediments forces infiltrated Tagliamento River water to emerge to the surface starting at

approximately river-km 114. The gaining zone is characterized by relatively stable flow conditions, except during high flow when Sections I and II are connected at the surface. The large alluvial aquifer serves as a major transient storage zone that stabilizes flow in the gaining zone (Baxter et al. 2000, Malard et al. 2002). However, even Section II experienced a slow seasonal expansion and contraction of surface waters (maximum length: ~1.5 km), most likely as a consequence of the slow emptying and refilling of the large alluvial reservoir. The continuous contraction during summer was most likely enhanced by groundwater extraction for irrigation and high evapotranspiration loss. Based on geochemical tracers (i.e., lower sulfate and strontium concentrations in Sections II compared to Section I) we think that the recharging of the alluvial reservoir primarily occurs during high autumnal precipitation and spring snowmelt (K. Tockner unpublished data).

In Section I infiltration rates were more than 10 times higher than exfiltration rates in Section II. Apart from groundwater abstraction, the vast alluvial aquifer expands laterally beyond the study area and therefore feeds rivers outside of the main corridor (Fontana et al. in press).

Spatio-temporal characteristics of expansion and contraction dynamics.

To evaluate lateral and longitudinal expansion and contraction dynamics in streams and rivers, simple models were used relating discharge or stage with inundated area or channel width (Benke et al. 2000, Van der Nat et al. 2002, Malard et al. 2006, this study).

The relationship between the Pinzano stage, and the length of the dry channel (Figure 6a) exhibited some scatter of the data resulting from the hysteretic relationship between the stage and the dry channel length (Figure 6b). Furthermore, the Tagliamento River is subject to some regulation upstream and to water abstraction downstream of the Pinzano stage. These factors imposed some uncertainties on the spatial extent of wetted channel length, which may have been over- or underestimated.

The model output indicates that the losing and gaining reaches became disconnected at the surface between 179 and 350 days per year. In the losing section (Section I), spatio-temporal distribution of dry and wet episodes is highly unpredictable. The river can fall dry at any time of the year, and the location of the maximum frequency of wet and dry cycles is shifting up- and downstream as a result of interannual flow variability. In contrast to the Tagliamento River, highly predictable expansion and contraction cycles of the wetted channel network were reported for the proglacial floodplain of the Roseg River (Malard et al. 2006), which are driven by seasonal snow and ice melt.

Table 2: Tagliamento catchment: Total number and length (km) of stream segments, and proportion (%) of temporary sections calculated for each stream order. n.d. = not determined.

Stream order	Number of stream segments	Average stream segment length (km)	Total stream segment length (km)	Relative proportion (%) that falls dry
1	1663	0.8	1405	62
2	416	1.5	631	51
3	90	3.6	320	6
4	21	7.4	155	n.d
5	6	14.1	85	32
6	2	8.0	16	0
7	1	114.0	114	20
Total	**2199**	-	**2726**	**ca. 46%**

The surface drying of the Tagliamento River is not restricted to the large alluvial corridor. A preliminary investigation in five headwater subcatchments showed that the proportion of temporary stream segments ranged from 6 to 62% per subcatchment (K. Tockner unpublished data). For the entire catchment we calculated that approximately 46% of the drainage network falls dry at the surface (Table 2). Extensive headwater surface drying reflects the catchment geology (dolomite and limestone), topography (i.e. steep slopes), and the highly variable precipitation patterns.

Ecological implications

World-wide, about one third of all streams and rivers are temporary (Poff 1992). In the near future their relative proportion will increase further due to increasing flow variability and increasing water consumption. Temporary streams are also unique because they provide habitats for characteristic aquatic and terrestrial biota. However, we are not aware of a single study that investigated simultaneously aquatic and terrestrial communities along temporary rivers.

This study provided important quantitative information about drying and rewetting cycling along a large gravel - bed river over a multi - year period. Small alterations of the flow regime can lead to major changes in duration, frequency, timing and extent of drying and rewetting with probably severe consequences for terrestrial and aquatic communities and ecosystem processes.

The abrupt losses of aquatic and terrestrial habitats lead to stranding and inundation of the resident biota (Stanley et al. 1994). Unpredictable and rapid changes between dry and wet periods are more difficult for organisms to deal with through evolved adaptations (Lake 2003). For example, for primary producers, rapid drying does not provide sufficient time for production of desiccation- resistant structures or physiological adjustment. Consequently, algae die typically within a short period after drying (Stanley et al. 2004). Stranded organisms such as macroinvertebrates and fish will perish or, if trapped in pools, will suffer from enhanced competition and predation (Boulton 2003, Matthews and Marsh-Matthews 2003, Schlaepfer and Rotach 2003, M. Doering personal observation). Aquatic and terrestrial communities are expected to react differently to expansion and contraction cycles. While terrestrial organisms can rapidly recolonize exposed channels, recolonization of wetted channels by aquatic organisms is often delayed. Recovering of aquatic organisms, for example from drought depends on the extent of desiccation and on the fashion in which water returns, i.e. by a slowly increasing water level or by floods associated with scouring (Stanley et al. 1994, Blinn et al. 1995). Both characteristics are part of the expansion and contraction dynamic of the Tagliamento River.

Drying and rewetting influence ecosystem processes such as nutrient cycling and respiration. As sediments dry out, bacterial biomass and activity decline. In contrast, rewetting flushes nutrients and enhances bacterial activity (JaapBloem et al. 1992, Baldwin and Mitchel 2000, Fierer and Schimel 2002). Frequent drying and rewetting cycles alter the composition of microbial communities by selecting for microbes that can survive rapid changes in water potential (Schimel et al 1999, Fierer et al. 2003), which subsequently affects respiration rates (Van Gestel et al. 1993, Clein and Schimel 1994).

In highly permeable vast aquifers water can travel exclusively in the hyporheic zone for kilometers where its chemistry can change substantially, for example by nitrification. At upwelling sites, nutrient - enriched water can stimulate algal primary production (Grimm et al. 1981, Stanley et al. 1997, Schlaepfer and Rotach 2003) and affects tree growth (Harner and Stanford 2003). At downwelling sites organic matter is trapped in the hyporheic zone, and respiration rates increase (Jones 1995).

This study provides important quantitative information about longitudinal changes of drying and rewetting patterns along a large gravel - bed river. How the different components of the expansion and contraction cycles control aquatic and terrestrial communities as well as ecosystem processes is a major challenge for future research.

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2. VERTICAL HYDROLOGIC EXCHANGE, HYPORHEIC RESPIRATION AND PERIPHYTON BIOMASS IN A LARGE FLOODPLAIN RIVER (TAGLIAMENTO, ITALY)

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In preparation

Abstract

Hyporheic respiration and periphyton biomass in a floodplain reach of the Tagliamento River were examined, focusing on the effect of hydrological linkage between the hyporheic and surface subsystem at the reach scale and the scale of bedform units (i.e., pool-riffle). The study area encompassed a 29 km long losing reach where the decrease of discharge averages 2.5 m^3 s^{-1} *per river km and a 12.5 km long gaining reach where the increase of discharge averages 0.3* m^3 s^{-1} *per river km. The vertical hydraulic gradient was used to characterize the direction of vertical hydrologic exchange. Periphyton biomass (ash-free dry mass) averaged 12.0 ± 12.2 g* m^{-2} *in the losing reach and 21.3 ± 18.9 g* m^{-2} *in the gaining reach. Corresponding hyporheic respiration normalized at 20 °C was 0.42 ± 0.19 mg* O_2 *kg sediment*$^{-1}$ h^{-1} *(losing) and 0.26 ± 0.15 mg* O_2 *kg sediment*$^{-1}$ h^{-1} *(gaining). In contrast to the reach scale, neither periphyton biomass nor hyporheic respiration significantly differed between riffle heads (local downwelling zone) and riffle tails (local upwelling zone). We hypothesize that the hydro-geomorphic characteristics at the reach level impose major constraints on the response of periphyton and respiration to local vertical exchange patterns.*

Introduction

Natural river corridors have been described as a sequence of alternating narrow canyon-constrained reaches and alluvial floodplains (Stanford and Ward 1993). In floodplain reaches subsurface flow can be substantial, depending on the hydraulic conductivity and vertical extent of the alluvial sediments. During dry periods, all river flow may be subterranean (Doering et al. 2007; Learned et al. in press). At the transition from a floodplain reach to constrained reach or where impermeable sediments intersect an otherwise permeable alluvium, subsurface water is forced to the surface. Such reach-scale losing-gaining phenomena are known from a few studies in relatively large rivers (Nyack River, NW Montana, USA, (Poole et al. 2002); Tagliamento River NE Italy; (Doering et al. 2007). Within alluvial reaches, relatively small scale vertical hydrologic exchange patterns are common; at the riffle head surface water infiltrates into the sediments and exfiltrates at the riffle tail (e.g., White 1993, Brunke and Gonser 1997, Franken et al. 2001).

Surface-subsurface water exchange is an important physical process influencing nutrient cycling, community structure, ecosystem processes, and, as a consequence, habitat diversity (Vallett et al. 1994, Jones 1995, Malard et al. 2006). At the pool-riffle scale, Jones (1995) demonstrated that sediment respiration was higher in downwelling areas than in upwelling areas because dissolved and suspended organic matter derived from the infiltrating surface water fuels respiration, and Vallett et al. (1994) found that nutrients released by decomposition of organic matter enhanced algal growth in upwelling areas. Several studies emphasized the importance of scale on interactions between geomorphologic and topographic features and surface-subsurface water exchange (e.g. Fernald et al. 2001, Kasahara and Wondzell 2003, Poole et al. 2004, Pool et al. 2006). But apart from few studies, e.g, on nutrient dynamics or bulltrout spawning (Baxter & Hauer 2000, Dent et al. 2001), studies were primarily focused on a single scale (mainly pool-riffle).

Stream systems can be described as a spatially nested hierarchy, where each level can be associated with geomorphic features and events, and where higher levels impose constraints on lower levels (Frissell et al. 1986). For example, vertical flow patterns at the pool-riffle level are not only controlled by local topography but also by hydro-geomorphic properties of the reach. To understand the effect of vertical hydrologic exchange on lotic ecosystem processes, information on the relative influence of different hierarchical levels is critical.

In this study we investigated the effect of vertical hydrologic exchange on sediment respiration (ecosystem process) and algal biomass (ecosystem property) at two different spatial scales (hierarchical levels) in the Tagliamento River, a large floodplain river in North Eastern Italy. A major feature of the lower Tagliamento River is a large-scale (41 km long) losing and gaining sequence delimited by a bedrock threshold at the upstream end and a zone where relatively impermeable sediment intersects the highly permeable alluvium. As a first step, we investigated sediment respiration and algal biomass in the large-scale losing and gaining areas. We expected that sediment respiration would be higher in the losing than in the gaining reach and an inverse pattern would be observed for algal biomass, similar to what has been observed at the riffle-pool scale (Vallett et al. 1994, Jones et al. 1995). As a second step, we studied the effect of vertical hydrologic exchange on both parameters at the pool-riffle scale thereby focusing on the question whether, or to which extent, local (pool-riffle scale) exchange patterns would shape respective patterns of sediment respiration and algal biomass.

Study system

The Tagliamento River (46° N, 12°30' E; Fig. 2) is a 7th order river originating in the southern limestone Alps and flowing unimpeded for 172 km to the Adriatic Sea (catchment area 2580 km^2; maximum elevation 2781 m a.s.l.).

The Alpine and prealpine areas consist mainly of limestone and flysch, occasionally intermixed with layers of gypsum (Tockner et al. 2003). The lowland section is part of the Venetian - Friulian Plain consisting mainly of carbonate bedrock (limestone and dolomites) that form a highly permeable and several hundred meters deep aquifer (Fontana et al. 2007).

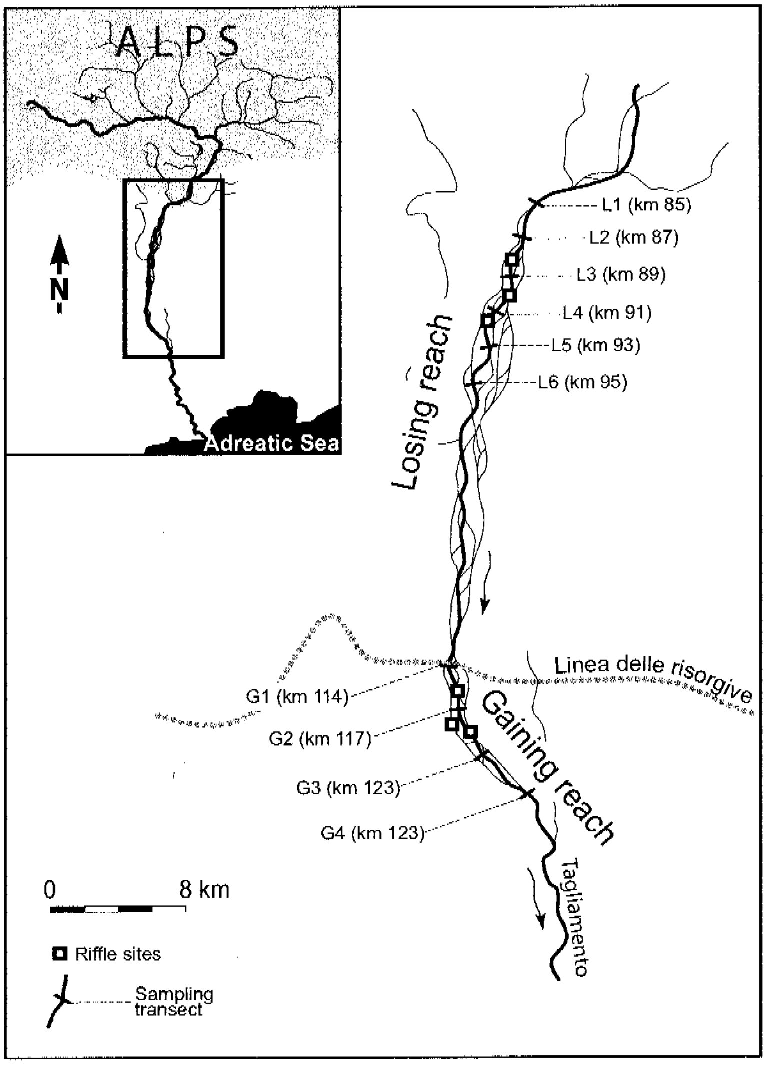

Figure 1: Map of the study reach with transects in the losing reach (L1 - L6) and the gaining reach (G1 - G4) sampled from July 2003 to April 2004. The open squares indicate the riffle sites sampled from October 2004 to July 2005. The insert shows the study area within the drainage of the Tagliamento River.

The flow regime is flashy pluvio nival with flow peaks in spring and autumn. However, flow and flood pulses (≥ bankful discharge) can occur at any time of the year (Arscott et al. 2002). Mean annual discharge at Pinzano (see below) averages 90 $m^3 s^{-1}$.

Our study focused on two adjacent reaches in the lowland plain that distinctly differed with respect to vertical hydrologic exchange. These two reaches are hereafter referred as the "losing" and "gaining" reach. The river corridor is up to 2 km wide and includes gravel (38 %), vegetated islands (7 %), riparian forest (24 %), and developed land (25 %). A more detailed description of the study reach has been given by Arscott et al. (2002) and Tockner et al. (2003).

The losing reach extends from river km 85 (Pinzano) to river km 114 (at river km 85 the river is laterally and vertically bedrock constrained for about 700 m). Downstream of Pinzano, about 2.5 $m^3 s^{-1}$ infiltrate into the highly permeable alluvial aquifer (Doering et al. 2007). At river-km 114, the "linea delle risorgive" (Figure. 1) an aquiclude of sediments rich in silt and clay, intersects the alluvial sediments and forces the water infiltrated in the losing reach to the surface (Fontana et al. 2007). In the adjacent gaining reach, which extends from river km 114 to 126.5, only a small fraction of infiltrated water returns to the bed of the river; i.e., discharge increases on average by 0.3 $m^3 s^{-1}$ per river km (Doering et al. 2007). The length of the wetted river course in the gaining reach is linearly related to the discharge at river km 85. If discharge is <60 $m^3 s^{-1}$, the losing and gaining reach become surface-disconnected. During the dry summer of 2003, surface flow ended downstream of river km 91.

Methods

To assess the effect of the large-scale vertical hydrologic exchange, we sampled six transects in the losing and four transects in the gaining reach from July 2003 to April 2004. The two lowermost transects (L5 and L6) in the losing reach were mostly dry in summer 2003 (Figure 1). These transects were located in runs to minimize the influence of local vertical hydrologic exchange at the pool-riffle scale. The distance between transects varied between two (losing reach) and three km (gaining reach). To asses the effects of small-scale vertical hydrologic exchange we randomly selected three riffles in the gaining and losing reach (Figure 1) and in each riffle we sampled one transect at the riffle head and one transect at the riffle tail. These samples took place on four different dates from October 2004 to July 2005.

In each transect we measured vertical hydraulic gradient (VHG), water chemistry of surface and subsurface water, sediment respiration, periphyton biomass, and organic matter content as described below.

Vertical hydraulic gradient (VHG)

VHG characterizes groundwater - stream water exchange direction and potential intensity. VHG is defined as:

$$VHG = \frac{\Delta h}{\Delta l}$$

where Δh is the difference in head between the water level in the piezometer and the level of the stream surface (cm), and Δl is the depth from the streambed surface to the first opening in the piezometer sidewall (Baxter et al. 2003). VHG is a dimensionless metric that is positive under upwelling conditions and negative under downwelling conditions. VHG was measured in five equally spaced mini-piezometers driven to a depth of ~50 cm depth across each transect.

Temperature and water chemistry

Surface water temperature was recorded hourly at river-km 88.5 (losing reach) and river-km 126.5 (gaining reach) from August 2004 until July 2005 using temperature loggers (TR MINILOG, VEMCO, Nova Scotia, Canada). Temperature was also measured at the conclusion of respiration measurements (spot measurements, see below).

Surface and interstitial water was collected with polyethylene bottles (one sample per transect). Interstitial water was pumped from a depth of ~50 cm from one piezometer installed in the middle of each transect. Conductivity was measured *in situ* (surface water) and in pumped interstitial water using a portable conductivity meter (LF 320 WTW, Weinheim, Germany). Analytical methods for ammonia (NH_4-N), nitrite (NO_2-N), nitrate (NO_3-N), dissolved nitrogen (DN), particulate nitrogen and phosphorus (PN, PP), soluble reactive-phosphorus (PO_4-P), dissolved phosphorus (DP), dissolved and particulate organic carbon (DOC, POC), and ash-free dry mass (AFDM) of suspended solids (SS) were identical to Tockner et al. (1997). Analytical methods for total inorganic carbon (TIC), sulfate (SO_4), and silica (SiO_2) were identical to those reported in Malard et al. (1999). Chloride (Cl) was measured using Ion Chromatography. Calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K) were measured using an inductive coupled emission spectrometer (SPECTRO, Analytische Geräte, Kleve, Germany). Interstitial water was analyzed for dissolved components only.

Periphyton

Periphyton biomass was assessed by randomly collecting five rocks along each transect. Rocks were placed in plastic storage bags and kept frozen until processed. To remove algae, rocks were scrubbed with a wire brush into a bucket with water, and the length and width of each rock were measured with a caliper. Aliquots of the algal suspension were filtered through glass fibre filters (Whatman GF/F) for determination of chlorophyll a and ash-free dry mass. Chlorophyll a was determined by HPLC after extraction with hot ethanol (Meyns et al., 1994). Area values of chlorophyll a were calculated for each site as described in Uehlinger (1991).

Sediment respiration and particulate organic matter (POM)

Respiration of aquatic sediments was measured as changes in O_2 concentration over time in Plexiglas tubes (5.2 cm diameter, 32 cm long) sealed with rubber stoppers (Uehlinger et al. 2002). Sediments sampled at 3 sites along each transect from 0 - 20 cm depth (the uppermost sediment layer with epilithic algae removed prior to sampling) were pre-sieved to exclude substrata >8 mm. Each tube was half filled with sediment before it was filled with water from the sampling site and subsequently incubated *in situ* for about 4 hours. Oxygen concentrations and temperature were measured with a portable oxygen meter (Oxi 340/bset, WTW, Weilheim, Germany). After incubation, sediments were kept frozen until analyzed for organic matter content and grain size distribution. Based on r, the oxygen consumption in the chamber water (g O_2 m^{-3} h^{-1}), we calculated the respiration per kg sediment R (g O_2 kg^{-1} h^{-1}) according to equation (1):

$$(1) \quad R = r \times V_w \frac{1}{G_w}$$

V_w is the volume of water in a tube (m^3) and G_w is the weight of the sediment in the tube. Respiration rates were normalized of a reference temperature of 20 °C using an Arrhenius equation:

$$(2) \quad R_{(20\,°C)} = R_{(T)}\, 1.072^{(T-20°C)}$$

$R_{(20°C)}$ is the respiration rate (g O_2 kg^{-1} h^{-1}) at 20 °C and T is temperature in the tube at the end of the incubation.

Sediment analysis

POM was elutriated with de-ionized water (Zah 2001) and separated by sieving into fractions >1 mm, 1 - 0.25 mm, and <0.25 mm. For the smallest fraction, an aliquot was filtered through a pre-weighted glass fiber filter (Whatman GF/F; Ø 47 mm). These POM fractions were dried at 60 °C for 24 hours, weighed, ashed at 500 °C for 3 hours, and re-weighed. After the elutriation of POM, the weight of the POM strongly attached to sediment particles >0.025 mm was determined by ashing the sediments at 500 °C for 3 hours. POM was expressed as ash-free dry mass per kg sediment.

Table 1: Mean ± 1 SD of physico-chemical parameters (surface water) in the losing (LR) and gaining (GR) reach and pooled data for riffle fronts and tails in the losing (RLR) and gaining (RGR) reach. Significant differences between LR and GR, and RLR and RGR, respectively, are highlighted in bold.

Site	**LR** **n =54**	**GR** **n =48**	**RLR** **n = 24*)**	**RGR** **n = 48**
Temperatur (°C)	15.32±4.97	**17.26±5.41**	13.46±7.4	**15.07±4.72**
O_2 (mg/l)	**10.92±1.97**	8.91±1.96	**11.48±1.57**	10.07±1.25
Conductivity (µS/cm)	**559.85±39.15**	513.11±50.9	**562.15±35.07**	477.84±37.87
NH_4-N (mg/l)	<0.001	<0.001	<0.001	<0.001
NO_2-N (mg/l)	<0.001	<0.001	<0.001	<0.001
NO_3N (mg/l)	0.747±0.048	**1.03±0.32**	0.69±0.06	**1.13±0.34**
DN (mg/l)	0.937±0.124	**1.25±0.42**	0.83±0.08	**1.36±0.41**
PN (mg/l)	0.018±0.02	0.013±0.010	6.50±11.60	2.47±5.00
PO_4-P (µg/l)	<5	<5	<5	<5
DP (µg/l)	<5	<5	<5	<5
PP (µg/l)	**2.65±2.26**	1.70±2.28	4.80±4.71	2.11±1.46
DOC (mg/l)	0.80±0.26	0.73±0.35	0.64±0.16	0.41±0.21
TIC (mg/l)	35.00±4.29	**39.74±10.75**	28.07±4.97	**35.39±3.94**
POC (mg/l)	**0.50±0.34**	0.22±0.14	**0.98±0.89**	0.32±0.23
SiO_2 (mg/l)	3.03±0.33	**4.08±1.14**	2.83±0.30	**3.55±0.40**
SO_4 (mg/l)	**144.79±20.25**	101.27±10.06	153.25±15.91	85.76±11.31
Cl- (mg/l)	**3.55±0.39**	3.31±1.23	3.20±0.67	3.11±0.45
Ca^{2+} (mmol/l)	77.31±11.86	70.78±7.78	84.59±11.16	71.24±6.43
Mg^{2+} (mmol/l)	19.92±1.33	20.07±2.63	19.92±1.55	19.45±1.43
K$^+$ (mg/l)	1.03±0.16	**1.13±0.28**	1.12±0.20	**1.28±0.47**
Na$^+$ (mg/l)	**3.39±0.41**	3.00±0.38	3.37±0.53	2.93±0.43
TSS (mg/l)	**4.10±4.29**	1.65±1.70	2.54±3.82	1.39±2.07
AFDM (mg/l)	**2.89±1.07**	1.94±0.91	3.55±1.44	2.95±0.93

* values only from surface samples

Total nitrogen content of the three POM fractions was determined as dissolved and particulate organic nitrogen components (DN, PN) and quantified as NO_3-N after digestion with $K_2S_2O_8$ at 121 °C. Total dissolved phosphorus (TDP) was determined as SRP after digestion with $K_2S_2O_8$ at 121 °C (Ebina et al. 1983). The molar C:N ratio of different POM fractions was calculated assuming a carbon organic matter content of 50 %.

Statistical analyses

All data were log (x+1) transformed to meet the assumptions of a normal distribution (Sokal and Rohlf 1995). Analyses were done separately for the 2003/2004 and 2004/2005 sampling period. Differences in VHG between the losing and gaining reach and between riffle heads and tails were evaluated using Kruskal Wallis ANOVA. One and two way ANOVA was applied to test for significant differences among sampling sites for hyporheic respiration, periphyton abundance and habitat variables such as hydrochemistry, POM, and N and P content of different POM fractions. A student *t*-test was used to evaluate for differences in periphyton abundance and hyporheic respiration between temporary and permanent wetted sites. Habitat variables were further analyzed by principal component analyses (PCA) to determine general spatiotemporal habitat patterns separating the different sampling sites. In general, data gaps were casewise deleted. All calculations were done with Microsoft Excel 2003 and Statistica 7.0 for Windows (Statsoft Inc. Tulsa OK, USA).

Results

Surface-subsurface water exchange

Measurements of the vertical hydraulic gradient (VHG) performed in runs clearly separated the losing from the gaining reach (Kruskal Wallis ANOVA, $\chi^2 = 129.79$, df = 1, p <0.001). VHG averaged -0.67 ± 0.55 (n = 116) in the losing reach and 0.03 ± 0.23 (n = 80) in the gaining reach. Between October 2004 and July 2005 when we tried to assess VHG at riffle heads and riffle tails, all measurements in the losing reach failed because Δl was zero (no water in the piezometer). In the gaining reach, VHG values were significantly lower at the riffle head (-0.20 ± 0.24, n = 60) than at the riffle tail (0.18 ± 0.19, n = 60) (Kruskal Wallis ANOVA, $\chi^2 = 48.13$, df = 1, $p < 0.001$).

Temperature and chemistry

Diel temperature amplitude ranged from 0.4 to 12.6 °C in the losing reach and from 0.4 to 6.2 °C in the gaining reach. The respective mean annual temperatures were 11.5 and 12.9 °C. Concentrations of NH_4, NO_2-N, PO_4-P and DP were typically lower than the detection limits of the analytical methods (Table 1), and were excluded from statistical analyses. Except for SiO_2, differences in the concentration of chemical parameters between surface and subsurface water were not significant (one-way ANOVA, $p < 0.001$).

In 2003/2004, when runs were sampled, temperature (spot measurements) and concentrations of NO_3-N, DN, TIC, SiO_2 and K^+ were significantly higher in the gaining reach in contrast to conductivity and concentrations of O_2, SO_4, Cl^-, Na^+, PP, POC, TSS and AFDM, which were significantly higher in the losing reach (one-way ANOVA, $p < 0.05$; Table 1). Within the losing and gaining reach riffle heads, and riffle tails did not significantly differ with respect to temperature and chemistry (sampling period 2004/2005). But if the data of riffle fronts and riffle tails were pooled separately for the losing and gaining reach almost the same pattern emerged as observed in 2003/2004, when runs were sampled, i.e., higher values of temperature, NO_3-N, DN, TIC, SiO_2 and K^+ in the gaining reach and lower values of O_2, DOC, SO_4, Ca^+, Na^+ and POC in the losing reach (two-way ANOVA, $p < 0.05$; Table 1).

Principle component analyses (PCA) using temperature and water chemistry distinctly separated the gaining and the losing reach but did not separate riffle heads and riffle tails (Figure 2).

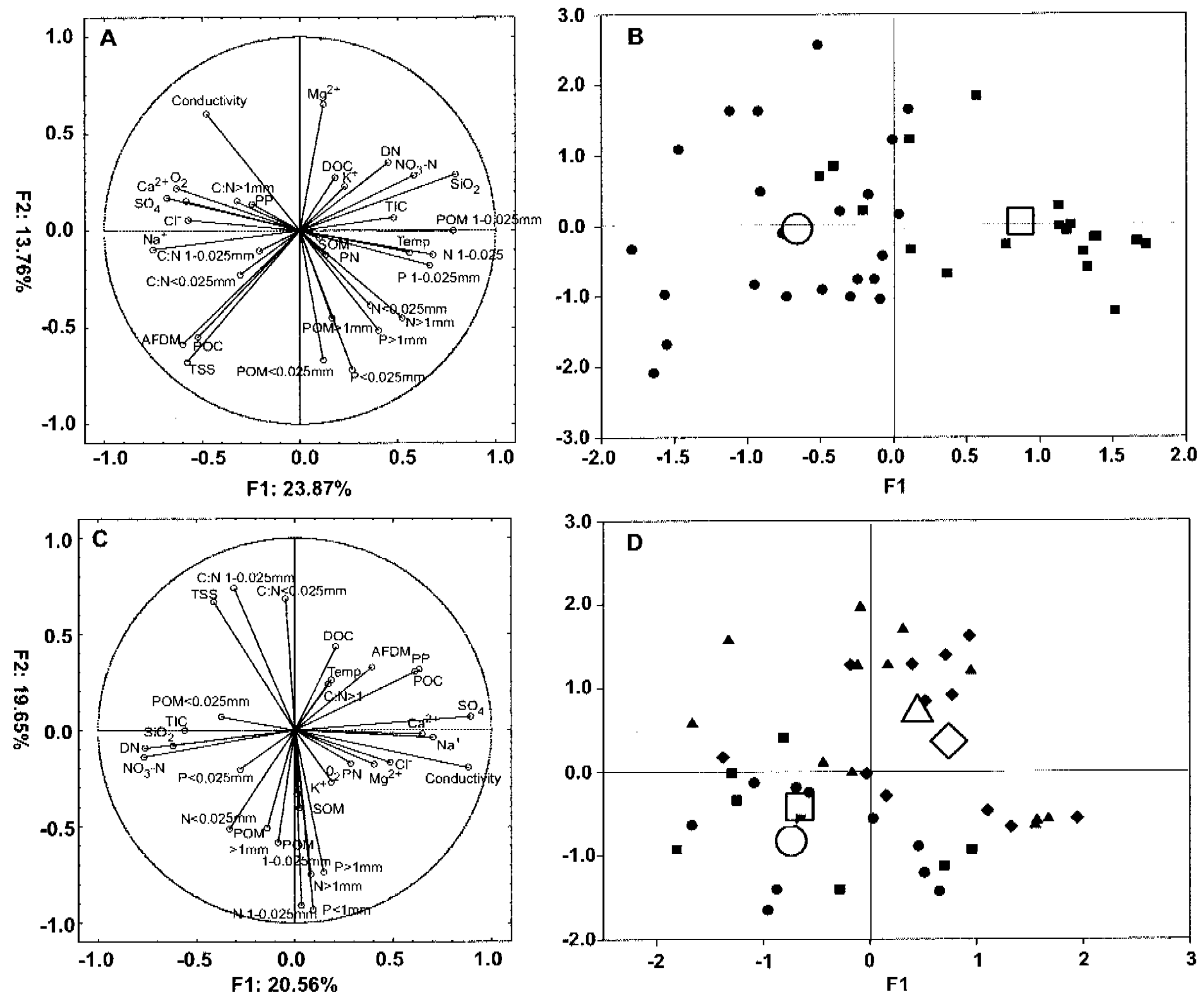

Figure 2: Ordination of principal component analyses using habitat parameters (see text). (A) Correlation circle and (B) factor map of habitat parameters sampled in runs from July 2003 to April 2004 in the losing (circles) and gaining reach (squares). SiO_2, POM 1 - 0.025 mm, Na^+, SO_4, N < 1 - 0.025 mm, N 1 - 0.025 mm, P 1-0.025 mm, and O_2 accounted for most of the definition of axis F1 (Factor loadings ≥ 60 %; in order of decreasing factor loadings). P 1-0.025 mm, TSS, POM < 0.025 mm, Mg^+, and conductivity accounted for most of the definition of axis F2 (Factor loadings ≥ 60 %). Large open symbols represent centroids of respective sites.

(C) Correlation circle and (D) factor map of habitat parameters sampled from October 2004 to July 2005 at riffle fronts (diamonds) and riffle tails (triangles) in the losing reach and at riffle fronts (squares) and riffle tails (circles) in the gaining reach. Axis F1 was mostly defined by SO_4, conductivity, NO_3-N, DN, Na^+, Ca^+, PP, SiO_2, and POC (Factor loadings ≥ 60%; in order of decreasing factor loadings). Axis F2 was mostly defined by, P 1-0.025 mm, N 1-0.025 mm, N>1 mm, C:N ratio 1-0.025mm, P>1 mm C:N ratio < 0.025, and TSS (Factor loadings ≥ 60%). Large open symbols represent centroids of respective sites.

Sediment parameters exhibited no consistent spatial patterns (Table 2). The C:N ratio of sediment POM >1 mm (run samples) was significantly higher in the losing reach (one-way ANOVA, $p < 0.001$) and the C:N ratio of POM 1 - 0.025 mm, N and P 1 - 0.025 mm was significantly higher in the gaining reach (one-way ANOVA, $p \leq 0.007$; Table 2). Strongly attached sediment POM exhibited significantly higher values in riffle heads and tails situated in the losing reach (two way ANOVA, $p < 0.001$) (Table 2).

Table 2: Mean ± 1 SD of different POM fractions (mg AFDM kg sediment^{-1}), nitrogen (µg N kg sediment^{-1}), phosphorous (µg P kg sediment^{-1}) content, CN ratio of POM fractions and SOM (g kg sediment) in the losing (LR) and gaining (GR) reach and pooled data for riffle fronts and tails in the losing (RLR) and gaining (RGR) reach. Significant values are highlighted in bold.

Site	**LR**	**GR**	**RLR**	**RGR**
POM >1 mm	94.2 ± 116.4	78.2 ± 83.4	51.8 ± 63.2	82.2 ± 150.2
N >1 mm	866 ± 1074	1201 ± 1857	1005 ± 1371	1099 ± 1396
C:N ratio >1 mm	**51.8 ± 23.1**	38.3 ± 30.0	39.3 ± 42.45	37.5 ± 36.2
P >1 mm	46.2 ± 82.5	72.4 ± 148.0	68.1 ± 122.4	46.6 ± 59.6
POM 1-0.025 mm	129.8 ± 154.8	208.2 ± 219.2	140.0 ± 256.6	156.4 ± 144.8
N 1-0.025 mm	3544 ± 5549	**6608 ± 8289**	3082 ± 4612	3452 ± 4978
C:N ratio 1-0.025 mm	31.5 ± 57.8	**32.6 ± 29.3**	120.5 ± 258.6	131.1 ± 288.9
P 1-0.025 mm	791.0 ± 1131.5	**1260 ± 1461**	1302 ± 2824	955 ± 1284
POM <0.025 mm	872.4 ± 585.0	923.0 ± 620.0	912 ± 505	990 ± 572
N <0.025 mm	12469 ± 10534	11479 ± 7267	11645 ± 8810	13772 ± 17766
C:N ratio <0.025 mm	55.8 ± 33.8	56.7 ± 45.1	56.6 ± 32.5	59.9 ± 39.1
P <0.025 mm	7227 ± 6233	7054 ± 5612	6499 ± 4823	7267 ± 7353
SOM	6.0 ± 1.5	5.9 ± 1.1	**7.0 ± 3.81**	5.7 ± 1.4

Periphyton biomass and hyporheic respiration

In 2003/2004, average chlorophyll *a* in runs was 19.7 ± 33.7 mg m^{-2} in the losing reach and 20.1 ± 33.2 mg in the gaining reach, but these differences were not significant in contrast to periphyton biomass (AFDM), which averaged 12.0 ± 12.2 g m^{-2} in the losing reach and 21.3 ± 18.9 g m^{-2} in the gaining reach (one-way ANOVA; $p<0.001$). The average hyporheic respiration normalized at 20 °C was 0.42 ± 0.19 mg O_2 kg sediment^{-1} h^{-1} in the losing reach and 0.26 ± 0.15 mg O_2 kg sediment^{-1} h^{-1} in the gaining reach (one-way ANOVA; $p<0.001$).

Permanently wetted sites of the losing reach showed significantly higher chlorophyll *a* and AFDM values (12.1 ± 25.6 mg chl. *a* m^{-2} and 7.1 ± 10.1 g AFDM m^{-2}) than the two intermittent sites of the same reach (7.9 ± 11.3 mg chl. *a* m^{-2} and 5.8 ± 4.2 g AFDM m^{-2}) (*t*-test; $p \leq 0.001$). Differences in hyporheic respiration between permanent and intermittent sites were not significant (permanent sites: 0.43 ± 0.23 mg O_2 kg sediment^{-1} h^{-1}; intermittent sites: 0.42 ± 0.18 mg O_2 kg sediment^{-1} h^{-1}; *t*-test, $p = 0.87$).

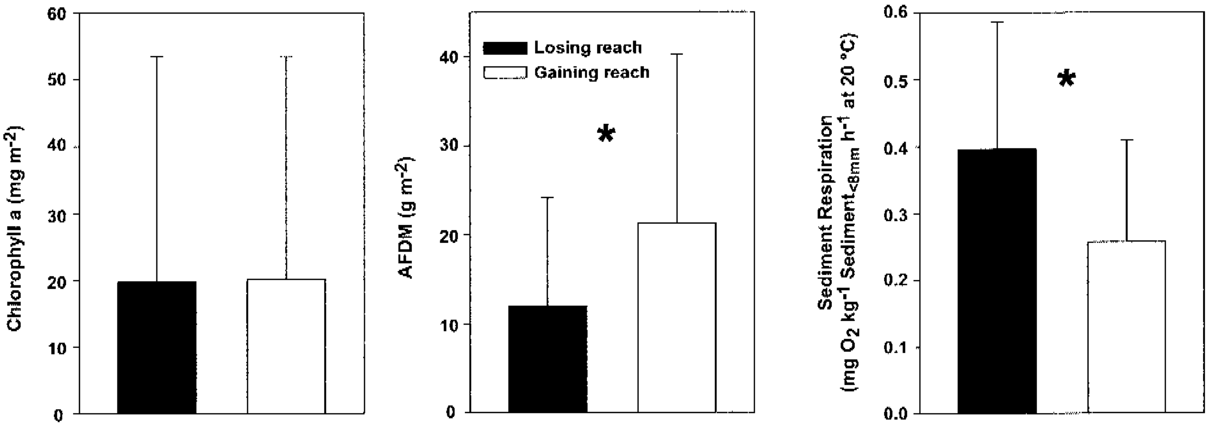

Figure 3: Average ± SD of chlorophyll a, ash free dry mass (AFDM) and hyporheic respiration in runs of the losing (black bar) and gaining (white bar) reach during the period from July 2003 to April 2004. Asterisks mark significant different differences between the losing and gaining reach.

Differences in chlorophyll *a* and AFDM between riffle heads and tails were not significant either in the losing or in the gaining reach. However, chlorophyll *a* in the gaining reach (average of riffle fronts and tails) was about twice as high than in the losing reach at 30.8 ± 60.8 and 12.8 ± 19.0 mg chl. *a* m^{-2}, respectively (two-way ANOVA, $p<0.001$; Figure 4) and showed much higher variability in the losing reach. Ash-free dry mass showed a consistent pattern with 18.2 ± 18.5 (gaining reach) and 12.2 ± 13.0 g m^{-2} (losing reach) (two way ANOVA; $p<0.001$). In the gaining reach, hyporheic respiration averaged 0.35 ± 0.15 mg O_2 kg sediment^{-1} h^{-1} at riffle fronts and 0.24 ± 0.12 mg O_2 kg sediment^{-1} h^{-1} at riffle tails. In the losing reach respective values were 0.46 ± 0.36 and 0.48 ± 0.34 mg O_2 kg sediment^{-1} h^{-1}. Neither in the gaining nor in the losing reach differences between riffle heads and tails were significant, but the average of riffle heads and tails was significantly higher in the losing reach (0.47 ± 0.34 mg O_2 kg sediment^{-1} h^{-1}) than in the gaining reach (0.30 ± 0.14 mg O_2 kg sediment^{-1} h^{-1}) (two-way ANOVA, $p < 0.001$; Figure 4). Hyporheic respiration rates correlated significantly with periphyton biomass (ash-free dry mass: $R^2 \leq 0.49$, $p < 0.036$; chlorophyll *a*: $R^2 \leq 0.23$, $p < 0.046$) but not with sediment organic matter ($p \geq 0.068$).

Discussion

At the reach scale periphyton accrual and hyporheic respiration reflected vertical hydrologic exchange. Vertical hydrologic exchange at the pool-riffle scale was not reflected by a respective response of periphyton and respiration. This suggests that both parameters are controlled by the hydro-geomorphic characteristics of the reach level rather than that of local pool-riffle systems.

Vertical hydrologic exchange

The losing reach of the investigated study area loses substantial surface flow into the highly permeable and deep alluvium. The average infiltration rate of 2.5 m^3 s^{-1} per river km is higher than values reported for rivers such as the Middle Fork of the Flathead River in Montana of 1.3 m^3 s^{-1} per river km or Homestead Creek (Australia) of 1.1 m^3 s^{-1} per river km (Dunkerley and Brown 1999, Stanford et al. 2005). Doering et al. (2007) showed that infiltration rates in the losing reach are rather constant throughout the annual cycle and independent of the discharge measured at the beginning of the reach over a relatively wide range (20 – 70 m^3 s^{-1}). In the gaining reach, the exfiltration of water is about one order of magnitude less intense; it equals on the average only 0.3 m^3 s^{-1} per km.

Most of the upstream infiltrated river water emerges outside of the Tagliamento River corridor, thereby feeding numerous springs (Fontana et al. 2007). This difference in the magnitude of vertical hydrologic exchange is also reflected in the average vertical hydraulic gradient (VHG), which is highly negative in the losing reach but only slightly positive in the gaining reach. In contrast to VHG measurements performed in runs in 2003/2004, the assessment of VHG at riffle heads and tails of the losing reach failed in 2004/2005; the vertical extent of the unsaturated hyporheic reach exceeded 0.5 m. Measuring VHG in the losing reach of the Tagliamento River, Malard et al. (2000) found that at some sites only the uppermost 20 - 40 cm of the sediments were saturated and only 10 cm from the shoreline groundwater was not reached until a depth of 1.7 m below the bed surface. Duration and magnitude of floods influence sediment permeability of bed sediments (Dunkerley and Brown 1999, Gasith and Resh 1999, Doering et al. 2007) and presumably depth and vertical extent of the saturated reach. Although we lack direct evidence from VHG measurements, we hypothesize that in the losing reach the downwelling marginalizes or prevents local upwelling (e.g., at riffle tails). In the gaining reach, VHG indicated approximately equal intensity of down- and upwelling at riffle heads and riffle tails, respectively. In contrast to the losing reach, the hydro-geomorphic settings apparently impose minor constraints on local vertical hydrologic exchange.

Habitat characteristics

Overall, hydro-chemical characteristics differed between the losing and gaining reach but not between riffle heads and riffle tails. Changes in water chemistry are apparently related to the length of the sub-surface flow path and discharge. They became evident at the reach scale, whereas discharge was too high and flow paths too short to exert a major influence on the chemical milieu at the local scale. In small streams, local vertical or lateral hydrologic exchange between sediments and surface water may strongly influence surface water chemistry, in particular nutrient concentrations such as nitrogen and phosphorus (e.g., Hendricks 1993, Vallett et al. 1994, Dent et al. 2001). In Sycamore Creek, surface NO_3 concentrations in local upwelling areas were two to three times higher than in corresponding downwelling reaches (Vallett et al. 1994). Downwelling areas are locations where suspended organic matter is expected to be retained in the uppermost sediments and subsequently processed. In the Tagliamento, differences in sediment organic matter between down- and upwelling areas were not significant and corresponds to the low POM load during base flow. Retained particulate organic matter such as sloughed algae is presumably subject to fast decomposition. In Sycamore Creek, Jones et al. (1995) found that after floods sediment POC was higher in downwelling than in upwelling areas but these differences disappeared during inter-spate periods. This suggests that floods rather than the continuous POM supply during base flow may account for differences in sediment organic matter between down- and upwelling areas.

Periphyton biomass and hyporheic respiration

Upwelling is known to enhance periphyton accrual, e.g., chlorophyll *a* is positively correlated with the vertical hydraulic gradient. This has been demonstrated at the pool-riffle scale (100 – 140 m) in small desert stream (Vallett et al. 1994) and at a larger scale (500 – 1000 m) in a medium sized floodplain river (Stanford et al. 2005). In the Tagliamento, periphyton biomass measured as ash-free dry mass was significantly higher in the gaining reach than in the losing reach but differences between riffle heads and riffle tails were not significant either in the gaining or in the losing reach. The spatial pattern of chlorophyll *a* was quite different, i.e., no significant differences at the reach level and distinct differences between riffle heads and riffle tails in the losing and gaining reach. Enhanced nutrient availability in riffle heads and tails of the gaining reach may account for the observed higher chlorophyll *a* content of the periphyton community. However, chlorophyll *a* is less suitable as biomass parameter than ash-free dry mass since the chlorophyll content of algae depends on environmental conditions. The chlorophyll content of algae has been shown to decline with increasing N or P limitation (Healey and Hendzel 1975, Rhee 1978, Uehlinger 1981) and to increase with declining light intensity (e.g., Hill and Boston 1991).

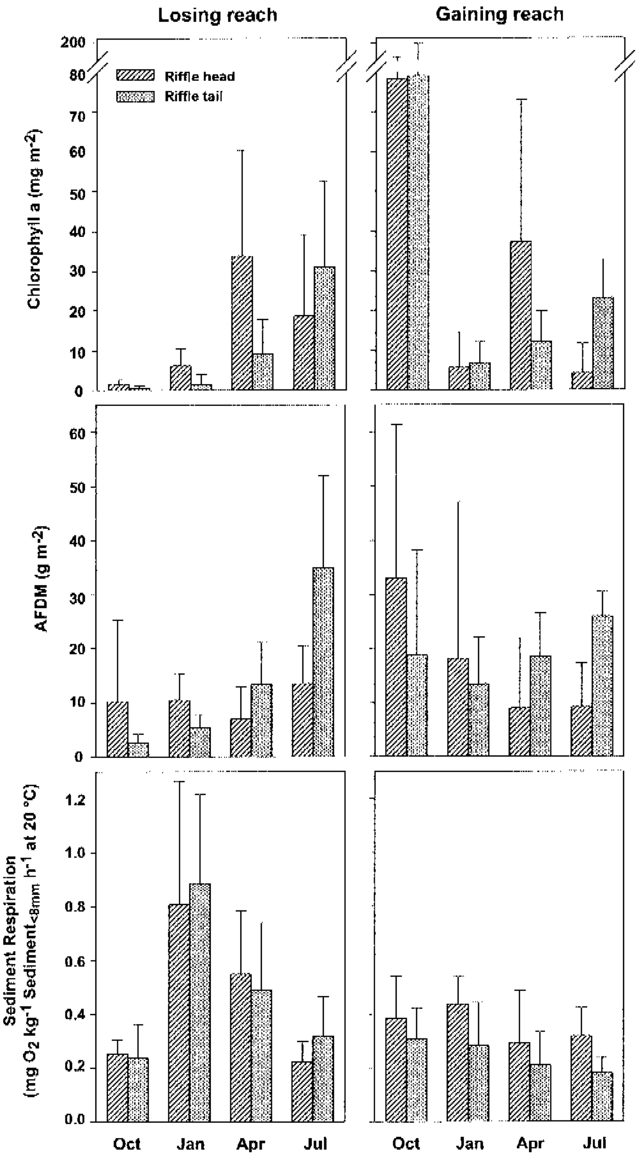

Figure 4: Chlorophyll *a*, ash-free dry mass (AFDM), and hyporheic respiration in riffle fronts and tails in the losing (left) and gaining reach (right) from October 2004 to July 2005.

Both chlorophyll *a* and ash-free dry mass were higher at permanent wetted sites. Fast contraction-expansion cycles triggered by local convective rain events hardly allows primary producers to develop desiccant resistant structures or physiological adjustment. During flow recession, the downstream end of the wetted channel in the losing reach may move upstream with up to 0.5 km h^{-1} (Doering et al. 2007). Consequently, algae are expected to die within hours after they fall dry (Angrawal and Singh 2002, Stanley et al. 2004). The upper end of the gaining reach is quite stable in time, during the extremely dry year it slowly moved downstream (Doering et al. 2007).

Table 3: Respiration in the hyporheic sediments of the Tagliamento River and other streams. Results of measurements with respiration chambers (Jones et al. 1995, Uehlinger et al. 2002, Uehlinger and Zah 2003)

Stream	**Depth (m)**	**Respiration (g O_2 m^{-3} d^{-1})**
Tagliamento (low elevation floodplain)		
(July 2003 - June 2005)		
Losing reach	0.1	9.4 ± 5.5
Gaining reach	0.1	6.9 ± 3.8
Val Roseg Alpine (high elevation floodplain)		
(March - October)		
Main channel	0.1	0.5 ± 0.4
Surface connected channel	0.1	0.9 ± 0.7
Surface-disconnected channels	0.1	1.9 ± 1.5
Sycamore Creek (desert stream), annual mean in		
downwelling zones	0.1	26.8
upwelling zones	0.1	11.0
Hassayampa River (desert stream), autumn	0.1	23.0 ± 2.6

Large scale vertical hydrologic exchange was apparently a major factor controlling hyporheic respiration. At the riffle scale, differences between downwelling and corresponding upwelling areas were not significant although respiration at riffle heads tended to be slightly higher than at riffle tails. The correlation between respiration and periphyton indicate that autochthonous production of organic matter, which includes the release of extracellular organic matter by algae and sloughed algal cells, may be an important energy source fueling hyporheic respiration (Jones et al. 1995). In the wide active channel area of the Tagliamento, allochthonous inputs from riparian forests and upstream areas are presumably of minor importance as an energy source for aquatic communities (Langhans et al. 2006). In autotrophic systems such as desert streams, autochthonous energy supply can support more than 80 % of the respiration in the hyporheic reach (Jones et al. 1995) in contrast to streams where the energy base is mainly allochthonous organic matter input as primary energy source (Pusch and Schwoerbel 1994, Naegeli et al. 1995).

In the Tagliamento River respiration rates were several times more than in the Alpine floodplain of the Roseg River but three to four times lower than in desert streams (Table 3).

Conclusion

The observed spatial pattern in periphyton biomass and hyporheic respiration in the losing and gaining reaches of the Tagliamento River matches findings from investigations performed at the scale of channel bedform units (pool-riffels); i.e., high biomass in upwelling areas and high respiration in downwelling areas. We hypothesize that the constraints imposed by the hydrogeomorphic characteristics at the reach level, as for example the high infiltration in the losing reach, reduces the vertical hydrologic exchange at the riffle scale, which is finally responsible for the lack of response in biomass and respiration in the local vertical hydrologic exchange. Lastly, relatively high discharge (e.g., 5 - 60 m^3 s^{-1} at river km 91) presumably reduces the effect of nutrient regeneration along the relatively short subsurface flow path between riffle heads and riffle tails.

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3. LINKING PATTERNS AND PROCESSES IN A FLOODPLAIN MOSAIC: SOIL AND SEDIMENT RESPIRATION ACROSS AN AQUATIC-TERRESTRIAL HABITAT GRADIENT

M. Doering, U. Uehlinger, T. Ackermann, M. Woodtli and K. Tockner.

In review

Abstract

Riverine floodplains are composed of a complex mosaic of contrasting aquatic and terrestrial habitats. These habitats are expected to differ widely in their structure and ecological function, although empirical data on their capacity to produce, store, and transform organic matter and nutrients are limited. The objectives of this study were (1) to measure the variation of respiration, a dominant carbon flux in ecosystems, across a floodplain gradient, (2) to identify the environmental drivers of respiration within floodplain habitats, and (3) to calculate whole-ecosystem respiration rates. We measured soil and sediment respiration (sum of auto- and heterotrophic respiration; SR) throughout an annual cycle at two aquatic (pond and channel) and four terrestrial (gravel, large wood, vegetated island, riparian forest) habitat types in the island-braided section of the Tagliamento River (NE Italy). The near natural Tagliamento River provides insight into the structural and functional complexity that must have characterized most Alpine rivers before regulation. Further, we studied the effect of surface inundation on SR rates in controlled laboratory experiments. Floodplain habitats greatly differed in substrate composition (soil to coarse gravel), organic matter content (0.63 % to 4.1 % AFDM), and temperature (seasonal range per habitat type: 8.6 to 33.1 °C). Average annual SR rate ranged from 0.54 ± 1.56 (exposed gravel) to 3.94 ± 3.72 μmol CO$_2$ m^{-2} s^{-1} (vegetated islands). Soil temperature was the most important predictor of SR rates. The Q_{10} value ranged from 1.62 (channel habitat) to 4.57 (riparian forest) *demonstrating major differences in the habitat-specific temperature sensitivity of the SR rate. Inundation led to a 69 to 91 % decline in the SR rate within six hours of inundation in all habitats except on surfaces of exposed gravel. Total annual SR rate in individual floodplain habitats ranged from 160 (ponds) to 1205 g C* m^{-2} *(vegetated islands). These rates spanned almost the entire range reported for various aquatic and terrestrial ecosystems world wide.*

Introduction

Riverine floodplains, i.e. the active tract and the fringing riparian zone along river corridors (Stanford et al. 2005, Fig. 1), can be portrayed as a mosaic of contrasting aquatic and terrestrial habitats (Naiman et al. 2005). These habitats are expected to differ widely in their structural properties and functional performance. For example, exposed gravel habitats are considered as harsh environments, with extreme temperature variations, high water stress, and therefore low productivity (Tockner et al. 2006); while the riparian forest is rich in resources that sustain high productivity (Tockner and Stanford 2002). The performance of individual habitats is not only controlled by intrinsic factors but also by the performance of the adjacent habitat types. Vegetated islands and riparian forests provide large amounts of bioavailable organic carbon to the aquatic habitats where it is either processed *in situ* or exported downstream (Cuffney 1988, Junk 1989, Langhans et al. 2006). Past process studies in riverine floodplains have focused either on permanent aquatic or on permanent terrestrial habitats (e.g., McTammany et al. 2003, Robinson et al. 2003, Rueda-Delgado et al. 2006). However, to understand the functional performance of ecosystems we need to study the effects of the composition, spatial configuration, and dynamics of individual habitat types on ecosystem processes. Natural floodplains are model systems to study the link between ecosystem structure and function.

Respiration is a central process in ecosystems that regulates organic matter decomposition, detrital storage, nutrient cycling, and flux of CO_2 to the atmosphere (Andrews and Schlesinger 2001). Therefore, respiration can be used to determine the functional integrity of ecosystems (VanVoris et al. 1980, Uehlinger and Naegli 1998, Euskirchen et al. 2003). Generally, respiration increases exponentially with temperature and often is limited by deficits in soil moisture and substrate availability (Buchmann 2000, Euskirchen et al. 2003, Tang et al. 2006). Thus, even marginal changes in temperature, water availability, or quantity and quality of organic substrates are likely to alter aquatic and terrestrial C exchange rates (Schimel et al. 1994, Jones 1995, Randerson et al. 1996, Buchmann 2000, Davidson et al. 2000, Xu and Qi 2001, Li et al. 2006). While the effect of rewetting on soil respiration has been studied extensively (e.g., Orchard and Cook 1983, Scheu and Parkinson 1994, Pulleman and Tietema 1999, Mamilov and Dilly 2002, Fierer et al. 2003), information about the effect of surface inundation on respiration is limited (Baldwin and Mitchel 2000, Valett et al. 2005).

To gain an advanced understanding of the factors governing soil respiration in a spatially complex and temporally dynamic ecosystem, we conducted detailed field studies in the island-braided section of the last remaining near-natural river corridor in Central Europe (Tagliamento River, NE Italy). The Tagliamento provides insight about the structural and functional complexity that must have characterized most Alpine rivers in their pristine state. We measured soil temperature, soil water content, grain size distribution, organic matter content, and soil and sediment CO_2 efflux rates in two aquatic and four terrestrial habitat types over an annual cycle. Further, we investigated the effect of surface inundation on soil respiration using controlled laboratory experiments. The main goals of the study were i) to measure the seasonal variation in total soil and sediment respiration (i.e. sum of root and heterotrophic respiration; SR) within and among the dominant habitat types, and ii) to quantify the predictive power of temperature, organic matter, and surface inundation on SR rates within these habitats, and iii) to quantify total annual SR at the ecosystem level.

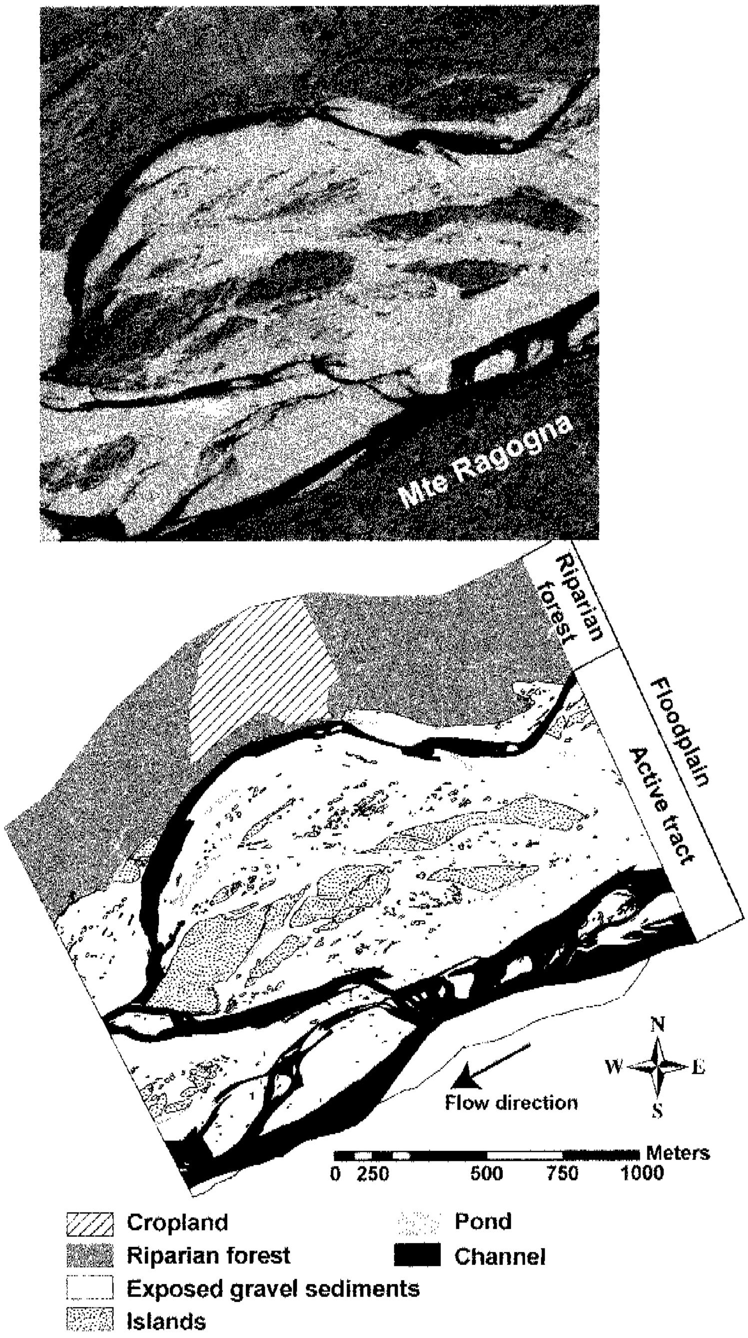

Figure 1: Aerial photo (May 2005) of the main study area (upper panel), and detailed map of the study area showing the spatial distribution of individual habitat types (lower panel). Large wood accumulations are too small to be shown on the map. All habitats were delineated by an intensive field survey in February 2005 at low discharge using a differential GPS.

Methods

Study site

This study was conducted from January through October 2005 in the island-braided section of the 7th order Tagliamento River in northeastern Italy (46° N, 12°30' E). The Tagliamento (catchment area: 2580 km^2) originates at 1000 m a.s.l. in the southern fringe of the European Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea.

The main study area was a 116 ha island-braided floodplain complex (river-km 79.8-80.8; 135 m a.s.l.) where maximum annual water level fluctuations are about 2 m (Tockner et al. 2003). This reach contains a spatially complex and temporally dynamic habitat mosaic dominated by extensive areas of exposed riverine sediments (Petts et al. 2000; Van der Nat et al. 2003) (Fig. 1). The 800 m wide active tract is fringed by a ribbon of intact riparian forest (right bank), with *Populus nigra* and five willow species as the dominant tree species (Karrenberg et al. 2003). Soil types of the riparian forest and vegetated islands are classified as Eutrochrept Fluvisols. The steep hillslope of Monte Ragogna fringes the left bank of the floodplain (Fig. 1).

At base flow (about 20 $m^3\ s^{-1}$), the floodplain contains exposed gravel habitats (60.3 ha, 52.8 % of total area), vegetated islands (10.4 ha, 8.9 %), large wood accumulations (0.4 ha, 0.3 %), the channel network (18.2 ha, 15.6 %), numerous ponds (0.6ha, 0.5 %), and the riparian forest (26.5 ha, 22.8 %).

The river has a flashy flow regime ($Q_{80} = 72\ m^3\ s^{-1}$; Ward et al. 1999) with frequent and short flow and flood pulses (*sensu* Tockner et al. 2000) throughout the year (Arscott et al. 2002). Flow pulses that inundate 20 % of the active tract last on average six days, floods that inundate 80 % last on average 1.5 days (van der Nat et al. 2002). Detailed information on the Tagliamento catchment and the main study area has been provided by Ward et al. (1999), Gurnell et al. (2001), and Tockner et al. (2003).

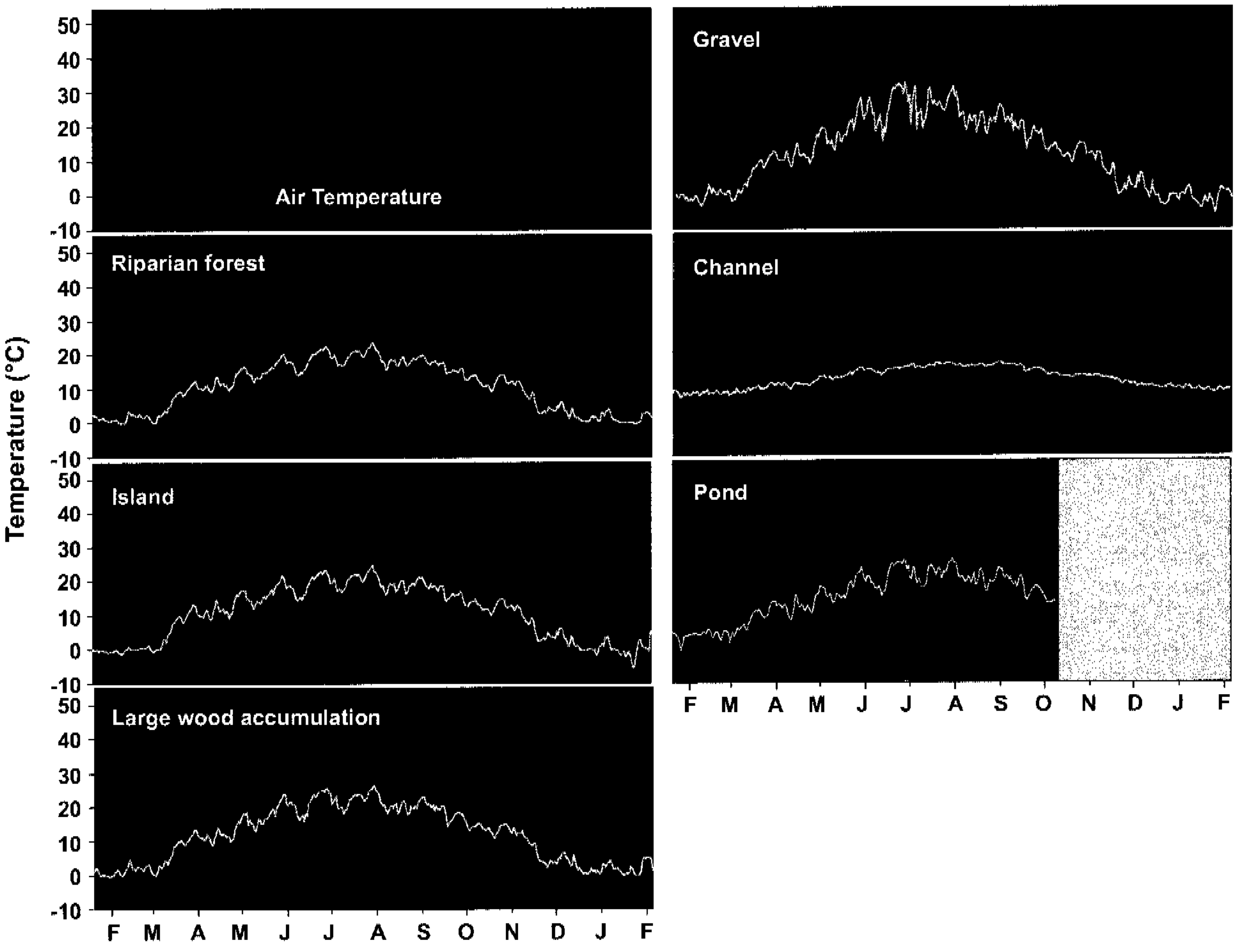

Figure 2: Average daily air temperature at the study site and average, minimum and maximum daily temperature in the six aquatic and terrestrial habitat types from January 2005 to February 2006.

Characterization of habitat patches

Two aquatic (channels, ponds) and four terrestrial (riparian forest, vegetated islands, large wood accumulations, exposed gravel sediments) habitat types were analyzed for grain size distribution, water content, % of maximum water holding capacity, and organic matter content. Soil and sediment water content (% of dry soil and sediment) was determined gravimetrically 3 -12 hours after sample collection. Samples were weighed, dried at 105 °C for 24 hours, and reweighed. Gravimetric water content (WC; % of dry sediment) of aquatic sediments was calculated according to equation (1).

$$(1) \quad WC = \frac{P}{\frac{S}{\partial} + P}$$

P is porosity, S dry sediment weight, and ∂ sediment density. Porosity was assumed to be 0.2 (Eglin 1990, Jussel 1992) and sediment density 3 kg dm^{-3} (Eglin 1990).

To measure the maximum water holding capacity (WHC; % of dry soil and sediment), sediment samples (five random samples per habitat type) were dried at 105 °C, weighed, saturated with deionized water for 24 hours, drained for 24 hours and weighted again.

Organic matter content of dry samples was measured as ash-free-dry-mass (AFDM; ashed at 500 °C for 3 hours) per kg dry soil or sediment. Ashed sediments were sieved to separate the grain size fractions <0.063 mm, 0.063-2 mm, 2-4 mm, 4-8 mm, and >8 mm.

Temperature was continuously recorded in terrestrial and aquatic habitat types. Five temperature loggers (DS1921G, Dallas Semiconductor, Dallas, USA) were exposed in each terrestrial habitat type at a depth of 5 cm. Five loggers (TR MINILOG, VEMCO, Nova Scotia, Canada and PDLR70; Ecotech, Germany) were exposed at the sediment surface of each aquatic habitat.

Measurement of SR in terrestrial habitats

Sediment respiration (i.e. sum of root and heterotrophic respiration; SR) was measured in January, April, July and October 2005 using a soil respiration chamber (Li 6400, LiCor, Lincoln, Nebraska, USA) attached to a portable Li-6400 infrared gas analyzer (IRGA). PVC collars of known volume (8 cm long, 10.5 cm inside diameter) were inserted into the sediment of the riparian forest (n = 16 per date), vegetated islands (n = 27), large wood accumulations (n = 13), and exposed gravel sediments (n = 81). The exact position of each randomly chosen sampling site was determined using a differential GPS (accuracy <0.5 m) to ensure that respiration was assessed at the same location on each sampling date. Collars were inserted to a depth of 5 to 7 cm. According to Norman et al. (1997), insertion of the collar results in initially high CO_2 fluxes that stabilize after 10 to 30 min. To minimize this effect, collars were installed at least 24 hours prior to the measurement (Buchmann 2000). The soil chamber was set on top of the collar to measure the undisturbed CO_2 flux. The IRGA measurement was repeated four times per date and collar and values were averaged. To estimate diel variation in CO_2 fluxes, five additional collars were exposed at each habitat type and measured three to four times from 7 am to 8 pm. Temperature was measured at 5 cm sediment depth next to the collar. After each seasonal measurement soil enclosed by each collar was collected, stored in sealed PVC bags, and transported to the laboratory for water, organic matter content, and grain size analyses (see above).

Measurement of SR in aquatic habitats

Aerobic respiration of aquatic sediments, excluding surface autotrophs, was measured as the change in O_2 concentration over time in plexiglas tubes (5.2 cm diameter, 32 cm long) sealed with rubber stoppers (Uehlinger et al. 2002). Channel (n = 25 per date) and pond (n = 13) sediments were collected from 0 - 20 cm depth (the uppermost sediment layer with epilithic algae was removed prior to sampling) and pre-sieved to exclude substrata >8 mm. Each tube was half filled with sediment, filled up with surface water from the sampling site, and subsequently incubated *in situ* for about 4 hours (Uehlinger et al. 2002). Oxygen concentration and temperature were measured with a portable oxygen meter (Oxi 340/bset, WTW, Weilheim, Germany). After incubation, sediments were stored frozen and later analyzed for organic matter content and grain size distribution (see above).

Short-term inundation experiments

Soil and sediment samples were collected in January and May 2005 in the riparian forest, on vegetated islands, large wood accumulations, and exposed gravel sediments (n = 5 per habitat type and date). Samples were pre-sieved to exclude the size fraction >8 mm and stored at 4 °C (Dilly 2001a). In the laboratory, plexiglas tubes, as described above, were half filled with soil, filled to the top with artificial floodwater, and sealed. Artificial flood water contained 26.14 mg TIC, 37.54 mg Ca^{2+}, 12.56 Mg^{2+}, 0.768 NO_3-N, 2.14 mg K^+, 50.04 mg Na^+, 66.41 mg Cl^- and 49.64 mg SO_4 per liter. This corresponded to the average concentrations of water collected during three flood events in 2004 along the Tagliamento. Oxygen concentration was measured at day 0.3, 0.9, 1.3, 1.9, 2.3, 3, 4, 5 and 6 using a portable meter (Oxi 340/bset, WTW, Weilheim, Germany). The January samples were incubated at 4 and 12 °C and the May samples at 12 and 20 °C in a dark climate room for six days.

A major difference between inundated sediments and soils is the higher amount of litter in floodplain soils leading to a pulse of nutrients following inundation (Baldwin and Mitchel 2000). This pulse may cause a rapid increase in microbial activity leading to the rapid onset of anoxia in the floodwater and the underlying soils. Measurements in the saturated subsurface sediments of the Tagliamento River indicated no oxygen limitation (average concentration: 8.8 mg/L, n = 97; Thalmann and Lüthi 2006). For this reason we reaerated sediment samples from large wood accumulation and exposed gravel fields at 12 and 20°C to prevent oxygen limitations (≤ 5 mg/L). At the end of the experiment grain size distribution and organic matter content were determined as described above.

Calculation of SR rates from sediment tube measurements

Based on the oxygen consumption in the chamber water r (g O_2 m^{-3} h^{-1}) we calculated the respiration rate R (μmol CO_2 $m^{-2}s^{-1}$) in the uppermost 20 cm sediment layer according to equation (2).

$$(2) \quad R = r \times \frac{10^6}{32} \times \frac{1}{3600} V_w \times \frac{Vs_{0\text{-}0.2}}{Vs_{chamber}} \times RQ$$

V_w is the volume of water in a chamber (m^3), $Vs_{chamber}$ the sediment volume including porosity (m^3) in a chamber, $Vs_{0\text{-}0.2}$ the sediment volume of the uppermost sediment layer (0 - 0.2 m) inclusive porosity below one m^2 and RQ the respiratory quotient (0.85; Dilly 2001b). The porosity of exposed gravel, channel, and pond sediments was assumed to be 20 % (Eglin 1990, Jussel 1992). The porosity of riparian forest and island soils was estimated to be 40 % (Kuntze et al. 1994), and the porosity of sediments in large wood accumulations was estimated to be 30 %. Results from 322 grain size analyses of exposed gravel sediments, collected from a total of 81 sites, showed that the size fraction >8 mm accounted on average for 54 % of the sediment volume. Therefore the SR rates in pond and channel habitats were multiplied by 0.54.

Temperature dependence of SR rates

We described the temperature-dependence of respiration as (3):

$$(3) \quad y = a * \exp^{(b*T)},$$

where T is the sediment temperature (°C) at 5 cm depth (terrestrial habitats) or the temperature of the chamber water. The model parameters a and b were identified using non-linear regression.

Residual analyses were performed to test for correlations between residuals of the temperature model and soil and sediment water content, organic matter content, and individual grain size fractions.

Q_{10} values were calculated according to equation (4) (Buchmann 2000):

$$(4) \quad Q_{10} = \exp^{10*b}$$

Sediment respiration at reference temperatures (T_r) 4, 12 and 20°C was calculated according equation (5):

$$(5) \quad R(T_r) = \exp^{b*(T-Tr)}$$

Table 1: Characterization of terrestrial and aquatic habitat types. Temperature (°C), water content (% of dry sediments), water content expressed as percentage of water holding capacity, organic matter (OM) content of two size fractions, total organic matter content (g kg sediment^{-1}), and grain size distribution (% of all size fractions) (average±SD; pooled data from four seasons). LWA=Large wood accumulation. GS = Grain size

Habitat	**Riparian forest** **n = 63**	**Island** **n = 114**	**LWA** **n = 52**	**Gravel** **n = 322**	**Channel** **n = 100**	**Pond** **n = 53**
Temperature (°C)	12.9 ± 7.4	14.2 ±8.9	14.9 ±9.8	16.8 ± 11.7	12.9 ± 4.6	13.5 ± 6.2
Water content (%)	25.7 ± 10.3	15.2 ± 10.5	15.7 ± 10.8	3.7 ± 8.7	9.4 ± 0.8*	9.8 ± 1.4*
% of water holding capacity	57.7 ± 22.7	36.6 ± 24.2	55.8 ± 29.8	41.11 ± 31.3	100	100
OM > 2mm ($g\ kg^{-1}_{sediment}$)	8.3 ± 6.0	5.4 ± 5.7	3.7 ± 4.9	3.3 ± 2.2	3.6 ± 1.3	2.3 ± 1.6
OM < 2mm ($g\ kg^{-1}_{sediment}$)	32.6 ± 12.4	17.9 ± 12.4	15.5 ± 13.0	3.0 ± 2.7	2.8 ± 1.3	3.7 ± 2.3
Total OM ($g\ kg^{-1}_{sediment}$)	40.9 ± 15.64	23.3 ± 16.4	19.2 ± 17.2	6.5 ± 2.9	6.3 ± 1.3	6.6 ± 1.9
GS >8 mm (%)	0.04 ± 0.07	0.06 ± 0.2	3.4 ± 9.2	46.1 ± 26.7	46.0 #	46.0 #
GS 8-4 mm (%)	0.06 ± 1.4	0.04 ± 0.1	1.8 ± 3.2	8.6 ± 5.6	20.1 ± 7.0	16.0 ± 8.6
GS 4-2 mm (%)	0.8 ± 1.3	0.5 ± 0.7	1.6 ± 2.0	5.1 ± 4.0	11.7 ± 3.3	8.1 ± 4.4
GS 2-0.063 mm (%)	80.1 ± 17.2	87.4 ± 15.3	86.2 ± 13.2	39.2 ± 31.9	21.8 ±8.4	29.4 ± 12.2
GS < 0.063 mm (%)	19.0 ± 17.5	12.0 ± 15.4	7.0 ± 5.2	1.0 ± 1.9	0.3 ± 0.3	0.5 ± 0.4

* Calculated values for permanent aquatic sediments

Values are from a total of 322 gravel samples

Statistics

ANOVAs (two way and repeated measures) with a posteriori tests (Bonferoni post hoc) were applied to separate the means. Data were log-transformed, if necessary, to meet the assumptions of normal distribution (Sokal and Rohlf 1995). A Principal Component Analysis (PCA) was used to separate the different habitat types by temperature, water and organic matter content, and grain size distribution. Spearman rank correlations were applied to describe the relationships between habitat variables and within-habitat respiration rates. Regression analyses were carried out to predict soil respiration from diel and seasonal temperature variation. Statistics were calculated using Statistica 6.0 (Statsoft Inc., Tulsa, Oklahoma, USA).

Results

Environmental characterization of habitat patches

We found distinct seasonal patterns in temperature within individual types of habitats (Fig. 2). The average daily temperature ranged seasonally from 8.6 °C (channel) to 33.1 °C (exposed gravel). Diel amplitude, averaged over the annual cycle, ranged between 2.7 °C (channel) and 9.7 °C (exposed gravel). Annual degree days (sum of average daily temperature) ranged from 4017 (riparian forest) to 4560 (exposed gravel).

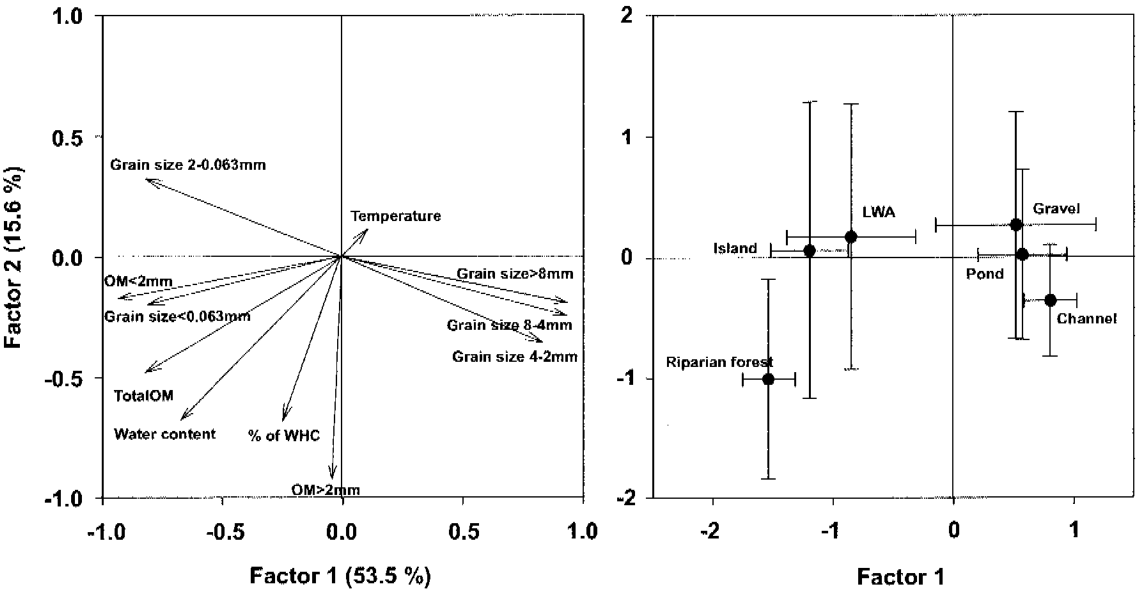

Figure 3: Principal component analyses based on eleven habitat variables. Correlation map of different habitat variables (left panel) and factor map (average ± SD) of individual habitat types (right panel). LWA = Large wood accumulation. WHC = Water holding capacity.

Grain sizes >8 mm prevailed in exposed gravel sediments and in aquatic habitats (>46 %), whereas the fraction 2-0.063 mm dominated other types of terrestrial habitats (>39.2 %). Average gravimetric water content ranged from

3.7 % (exposed gravel sediments) to 25.7 % (riparian forest). Average water content (WC), expressed as % of WHC, was lowest in vegetated islands (36.6 %) and highest in the riparian forest (57.7 %). Total organic matter (TOM; g AFDM $kg^{-1}_{sediment}$) in terrestrial habitats ranged from 6.5 g (0.65 %) in exposed gravel sediments to 40.9 g (4.1 %) in the riparian forest, with the size fraction <2 mm as the dominant OM fraction. OM content in aquatic habitats was similar to the content in exposed gravel sediments (Table 1).

Terrestrial habitats were arranged across an environmental gradient determined by organic matter and water content, and to a lesser extent by temperature. Differences in the grain size fractions >0.063 mm separated the aquatic from the terrestrial habitats (PCA; Fig. 3). Axes F1 and F2 explained 58.2 and 15.8 %, respectively, of the total variation.

Table 2: Seasonal soil and sediment respiration rates (μmol CO_2 m^{-2} s^{-1}) in aquatic and terrestrial habitats (average $\overline{X}$ ± SD). LWA = Large wood accumulation. CV = Coefficient of variation.

Habitat	**n**	**Month**	**January**	**April**	**July**	**October**
Riparian forest	**63**	$\overline{X}$ ± SD	0.97 ± 0.51	3.10 ± 0.96	7.44 ± 2.04	2.67 ± 1.36
		CV	53	31	27	51
Islands	**114**	$\overline{X}$ ± SD	0.86 ± 1.14	3.13 ± 1.35	8.22 ± 3.79	3.38 ± 3.17
		CV	133	43	46	94
LWA	**52**	$\overline{X}$ ± SD	0.37 ± 0.54	1.50 ± 0.85	5.51 ± 2.34	1.46 ± 1.26
		CV	146	57	42	86
Gravel	**322**	$\overline{X}$ ± SD	0.04 ± 0.24	0.52 ± 0.82	1.29 ± 2.65	0.30 ± 0.58
		CV	573	158	206	194
Channels	**100**	$\overline{X}$ ± SD	0.57 ± 0.32	1.00 ± 0.59	1.03 ± 0.54	0.62 ± 0.5
		CV	56	59	52	81
Pond	**53**	$\overline{X}$ ± SD	0.23 ± 0.19	0.47 ± 0.28	1.09 ±0.46	0.62 ± 0.37
		CV	83	60	42	60

Diel variation of SR

Within-habitat diel variation in SR rate was highest in July and ranged between 0.99 (vegetated island) and 1.63μmol CO_2 m^{-2} s^{-1} (large wood accumulation). Diel amplitudes in SR rates were significantly correlated to variations in temperature ($R^2 \geq 0.82$; $p < 0.001$).

Table 3 Spearman rank correlations of total soil and sediment respiration (μmol CO_2 m^2 s^{-1}) and different habitat variables (pooled data from four seasons). Significant correlations ($p \leq 0.05$) are highlighted in bold. OM: organic matter. LWA = Large wood accumulation. GS = Grain size

Independent variable	**Riparian forest n=63**		**Islands n=114**		**LWA n=52**		**Gravel n=322**		**Channels n=100**		**Pools n=53**	
	R	**p**	**R**	**p**	**R**	**p**	**R**	**p**	**R**	**p**	**R**	**p**
Temperature (°C)	**0.85**	**<0.001**	**0.72**	**<0.001**	**0.73**	**<0.001**	**0.35**	**<0.001**	**0.32**	**<0.001**	**0.73**	**<0.001**
Water content (%)	**-0.37**	**0.002**	**-0.22**	**0.018**	**-0.28**	**0.046**	**0.17**	**0.002**	-0.19	**0.099**	-0.18	0.278
% of water holding capacity	**-0.37**	**0.002**	**-0.22**	**0.018**	**-0.28**	**0.046**	**0.17**	**0.002**	-	-	-	-
OM > 2mm ($g\ kg^{-1}_{sediment}$)	**0.27**	**0.036**	0.10	0.273	0.12	0.194	0.22	0.148	**0.27**	**0.001**	0.14	0.394
OM < 2mm ($g\ kg^{-1}_{sediment}$)	**0.27**	**0.030**	0.10	0.286	0.18	0.391	**0.08**	**<0.001**	0.13	0.210	0.19	0.175
Total OM ($g\ kg^{-1}_{sediment}$)	0.24	0.054	0.10	0.301	0.17	0.224	**0.21**	**<0.001**	-0.02	0.830	-0.08	0.555
GS >8 mm (%)	**-0.43**	**<0.001**	**-0.33**	**<0.001**	0.19	0.169	**-0.19**	**0.001**	-	-	-	-
GS 8-4 mm (%)	**-0.58**	**<0.001**	**-0.42**	**<0.001**	0.18	0.190	**-0.19**	**0.001**	-0.03	0.742	-0.00	0.990
GS 4-2 mm (%)	-0.22	0.077	0.02	0.866	0.15	0.297	**-0.19**	**0.001**	**-0.27**	**0.006**	0.01	0.945
GS 2-0.063 mm (%)	**-0.67**	**<0.001**	**-0.32**	**<0.001**	**-0.32**	**0.020**	**0.18**	**0.001**	0.15	0.132	-0.02	0.868
GS < 0.063 mm (%)	**0.69**	**<0.001**	**0.33**	**<0.001**	**0.44**	**0.001**	**0.23**	**<0.001**	**0.46**	**<0.001**	**0.32**	**0.018**

Seasonal variation of SR

The average annual SR rate (μmol CO_2 m^{-2} s^{-1}) ranged from 0.54 ± 1.56 μmol (exposed gravel sediment) to 3.94 ± 3.72 μmol (vegetated island). Over the annual cycle, average SR rate varied in exposed gravel sediments from 0.04 (January) to 1.29 μmol CO_2 m^{-2} s^{-1} (July) and in vegetated islands from 0.86 (January) to 8.22 μmol CO_2 m^{-2} s^{-1} (July). In aquatic habitats seasonal variation was relatively low (Table 2). Differences in the SR rate were significant among habitat types (df = 5; F = 169.58; $p < 0.001$), although SR rates in the riparian forest and in vegetated islands were not significantly different (Bonferoni post hoc; $p > 0.05$). SR rate varied significantly with time (season) (df = 3; F = 121.06; $p < 0.001$), and there was a significant interaction between time and habitat type (df = 15; F = 10.31; $p < 0.001$). Average spatial variation in the SR rate, expressed as the coefficient of variation (CV), was lowest in the riparian forest (CV: 41 %) and highest in exposed gravel sediments (282 %). Within habitats, the CV decreased with increasing temperature and was therefore lowest in July (Table 2).

Table 4: Regression models between total respiration rates (µmolCO_2 $m^{-2}s^{-1}$) and sediment (s; 5 cm depth) and water (w) temperatures calculated for six habitat types. LWA=Large wood accumulation. SE = Standard error. Q_{10}=Temperature sensitivity. n = number of replicates.

Habitat	Model	Parameter	SE	Q_{10}	n	F	R^2	p
Riparian forest	R=a*exp(b*Ts)	a=0.305 b=0.152	0.094 0.016	4.57	63	266.57	0.72	<0.0001
Island	R=a*exp(b*Ts)	a=1.292 b=0.068	0.287 0.010	1.97	114	131.34	0.38	<0.0001
LWA	R=a*exp(b*Ts)	a=0.394 b=0.093	0.116 0.011	2.53	52	116.59	0.67	<0.0001
Gravel	R=a*exp(b*Ts)	a=0.165 b=0.056	0.086 0.018	1.75	322	24.71	0.05	<0.0001
Channel	R=a*exp(b*Tw)	a=0.423 b=0.048	0.089 0.014	1.62	100	134.12	0.11	<0.0001
Pond	R=a*exp(b*Tw)	a=0.168 b=0.085	0.034 0.010	2.34	53	148.38	0.59	<0.0001

Potential drivers of SR

Among habitats, PCA factor scores of axis F1 (Fig. 3) were significantly correlated with respiration rates (R^2 = 0.76; $p < 0.0001$). Within habitats, we found a high correlation between temperature and SR rate ($0.32 < r < 0.85$) except for the channel habitat (Table 3). The relationship between temperature and SR rate was best described by an exponential equation. Temperature explained a high proportion of SR variation (R^2 between 0.38 and 0.72), except for exposed gravel and channel habitats (R^2 = 0.05 and 0.11, respectively), although all models were highly significant ($p < 0.0001$) (Table 4). Residual analyses confirmed temperature as the dominant variable explaining respiration within individual habitat types. The calculated Q_{10} values ranged from 1.62 (channel habitats) to 4.57 (riparian forest) (Table 4). In terrestrial habitats, temperature-corrected SR rates (reference temperature: 12 °C, equation 5) peaked in July except in the riparian forest. In aquatic habitats, temperature-corrected SR rates remained fairly constant throughout the year (Fig. 4).

Annual SR

Annual SR, calculated from the exponential equations derived from empirical field data (cf Table 4), were modeled for the individual habitat types, as well as for the entire floodplain system. Annual SR rates (Feburary 2005 to January 2006) ranged from 160 (ponds and exposed gravel sediments) to 1205 g C $m^{-2} y^{-1}$ (islands) (Table 6). This corresponded to a total annual flux of 545 t C for the 116 ha island-braided floodplain section.

Effect of surface inundation on SR

Surface inundation led to a 66-91 % decrease in SR rates (standardized at 4, 12, and 20 °C) in all habitat types except in exposed gravel sediments. In exposed gravel, SR rate increased by 6 % at a reference temperature of 12 °C but declined by 26 % and 77 % at 20 °C and 4 °C, respectively. SR rates of inundated soils varied significantly among habitat types, incubation temperatures, and time (Two-way ANOVA repeated measures; $p < 0.0001$), although differences between the riparian forest and island habitats were not significant (Bonferoni post hoc; $p > 0.05$). After six hours of inundation, the SR rates ranged from 0.11 ± 0.11 µmol CO_2 m^{-2} s^{-1} (exposed gravel sediments) to 0.67 ± 0.54 µmol CO_2 m^{-2} s^{-1} (riparian forest). Respiration values peaked after 1.25 days of inundation at 4 °C and after 6 hours at 12 °C and 20 °C in the riparian forest and in vegetated islands. Soils from the riparian forest and vegetated islands reached oxygen limitation after three days of inundation (12 °C and 20 °C; Fig. 5). Respiration values for large wood accumulations and exposed gravel sediments remained fairly constant over time (Fig. 5). As expected, temperature was the key predictor of the SR rate in inundated habitats (after six hours of inundation), and the relationship between temperature and SR rate was best described by exponential equations (Table 5). Subsequent residual analyses confirmed the dominant role of temperature in explaining the SR rate. After six hours of inundation the Q_{10} value ranged from 2.31 (riparian forest) to 3.11 (large wood accumulations; Table 5).

Table 5: Regression models of water temperatures (in chambers) and respiration rates (μmol CO_2 m^{-2} s^{-1}) for the four terrestrial habitat types after six hours of inundation. LWA=Large wood accumulation. SE = Standard error. Q10=Temperature sensitivity. n= number of replicates.

Habitat	Model	Parameter	SE	n	Q_{10}	F	R^2	p
Riparian forest	R=a*exp(b*T)	a=0.243 b=0.084	0.059 0.021	20	2.31	62.14	0.58	<0.0001
Islands	R=a*exp(b*T)	a=0.154 b=0.108	0.067 0.022	20	2.95	77.85	0.72	<0.0001
LWA	R=a*exp(b*T)	a=0.073 b=0.113	0.019 0.014	20	3.11	155.30	0.83	<0.0001
Gravel	R=a*exp(b*T)	a=0.037 b=0.095	0.037 0.095	20	2.58	27.00	0.42	<0.0001

Discussion

Soil and sediment respiration (SR) is one of the most important carbon flux in ecosystems and is therefore a well-studied process in permanent aquatic and terrestrial ecosystems (del Giorgio and Williams 2005, Luo and Zhou 2006). However, information from morphologically complex and temporally dynamic ecosystems, such as riverine floodplains, is almost completely lacking (but see Valett et al. 2005). The floodplain along the Tagliamento River, a model ecosystem of European importance, provides the optimal framework to study the linkage between ecosystem structure and function across habitat gradients and over various temporal scales. Our study clearly demonstrates that SR rates were highly variable in space and time reflecting the seasonal dynamics of the floodplain mosaic. We identified temperature as the main factor controlling SR rates within the various habitat types.

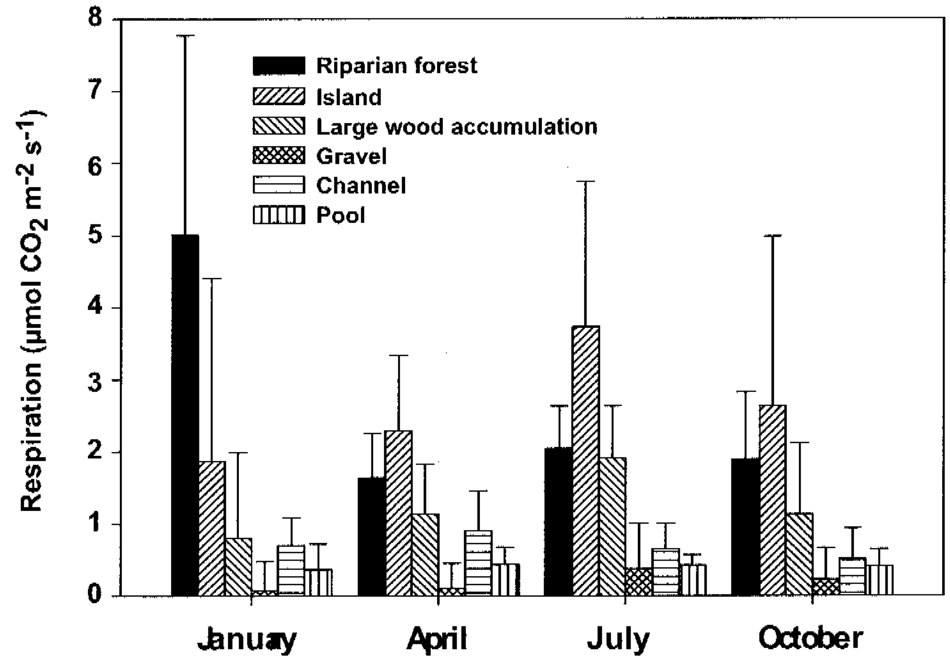

Figure 4: Total soil and sediment respiration rate (average ± SD) in individual habitat types standardized at 12 °C. N = 52 to 322 per habitat type (see table 2).

Methodological aspects in assessing SR

The different methods used to measure respiration rates in terrestrial and aquatic habitats constrained to some extent comparability. The assessment of terrestrial respiration provided area-specific rates, and sediment or soil patches remained relatively undisturbed. In aquatic systems, enclosures were used to quantify SR rates (e.g., Pusch and Schwoerbel 1994, Jones 1995, Jones et al. 1995, Naegeli et al. 1995). Enclosures created an artificial sediment structure that may have disrupted the enclosed microbial communities (Uehlinger and Brock 1991, Naegeli et al. 1995). Moreover, the conversion of SR rates from chamber to area-related values required information about the change in SR rates with sediment depth, a difficult task in aquatic environments (Naegeli and Uehlinger 1997). Open-system methods (Odum 1956) can circumvent such methodological constraints. However, in braided systems the divergence and convergence of channels around bars and islands and the intense vertical exchange of surface and ground waters prevented determination of reliable oxygen balances. By integrating the measured aquatic respiration over a depth of 20 cm we likely underestimated aquatic sediment respiration. In terrestrial habitats, SR measurements using IRGA most likely integrated the SR rates in the uppermost 20-40 cm soil and sediment layers (Luo and Zhou 2006). Further, respiration included different functional compartments. In aquatic habitats respiration included only the contribution of the hyporheic zone. In gravel deposits and large wood accumulations, where an autotrophic compartment was almost completely missing, SR presumably represented microbial respiration. In islands and riparian forest SR included heterotrophic and autotrophic (i.e. root) respiration. Root/rhizosphere respiration can account for as little as 10 percent to more than 90 percent of total *in situ* soil respiration depending on vegetation type and season of the year (Hanson et al. 2000). Despite these methodological shortcomings, our study provides a robust estimate of the spatiotemporal patterns of SR rates in a highly complex and dynamic riverine landscape.

Spatiotemporal variation of SR rate

Average SR rates differed among habitat types by an order-of-magnitude (Fig. 3). The riparian forest and in particular vegetated islands exhibited high SR rates. The availability of large pools of organic matter and the contribution of autotrophic respiration to total SR most likely explained these high rates. Microbial activity depends on the availability of labile fractions of OM derived from fresh litter input and in-site productivity (Schimel et al. 1994, Janssens et al. 2001). In the Tagliamento, islands are young (maximum age 20 years) and the most productive habitats (Langhans 2006). High input and storage rates of bioavailable OM are expected to favor heterotrophic SR on vegetated islands. Our results also underpin the importance of vegetated islands as 'hot spots' for ecosystem processing (this study; Langhans 2006), as well as for biodiversity (Gurnell et al. 2005; Tockner et al. 2006). Islands exhibit a high perimeter to area ratio and are expected to influence adjacent habitats that are less productive and diverse e.g., by transfer of organic matter and organisms. Islands are also among the first habitats that disappear as a consequence of flow and channel regulation. Therefore they are sensitive indicators for assessing functional integrity of floodplain rivers.

Within habitat types, SR rate exhibited distinct diel and seasonal trends strongly correlated to temperature variation. We identified temperature as one of the most important predictors for SR (see also Gansert 1994, Burton et al. 1998, Buchmann 2000). The average Q_{10} value was similar to other terrestrial ecosystems (Davidson et al. 1998, Buchmann 2000, Raubuch et al. 2002), although differences among habitat types were very distinct (1.62 to 4.57; Table 3 and 4). SR rates represented the sum of autotrophic (root) and heterotrophic respiration, for which the Q_{10} can be very different (Buchmann et al. 1997, Boone et al. 1998). In most habitats, the temperature-corrected (standardized at 12 °C) seasonal trend of SR rates reflected the potential influence of root respiration, with higher respiration during the growing season (Fig. 4; Buchmann 2000, Hanson et al. 2000). In the riparian forest, however, the normalized respiration rates exhibited a peak in January, contradicting the hypothesis of seasonality of root respiration. Frequent flood disturbances (Jones et al. 1995, Uehlinger 2000, Uehlinger 2006) and high temperature amplitudes that can affect abundance, physiology, and composition of microbial communities (Lloyd and Taylor 1994, Palmer Winkler et al. 1996) might explain the low temperature dependence of SR rates in channel habitats and in exposed gravel sediments (Table 4). Periods of heterotrophic activity do not necessarily coincide with periods of autotrophic activity. It is the interplay between these processes that determine the seasonality of SR rates, and hence the differences among habitat types.

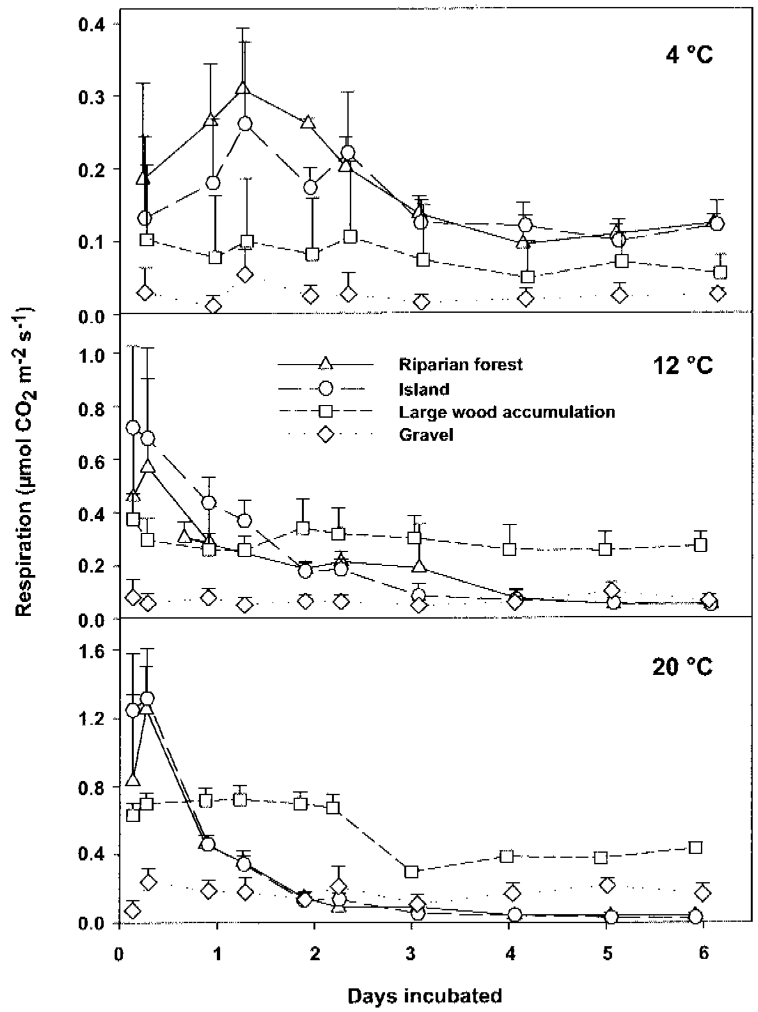

Figure 5: Total soil respiration rate (average ± SD) from terrestrial sediment samples following inundation over a six day incubation period at 4, 12 and 20°C. Notice different scales. Samples of the riparian forest and island reached oxygen limitation after three days at 12 °C and after two days at 20°C.

In addition to temperature, moisture (Davidson et al. 2000, Xu and Qi 2001, Li et al. 2006) and OM content (Schimel et al. 1994, Randerson et al. 1996) are known to control SR rates. For example, Carlyle and BaThan (1988) found a significant correlation of SR rate with moisture when water content dropped below 12.5 %. Amalfitano et al. (in press) found that a water content of 20 % (% of max. WHC; grain size <2 mm) was the critical threshold for bacterial carbon production (BCP). Below this value, BCP ceased although a considerable proportion of bacteria remained alive. In our floodplain system, water content was always well above this critical threshold level (Table 1).

Although OM and water content did not explain within-habitat variation of SR, OM content was closely linked to differences in SR rates among habitat types. Factors such as OM quality, water availability, and root density, which were not assessed in the present study but are known to be highly variable in space (Buchmann 2000), may explain the observed within-habitat variability of SR rates.

Annual soil and sediment CO_2 flux

In the Tagliamento, habitat-specific efflux of CO_2 from soils and sediments spanned almost the entire range reported from various aquatic and terrestrial ecosystems. While exposed gravel sediments and pond habitats exhibited CO_2 fluxes similar to Antarctic and desert ecosystems, fluxes from vegetated islands were as high as rates in moist tropical forests (Raich and Schlesinger 1992, Burkins et al. 2001; Table 6). Hence, in the natural floodplain mosaic of the Taglaimento River, "desert-like" habitats are located in close proximity to "rainforest-like" habitats.

Effect of inundation on SR rate

In contrast to most rewetting studies (e.g., Orchard and Cook 1983, Carlyle and BaThan 1988, Fierer and Schimel 2002) resulted in increasing SR rates, surface inundation led to a major reduction in the SR rate of up to 91% in our study. This sharp decline in SR rate might be explained by the drastic change from the terrestrial to the aquatic environment leading to reduced diffusion of oxygen (Davidson et al. 2006), to the death of "terrestrial" microbes (one third to one half after rewetting in dry soils; Belnap et al. 2005), and to a lower microbial diversity (Rees et al. 2006). Since exposed gravel habitats are subject to frequent inundation, a slight increase in SR rate after inundation can be explained by the potential adaptation of the microbial community to changing environmental conditions (Van Gestel et al. 1993, Lundquist et al. 1999, Fierer and Schimel 2002, Fierer et al. 2003). In an experimentally flooded floodplain forest of the Middle Rio Grande, Valett et al. (2005) found a more than 200-fold increase in soil respiration after a few days of inundation, which contrasts with our findings. However, respiration rates before inundation were much smaller in the Rio Grande floodplain than in the Tagliamento riparian forest.

Table 6: Annual respiration rates (average ± SD; gC m^{-2} y^{-1}) for global soil and aquatic ecosystems (Raich and Schlesinger 1992, Uehlinger, 1993) and for aquatic and terrestrial floodplain habitat types (in bold; this study; * n: see table 2)

Global soil ecosystems and floodplain habitat types	Respiration (gC m^{-2} y^{-1})	n
Tundra	60±20	11
Northern bogs and mires	94±55	12
Pools	**160**	*
Gravel	**168**	*
Desert scrub	224±66	3
Channels	**292**	*
Boreal Forests and Woodland	322±124	16
Marshes	413±186	6
Temperate grasslands	442±234	9
Croplands, fields, etc.	544±408	26
Large wood accumulations	**624**	*
Tropical savannas and grasslands	629±159	9
Temperate decidous forests	647±275	29
Temperate streams	769 ± 316	13
Tropical dry forests	673±268	4
Temperate coniferous forests	681±456	23
Mediteranean woodlands and heath	713±317	13
Desert streams	807 ± 668	9
Riparian forest	**982**	*
Islands	**1205**	*
Tropical moist forests	1260±180	10

SR of inundated terrestrial sediments varied distinctively among habitat type, incubation time, and temperatures (Fig. 5). The differences in OM content are most likely responsible for the large among site variation in SR (see above). SR peaked at the beginning of the inundation experiment in riparian forest and islands soils, while respiration in sediments from large wood accumulation and exposed gravel habitats remained fairly stable (Fig. 5). This can be simply due to a reduced amount of available organic matter, a lower microorganism pool or a physical adjustment resulting in a lower shock reaction of the microorganisms to frequently changing environmental conditions such as inundation (Fierer and Schimel 2002). The large wood accumulations and the gravel habitat are subject to frequent inundation while the riparian forest and the islands are rarely flooded. Temperature was a better predictor of respiration and Q_{10} values showed a lower range compared to *in situ* values (Table 5). This probably results from excluding root respiration from the experimental sediments.

Conclusion

We found a tight link between habitat structure and sediment respiration across an aquatic-terrestrial environmental gradient. SR rates differed by an order-of-magnitude among habitat types, with organic matter content, temperature, and inundation regime as the most important variables determining SR. Hence, even small changes in the relative proportion of individual habitat types, in temperature, and in the inundation regime can substantially alter the whole-floodplain efflux of CO_2. This is important in the context of river modifications and changing climate. Channelization and flow regulation decrease habitat complexity in floodplain systems, with severe consequences for the spatial variation in SR (Langhans et al. 2006). Global warming will increase soil and sediment temperature, and therefore SR. As a consequence, decomposition can exceed net primary production leading to a decrease in soil and sediment organic matter content (Kirschbaum 1995), and therefore in process heterogeneity and carbon cycling in floodplain systems.

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4. FROM PATCH TO LANDSCAPE: APPLYING A GIS-BASED APPROACH TO MODEL FLOODPLAIN RESPIRATION

M. Doering, U. Richard, U. Uehlinger, and K. Tockner

In review

Abstract

Riverine floodplains are among the most diverse and productive landscapes, while at the same time they are very threatened ecosystems. However, we lack basic information for predicting their functional response to human alterations. We present a simple heuristic model to upscale soil and sediment respiration (SR) from the patch to the entire floodplain scale. To identify the key predictors of SR rate, we carried out controlled laboratory experiments and intensive field surveys within different habitat types along a morphologically intact river (Tagliamento River; NE Italy). A one-dimensional empirical floodplain respiration model was implemented into a three dimensional GIS-based model. This model allowed us to simulate the response of the SR rate to flow, temperature, and habitat alterations. Average annual SR rates ranged from 144 g C $m^{-2} yr^{-1}$ *in exposed gravel sediments to 1149 g C* $m^{-2} yr^{-1}$ *in vegetated islands; and therefore spanned the entire reported range for various aquatic and terrestrial ecosystems world wide. The SR rate was highly sensitive to temperature variations while inundation had a low predictive power. A simulated 4°C increase in air temperature caused a 6 % (14 g C* $m^{-2} yr^{-1}$*) increase in SR in aquatic habitats, but a 70 % (691 g C* $m^{-2} yr^{-1}$*) increase in the riparian forest. On the other hand, the elimination of vegetated islands, covering only 9 % of the entire system, resulted in an 18 % decrease in total floodplain SR rate. Our model emphasizes the strong linkage between environmental heterogeneity and ecosystem functioning, and can therefore be used to predict the response of respiration to future anthropogenic alterations.*

Introduction

Although ecosystem managers and conservationists are aware of the dynamic nature of ecological systems, they often lack the information required to make management decisions about systems that naturally undergo major changes in space and time (Borman and Likens 1979). Yet our ability to predict the dynamics of such ecosystems, especially in response to anthropogenic alterations, is central to maintaining their long-term integrity (Clark et al. 2001, Nilsson et al. 2003). Hence, we need specific models which allow us to make predictions about the future behaviour of highly dynamic ecosystems (Canham et al. 2003, Dole and Niemi 2004).

In their natural condition, riverine floodplains (*sensu* Stanford et al. 2005) are amongst the most dynamic and heterogeneous ecosystems, showing complex patterns of variation over a wide range of temporal and spatial scales. These patterns arise through the interactions between the dominant hydrogeomorphological processes and ecosystem processes such as primary productivity and sediment respiration. Therefore, floodplains are excellent model systems to study the linkages between the structure and the functioning in ecosystems (Ward et al. 2002).

So far, there have been few attempts to model habitat and ecosystem processes on floodplains. Glenz (2005) recently developed a coupled model of ecological and hydraulic processes to simulate riparian forest dynamics for Central European conditions. (Gergel et al. 2005) developed a spatially-explicit biogeochemical model simulating the effects of flood alterations on floodplain denitrification. In this model, terrain was simulated to create replicate floodplains with various inundated areas. When flooded, depressions received NO_3-N, dissolved organic carbon and well-oxygenated water. As ponds drained, biotic assimilation and denitrification were determined for both the water column and the underlying sediments.

The model we propose is a simple heuristic model to upscale ecosystem processes from small-scale field investigations and controlled laboratory experiments to the entire floodplain mosaic. It is a spatially-explicit, grid-based model by applying a generic ecosystem process model to all grid elements of a floodplain reach. We focus on sediment respiration (sum of auto- and heterotrophic respiration rates; SR) as a key process in the carbon cycle that integrates the energy flow through the biotic compartments of aquatic and terrestrial ecosystems (Van Voris et al. 1980, Uehlinger and Naegli 1998, Euskirchen et al. 2003). Based on literature studies of the most important influences on SR, combined with data from extensive field and laboratory experiments, we developed a simple parameterization of SR. We implement a one-dimensional empirical floodplain respiration model into a three dimensional GIS-based application. Our model can be applied for short-term simulations of SR rates (average daily intervals over an annual cycle). These simulations will improve our quantitative understanding of ecological processes in braided floodplain, and will allow us to identify areas with intensive SR rates. Finally, it will allow us to simulate responses of SR rates to different types of flow, temperature, and channel alterations. This is an important step towards a better understanding of the past and future responses of ecosystem processes to various scenarios of environmental change (Omlin and Reichert 1999, Gergel et al. 2005).

Methods

Study site

The Tagliamento (46°N, 12°30'E) is a 7th order gravel-bed river with a total catchment area of 2580 km^2. The corridor is fringed by continuous riparian woodland. Despite local water and gravel abstractions and a channelized downstream section, the river retains its essentially pristine morphological and hydrological characteristics. The flow regime is highly dynamic with frequent flow pulses (*sensu* Tockner et al. 2000) throughout the year (Petts et al. 2000, Arscott et al. 2002, Van der Nat et al. 2002). The main study ecosystem is a 1.9 km^2 island-braided floodplain in the mid-section of the river corridor (river km 79.5 – 80.4; 135 m a.s.l.; Figure 1).

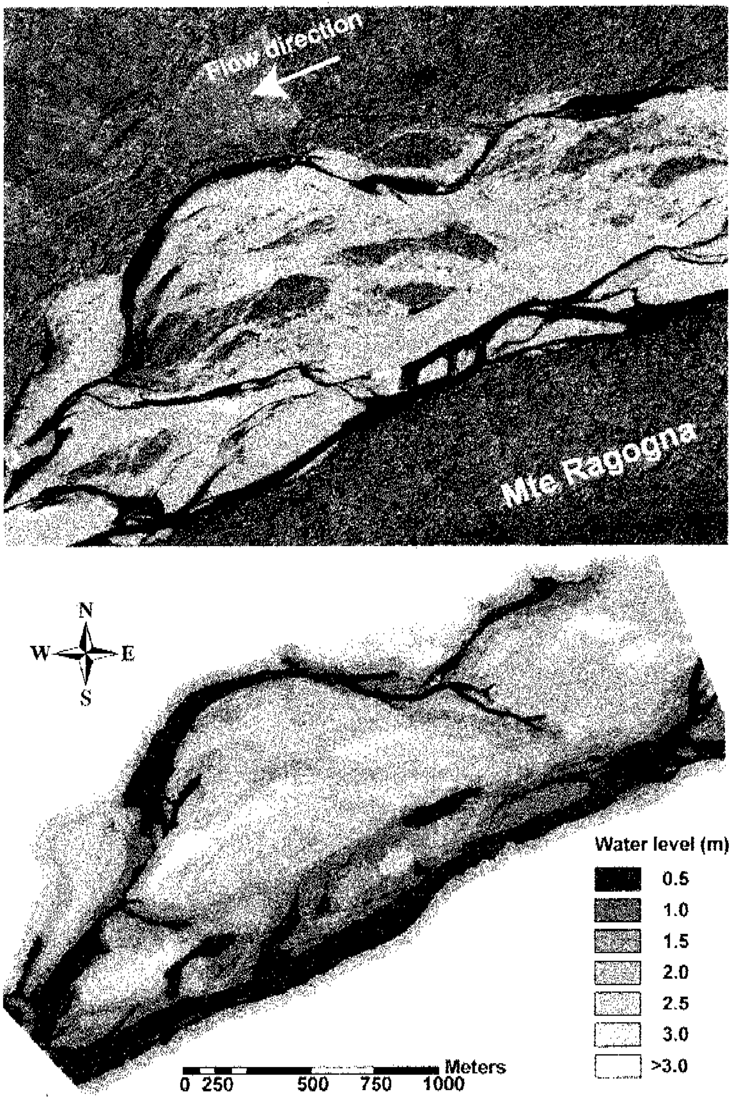
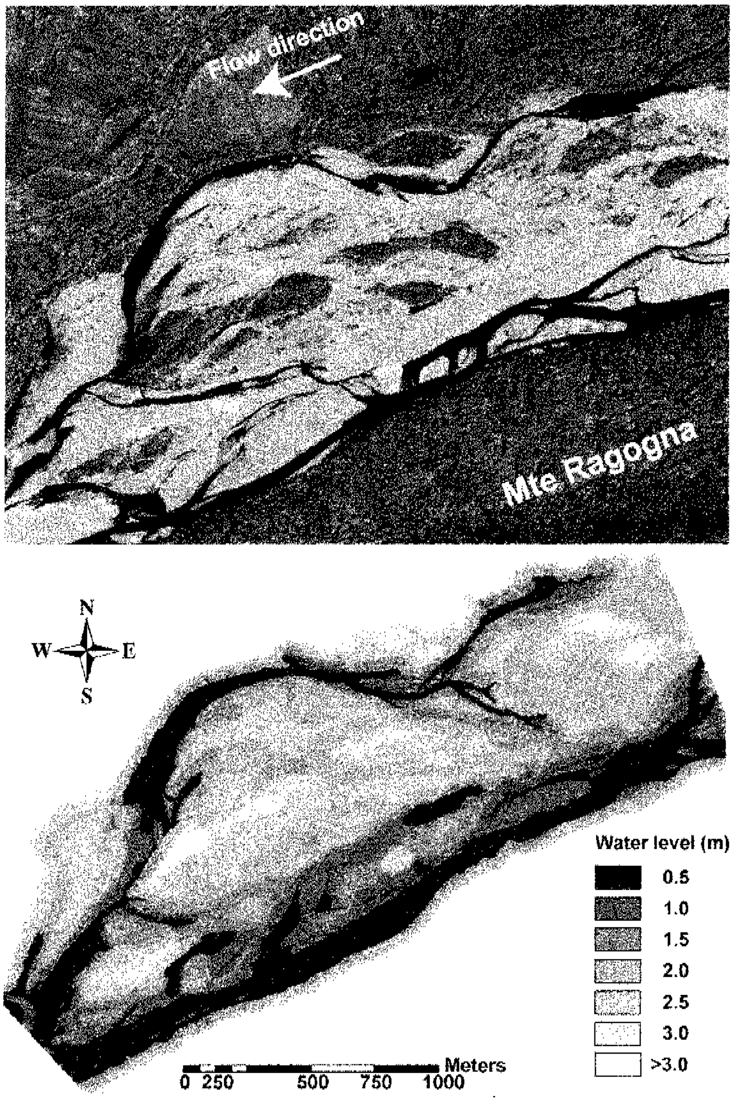


Figure 1: Aerial photo of the main study area (upper panel) and map of inundation patterns (lower panel). Water levels are from a gauging station 2 km downstream of the study area. Inundation of the riparian forest occurs at a water level above 3 m.

It consists of a complex network of aquatic habitats (17.6 % of total floodplain area), gravel bars (47.0 %), wooded islands (8 %), large wood accumulations (0.4 %) and a fringing riparian forest (27 %). The local climate is typical of the flow pulses (*sensu* Tockner et al. 2000) throughout the year (Petts et al. 2000, Arscott et al. 2002, Van der Nat et al. 2002). The main study ecosystem is a 1.9 km^2 island-braided floodplain in the mid-section of the river corridor (river km 79.5 – 80.4; 135 m a.s.l.; Figure 1).



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Assessment of model parameters

Our floodplain respiration model is based on an empirical model developed through intensive field and laboratory studies. We measured soil and water temperature, soil moisture, organic matter content, grain size distribution and soil and sediment respiration (SR) in all dominant aquatic and terrestrial habitat types (Doering et al. in review). Further we investigated the effect of surface inundation on terrestrial SR using controlled laboratory experiments. Temperature and inundation had been identified as the key variables determining SR. We developed an empirical model that acted as the basis for the spatially explicit floodplain model. In the following section we briefly describe the methods used to develop the empirical model. A detailed description of the model development is given by Richard and Woodtli (2006) and Doering et al. (in review).

In situ measurements of SR in terrestrial habitats

SR was measured in January, April, July and October 2005 using a soil respiration chamber (Li 6400, LiCor, Lincoln, Nebraska, USA) attached to a portable Li-6400 infrared gas analyzer (IRGA). PVC collars of known volume (8 cm long, 10.5 cm inside diameter) were inserted into the sediment of the riparian forest (n = 16 per date), vegetated islands (n = 27), large wood accumulations (n = 13), and exposed gravel sediments (n = 81). The soil chamber was set on top of the collar to measure the undisturbed CO_2 flux. The IRGA measurement was repeated four times per date and collar and values were averaged. Temperature was measured in 5 cm sediment depth next to the collar.

In situ measurements of SR in aquatic channel habitats

Aerobic respiration of aquatic channel sediments was measured as the change in O_2 concentration over time in plexiglas tubes (5.2 cm diameter, 32 cm long) sealed with rubber stoppers (Uehlinger et al. 2002). In channel habitats ($n = 25$ per date) sediments were collected from 0 - 20 cm depth (the uppermost sediment layer with epilithic algae was removed prior to sampling) and pre-sieved to exclude substrata > 8 mm. Each tube was half filled with sediment, filled up with surface water from the sampling site, and subsequently incubated *in situ* for about 4 hours (Uehlinger et al. 2002). Oxygen concentration and temperature were measured with a portable oxygen meter (Oxi 340/bset, WTW, Weilheim, Germany).

Short-term inundation experiments

Soil samples were collected in January and May 2005 in the riparian forest, on vegetated islands, large wood accumulations, and exposed gravel sediments ($n = 5$ per habitat type and date). Samples were pre-sieved to exclude the size fraction > 8 mm and stored at 4 °C (Dilly 2001). In the laboratory, plexiglas tubes, as described above, were half filled with soil, filled to the top with artificial floodwater, and sealed. Artificial flood water contained 26.14 mg TIC, 37.54 mg Ca^{2+}, 12.56 Mg^{2+}, 0.768 NO_3-N, 2.14 mg K^+, 50.04 mg Na^+, 66.41 mg Cl^- and 49.64 mg SO_4 per liter. This corresponded to the average concentrations of flood water collected in 2004 (three events) along the Tagliamento. Oxygen concentration was measured at day 0.3, 0.9, 1.3, 1.9, 2.3, 3, 4, 5 and 6 using a portable meter (Oxi 340/bset, WTW, Weilheim, Germany). The January samples were incubated at 4 °C and 12 °C and the May samples at 12 °C and 20 °C in a dark climate room for six days.

A major difference between inundated sediments and submerged soils is the higher amount of litter in the floodplain soils, leading to a pulse of nutrients following inundation. This pulse may cause a rapid increase in microbial activity leading to a rapid onset of anoxia in the floodwater and the underlying soils (Baldwin and Mitchel 2000). In the Tagliamento floodplain oxygen measurements in the saturated subsurface sediments indicated no oxygen limitation (average concentration: 8.8 mg/L; n = 97; Thalmann and Lüthi 2006). Therefore, samples from large wood accumulation and exposed gravel areas were reaerated at 12 °C and 20 °C to prevent oxygen limitation (≤ 5 mg/L).

Calculation of SR rates from sediment tube measurements

Based on the oxygen consumption in the chamber water r (g O_2 m^{-3} h^{-1}) we calculated the respiration rate per m^2 in the uppermost sediment layer (0 and 0.2 m depth) R (μmol CO_2 m^{-2} s^{-1}) according to the equation:

$$R = r \times \frac{10^6}{32} \times \frac{1}{3600} V_w \times \frac{Vs_{0-0.2}}{Vs_{chamber}} \times RQ$$

V_w is the volume of water in a chamber (m^3), $Vs_{chamber}$ the sediment volume including porosity (m^3) in a chamber, $Vs_{0\text{-}0.2}$ the sediment volume of the uppermost sediment layer (0 - 0.2 m) inclusive porosity below one m^2 and RQ the respiratory quotient (0.85; Dilly 2001). The porosity of exposed gravel, channel, and pond sediments was assumed to be 20 % (Eglin 1990, Jussel 1992). The porosity of riparian forest and island soils was estimated to be 40 % (Kuntze et al. 1994), and the porosity of sediments in large wood accumulations was estimated to be 30 %.

Empirical model

SR rate in terrestrial and aquatic channel habitats

The SR rate of terrestrial and aquatic channel habitats exhibited an exponential relationship with temperature (soil/sediment temperature, Ts; water temperature, Tw) (eq. 1):

(1) $SR=a*\exp(b*Ts,w)$

SR rate in inundated habitats

The SR of the inundated soils from the riparian forest and island habitats varied with water temperature (Tw) and duration of inundation (t). The SR was best described by an exponential decay function (eq. 2). Respiration (SR) of the inundated large wood accumulation and of exposed gravel sediments varied only with water temperature (Tw), best described by an exponential function (eq. 3).

(2) $SR=a*Tw*exp(-b*t)$

(3) $SR=a*exp(b*Ts)$

Model parameters a and b, including standard errors, and R^2 are listed in table 1.

Table 1: Model parameters a and b (± SE) and R^2 of exponential relations between temperature and respiration (equation 1) and between temperature, duration of inundation and respiration after short term inundation (equation 2 and 3). LWA = Large wood accumulation.

	Temperature			**short term inundation**		
Habitat	**a ± SE**	**b ± SE**	**R^2**	**a ± SE**	**b ± SE**	**R^2**
Riparian forest	0.305 ± 0.094	0.152 ± 0.016	0.72	0.152 ± 0.003	-0.748 ± 0.086	0.62
Island	1.292 ± 0.287	0.068 ± 0.010	0.38	0.068 ± 0.004	-0.932 ± 0.079	0.80
LWA	0.394 ± 0.116	0.056 ± 0.018	0.67	0.093 ± 0.016	0.129 ± 0.012	0.70
Gravel	0.165 ± 0.086	0.048 ± 0.014	0.05	0.056 ± 0.002	0.096 ± 0.012	0.49
Channel habitats	0.308 ± 0.073	0.093 ± 0.011	0.11	-	-	-

A detailed description of *in situ* measurements, laboratory experiments, and the functional relationship between respiration, temperature, and inundation are given in (Richard and Woodtli 2006, Doering et al. in review).

Temperature

For the estimation of habitat-specific temperature, average daily values of soil, sediment (Ts), and water (Tw) temperatures (n = 382 per habitat type; January 2005 to February 2006) were regressed against average daily air temperature (T_{air}) recorded at a station 10 km from our study reach (Fagagna; 46° 1004'N, 13° 0903'E) (eq. 4):

(4) $Ts,w = a*T_{air}+b$

Model parameters a and b, including standard errors, and R^2 are given in Table 2.

Table 2: Model parameters a and b (± SE) and R^2 of linear regressions between air and soil/sediment temperatures and between air and water temperatures in terrestrial and aquatic channel habitats (equation 4). LWA = Large wood accumulation.

Habitat	a ± SE	b ± SE	R^2
Riparian forest	0.870 ± 0.009	0.390 ± 0.126	0.96
Island	0.967 ± 0.010	-0.780 ± 0.145	0.96
LWA	0.990 ± 0.008	0.246 ± 0.118	0.97
Gravel	1.209 ± 0.010	-2.060 ± 0.152	0.97
Channel habitats	0.329 ± 0.007	8.227 ± 0.101	0.85

Developing a spatially-explicit floodplain SR model

A one-dimensional empirical model as described above was implemented into a three-dimensional raster application based on a Geographic Information System (GIS; ArcGIS 9.1; ESRI, Redlands, California, USA) to simulate and to model (upscale) spatial and temporal variation of SR rates in the floodplain mosaic. Major components of this application included a digital elevation model (DEM), a raster layer defining the extent and spatial distribution of individual habitat types, continuous stage records, temperature data, and the empirical functions of SR rates as described above.

Digital Elevation Model (DEM) and habitat raster

For the generation of the digital elevation model (DEM), we produced georeferenced maps from oblique aerial photographs taken from a bluff at the left bank of the floodplain (Mte Ragogna). In 2003 and 2004, twelve sets of photos were taken at ~20 cm water level intervals, from baseflow to bankful level. Each set of photos was orthorectified based on a detailed dGPS mapping (accuracy <0.5 m) conducted in March 2003 and in January 2005 providing sufficient ground control points (floodplain margins, island tips, large wood accumulations) for rectification. Rectified images were digitized using ArcGis 9.1 (ESRI, Redlands, California). The shorelines were extracted from each map and used as contour (bathymetric) lines to interpolate a DEM using inverse distance weighting (IDW). The DEM was represented by a map of grid cells (3×3 m) storing the height of each individual cell. The definition of the habitat types was provided by a second raster layer (3×3 m) derived from a detailed habitat mapping using dGPS in January 2005. The selected grid-cell size restricted the incorporation of ponds into the DEM.

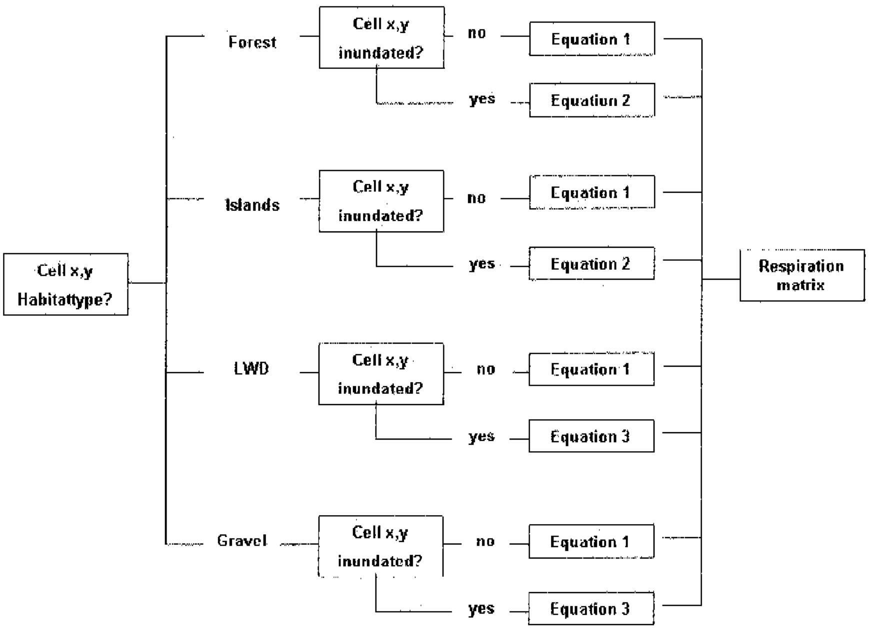

Figure 2: Conceptional respiration model. Model parameters of individual equations are listed in table 1. LWA = Large wood accumulation.

Simulation of inundation patterns

After the definition of habitat types the inundated area was calculated at different water levels (Figure 1). The duration of inundation at each time step (daily intervals) was stored in each single cell. The resulting matrix was combined with the corresponding temperature data stored in a table. Both data sets were used as model parameters for the equations described above to generate a matrix representing the actual respiration rates (daily time steps; Figure 2).

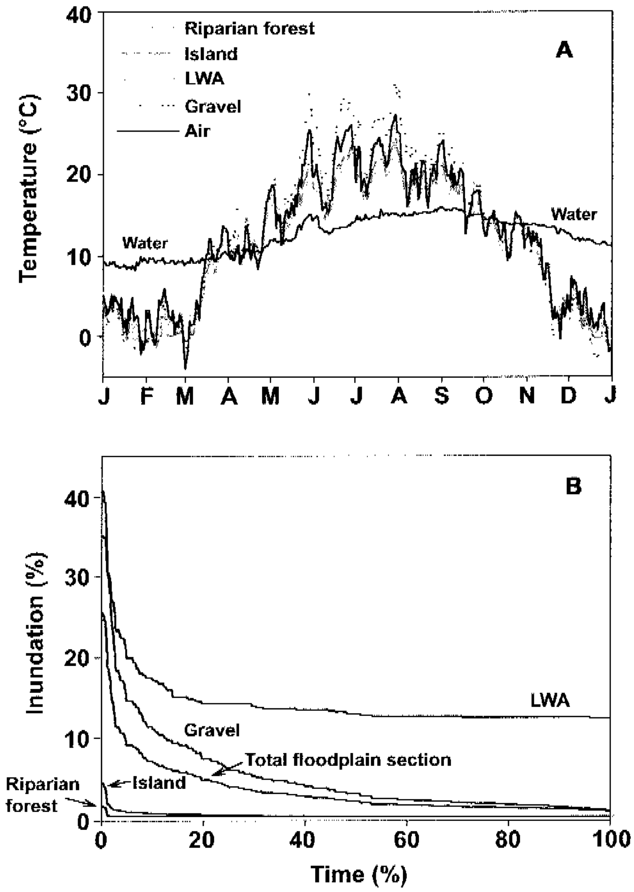

Figure 3: a) Annual temperature variation (°C; daily averages in 2005) in the individual habitat types. b) Duration curve of annual inundation (%) of individual habitat types and of the total floodplain (2005). LWA=Large wood accumulation.

Stage records and temperature data

Water level was continuously recorded at a gauging station 1.5 km downstream of the study reach (S. Pietro). Temperature was recorded continuously in terrestrial habitats using temperature loggers exposed at 5 cm soil depth (n = 5 per habitat type; DS1921G, Dallas Semiconductor, Dallas, USA). Temperature in aquatic channel habitats was recorded using the temperature probe of two stage level recorder (PDLR70; Ecotech, Germany) installed in channels at the left and right margins of the floodplain.

Simulated response of respiration to environmental alterations

Using the measured average daily stage level data, and the average daily soil, sediment and water temperatures of the 2005 field campaign, we calculated annual aquatic and terrestrial respiration rates within the individual habitat types. Missing temperature data from January 1 to January 19 were calculated using equation (4).

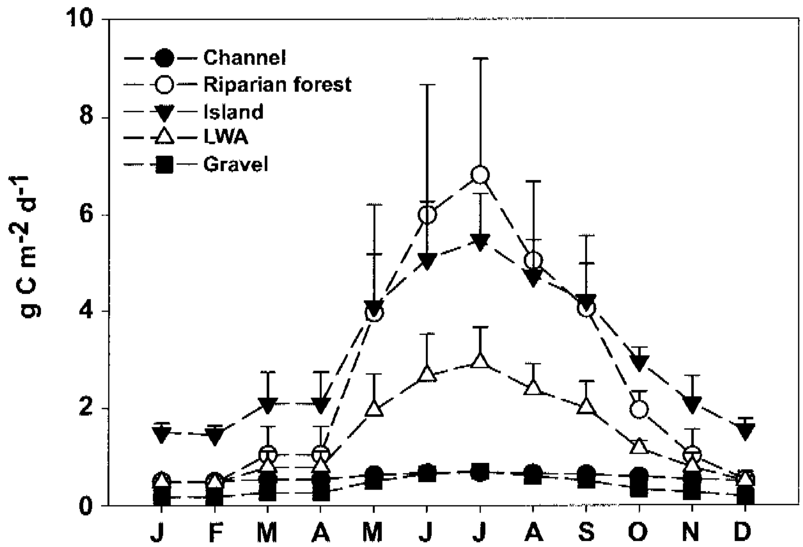

Figure 4: Temporal patterns of soil and sediment respiration rates in aquatic and terrestrial habitats (g C m^{-2} d^{-1}; monthly averages ± SD; 2005). LWA=Large wood accumulation.

To separate the effect of temperature and inundation on SR rates we used stage level and temperature data of a wet and cold year (2002) and a dry and hot year (2003). Soil and water temperatures were calculated from average daily air temperature data according to equation (3). The effects of temperature and inundation were evaluated by activating and deactivating inundation patterns in both years. To test for temperature sensitivity we increased average daily air temperatures in the 2005 model by 0.5, 1, 2, and 4 °C. Corresponding water and soil temperatures were calculated according to equation (4). To evaluate the effect of habitat alterations on SR rates we increased the area of the riparian forest by 20 % and eliminated all vegetated islands from the active tract, respectively. Both scenarios reflected potential consequences of river regulation.

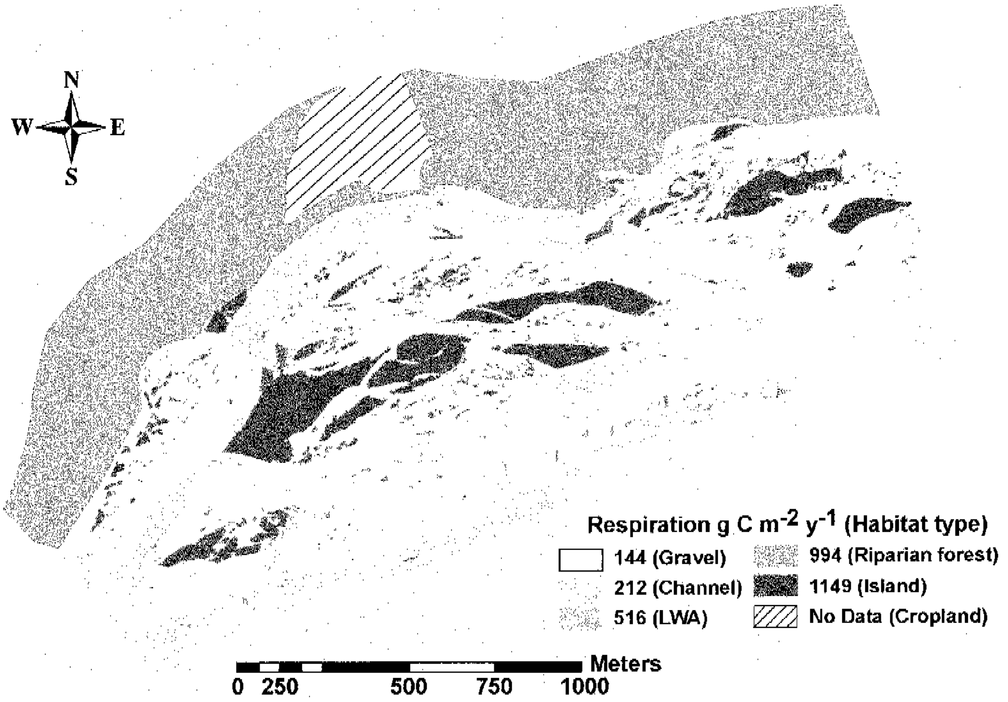

Figure 5: Spatial variation of total annual soil and sediment respiration rates (g C $m^{-2} y^{-1}$) in the modeled floodplain section in 2005. Respiration rates in large wood accumulations (LWA) are too small to be shown on this map.

Results

Temperature and inundation dynamics

In 2005, annual degree days ranged from 4’060 (riparian forest) to 4’605 (exposed gravel sediments; Figure 3a). However, the seasonal amplitude was very distinct in exposed gravel sediments (range: 34.7 °C), compared to 10.1 °C in aquatic channel habitats. In 2005, up to 25 % of the terrestrial part (area above base flow) of the floodplain was inundated, ranging from 1 % for the riparian forest area to 34 % for large wood accumulations. During 95 % of the time the inundated area was <1 % (riparian forest) and <21 % (large wood accumulation), respectively, corresponding to a total area of 10 % of floodplain area above base flow level (Figure 3b).

Spatiotemporal pattern of SR rates

During 2005, the average monthly SR ranged from 0.2 to 0.7 g C $m^{-2} d^{-1}$ (exposed gravel sediments) and from 0.5 to 6.8 g C m^{-2} d^{-1} (riparian forest), respectively. Annual variability of SR rates, expressed as the coefficient of variation, ranged from CV = 14 (aquatic channel habitats) to CV = 88% (riparian forest; Figure 4).

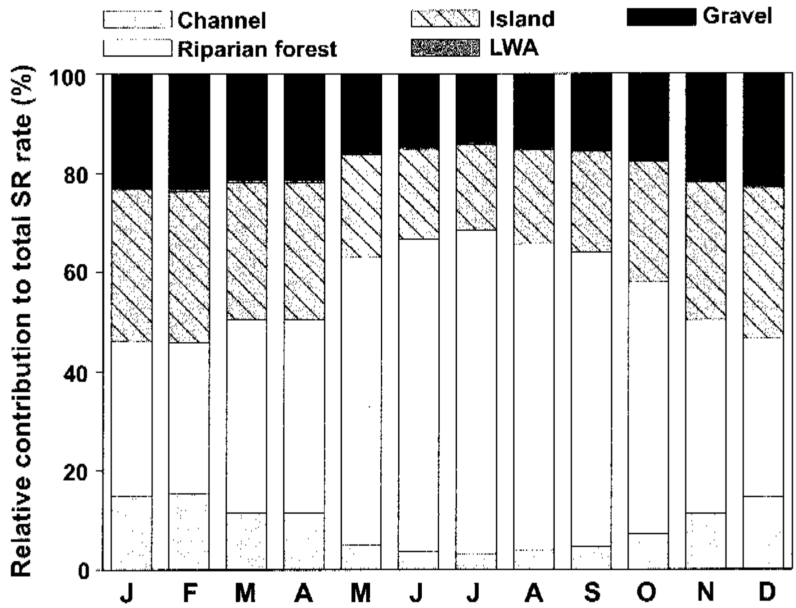

Figure 6: Relative contribution (%) of the dominant habitat types to total soil and sediment respiration (SR; monthly averages; 2005). LWA = Large wood accumulation.

The annual SR rate ranged from 144 g C $m^{-2} yr^{-1}$ (exposed gravel sediments) to 1149 g C $m^{-2} yr^{-1}$ (vegetated islands; Figure 5). The total annual SR rate (i.e., area-weighted mean) for the entire floodplain was calculated as 463 g C $m^{-2} yr^{-1}$; corresponding to a total carbon efflux of 863 t. The riparian forest covered 27 % of the total floodplain area but contributed on average 57 % to total respiration, while exposed gravel sediments covered 47 % of the area, but contributed only

16 % to total floodplain respiration (Figure 6). The relative contribution of individual habitats to total SR rate changed with season. For example, the relative contribution of the riparian forest was highest in summer.

Separating the effect of temperature and inundation on SR rates

Average daily air temperature in 2002 and 2003 was 12.6 °C and 12.7 °C, respectively. Annual degree days (sum of average daily values) were 4871 °C in 2002 and 4965 °C in 2003. The total inundated areas above base flow level were 1766 ha y^{-1} (sum of average daily values of the inundated area) and 7066 ha y^{-1} in 2003 and 2002, respectively. Consequently, the total calculated annual SR rates (area-weighted mean for the entire floodplain) were 475 and 581 g C m^{-2} y^{-1} in 2002 and 2003, respectively. The higher SR rate in 2003 (18 % above the rate calculated for 2002) was primarily a consequence of higher temperature in 2003. In order to evaluate the sole effect of temperature, we simulated SR under permanent base flow conditions. Results revealed a temperature-related SR increase of 16 % (i.e. 172 g C m^{-2} y^{-1}) in 2003 compared to 2002 (Table 3).

Temperature sensitivity of SR rates

An increase in air temperature between 0.5 °C and 4° C resulted in a predicted temperature increase from 0.1 °C to 1.6 °C in aquatic channel habitats and from 0.6 °C to 4.8 °C in exposed gravel areas (Figure 7a). Habitat-specific increase in the SR rate, as a consequence of a 0.5 to 4.0 °C increase in air temperature, was predicted to range from 1 % to 6 % (1.7 to 14 g C $m^{-2}yr^{-1}$) in permanent aquatic channel habitats and from 6 % to 70 % (67 to 691 g C $m^{-2}yr^{-1}$) in the riparian forest (Figure 7b). At the floodplain scale, an increase in air temperature from 0.5 and 4 °C was predicted to increase the annual SR rate (area-weighted mean) by 4 % and 33 % (67 and 230 g C m^{-2} yr^{-1}), respectively.

Habitat sensitivity of SR rate

The floodplain SR rate was expected to be very sensitive to changes in habitat composition. The relative increase in the areal extent of the riparian forest by 20 % was calculated to increase the floodplain SR rate by 18 %. On the other hand, the clearance of all vegetated islands (9 % of total area), as it was the case during World War I and II would lead to a decrease in the calculated floodplain SR rate of 16 %.

Table 3: Model results of annual respiration rates (2002 and 2003) calculated for individual habitat types under terrestrial and inundated conditions using natural and modified flow conditions (base flow: ~20 $m^3 s^{-1}$). Ra = respiration in the permanent aquatic habitat (channel), RFt = respiration in the riparian forest (terrestrial), RFi = respiration in the floodplain forest (inundated), RIt = respiration in the island habitat (terrestrial), RIi= respiration in the island habitat (inundated), RWt = respiration in large wood accumulations (terrestrial), RWi = respiration in the large wood accumulations (inundated), RGt = respiration in exposed gravel sediments (terrestrial), RGi = respiration in exposed gravel sediments (inundated). bf = base flow

Year	Unit	Ra	RFt	RFi	RIt	RIi	RWt	RWi	RGt	RGi	Sum
2002	tC	49	522	0.10	183	0.21	3	0.14	119	7	884
	gC m^{-2}	217	1050	0.20	1170	1	458	22	122	7	475
2002 bf	tC	49	524	0	188	0	3	0.07	150	0	915
	gC m^{-2}	216	1053	0	1199	0	541	10	154	0	491
2003	tC	49	668	0.02	202	0.03	4	0.09	158	1	1082
	gC m^{-2}	217	1342	0.03	1287	0.18	609	14	162	1	581
2003 bf	tC	49	668	0	203	0	4	0.08	163	0.00	1086
	gC m^{-2}	217	1343	0	1290	0	617	13	167	0.00	583

Discussion

Given the size, complexity and dynamic of most floodplains it is difficult to investigate large scale ecosystem processes empirically or experimentally, and modeling approaches are essential to understand how floodplain ecosystems function at various scales (e.g. Canham et al. 2003). Here, we developed a simple heuristic model combining a one dimensional empirical model based on intense field and experimental work (Doering et al. in review) with a three dimensional spatial model to quantify the effects of temperature, inundation, and landscape composition on soil and sediment respiration (SR). This model allowed us to investigate the link between habitat structure and function in riverine floodplains and to make predictions about the future behaviour of a highly dynamic ecosystem.

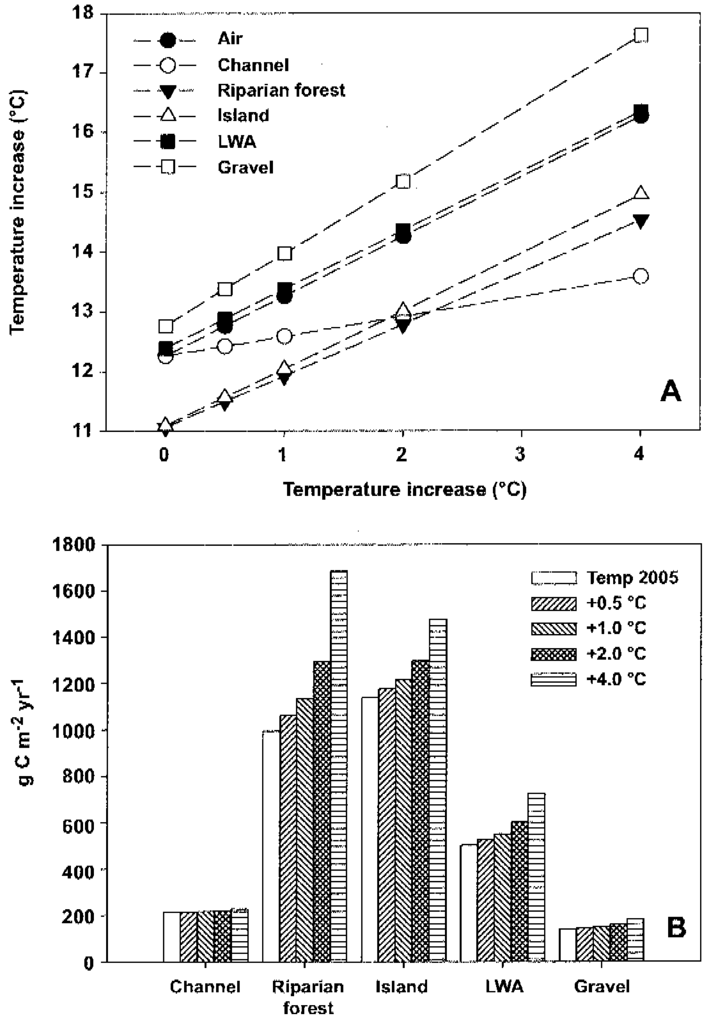

***Figure** 7*: a) Calculated temperature (°C) increase in individual habitat types as a consequence of an increase in air temperature of 0.5, 1, 2, and 4 °C. b) Annual soil and sediment respiration rates in permanent aquatic and in terrestrial habitat types in 2005 as a consequence of an increase in air temperature of 0.5, 1, 2, and 4 °C. LWA = Large wood accumulation.

Model evaluation

Our modeling approach was similar to that introduced by (Fitz et al. 1996) and further developed by (Voinov et al. 2004). Based on literature studies of the most important influencing factors on SR and on the empirical and experimental work a simple parameterization of SR rates was done. We are aware that this is an oversimplified approach that did not account for all potential predictors of SR. At the floodplain scale, we aggregated process rates measured in various habitat types without taking into account the potential functional linkages among the individual habitat types. In our model we did not consider soil moisture, organic matter content, and grain size distribution; factors that potentially could influence our model results. Instead, we focused on habitat type (which indirectly reflects OM and water content), temperature, and surface inundation as the key predictors of the SR rate. These variables were identified as being important during an intense previous investigation in this floodplain section (Doering et al. in review).

The spatial model is to some extent subject to limitations. Due to the spatial resolution of the oblique air photos, small ponds were not included in our model. However, ponds covered only 0.5 % of the total floodplain area and they exhibited low SR rates (Doering et al. in review). Therefore, their contribution to total floodplain respiration was expected to be of limited importance. Our model was spatially conservative, i.e. it was not able to describe changes in morphology through floods. In their natural state, floodplains are described as a shifting mosaic of habitat patches (Stanford et al. 2005). Although the spatial configuration of habitats can drastically change with floods, their relative composition remains relatively constant (Arscott et al. 2002, Van der Nat 2003). Thus, our model can be applied to simulate SR rates on time-scales from months to years. Floods can however scour the river bed, leading to significant reductions in SR rates (Jones et al. 1995, Naegeli and Uehlinger 1997, Uehlinger 2006). However, respiration is considered to be highly resilient ecosystem process that can recover within a few weeks after flood disturbance to pre-disturbance rates (Uehlinger 2006).

Our model exhibited a relatively high degree of uncertainty. Using the standard errors of the model parameters (Table 1), total annual respiration differed from +61 % to -52 % of the calculated average (Table 4). A high degree of uncertainty was expected (Ryan and Law 2005) since the SR rate is the sum of microbial, root, and micro- and macrofaunal activity; all these processes react differently to change in environmental conditions and over several scales (Buchmann 2000, Hanson et al. 2000, Doering et al. in review).

Despite these limitations, our model allowed us to provide a first estimation of SR rates in a highly dynamic and complex floodplain ecosystem. The predicted SR rates were plausible and comparable with values reported in the literature (e.g., Raich and Schlesinger 1992, Buchmann 2000, Doering et al. in review)

Spatiotemporal patterns in SR rates

SR rates exhibited distinct spatial and seasonal patterns (Figures 1, 4 and 5). The annual SR rate in vegetated islands (1149 g C m^{-2} yr^{-1}) was 8X higher than in exposed gravel areas (144 g C m^{-2} yr^{-1}; Figure 5). These results were consistent with the data from a previous study at the habitat level (Doering et al. in review). Annual SR rates spanned nearly the entire range reported for various aquatic and terrestrial ecosystems, from tropical moist forests to subarctic bogs (Raich and Schlesinger 1992).

Our model results confirmed the overriding importance of temperature (e.g., Lloyd and Taylor 1994, Davidson et al. 1998, Buchmann 2000), and to a lesser extent of inundation (Valett et al. 2005, Doering et al. in review), in controlling SR rates; but they also revealed some new perspectives. Although inundation had a strong impact on the SR rate at the habitat level, its impact on the landscape level was rather low; at least at the seasonal time scale considered

(Table 3). For example, floods were too short to substantially affect the SR rate at the floodplain scale. Between 2001 and 2005 flow pulses affecting more than 20 % of the active floodplain tract lasted on average for less than 6 days. Floods affecting more than 80 % of the active tract on average lasted less than 2 days (Van der Nat et al. 2002). Further, floods inundated primarily exposed gravel sediments that in any case exhibited the lowest SR rate.

Temperature was identified as the most important predictor of SR in all habitat types; which is in accordance to existing models focusing on various terrestrial and wetland ecosystems (e.g., Rothamstad model, FAEWE model; Burke et al. 2003). Since the relationship between temperature and SR is non-linear, even a small increase in temperature can lead to a major change in the SR rate. We predicted that an increase in the air temperature by 4 °C, a likely scenario during the next century, will lead to a 33 % increase in the CO_2 efflux from the entire floodplain. Furthermore, river regulation in concert with an increase in temperature may exacerbate the effect of temperature on the SR rate. Most formerly braided rivers had been converted into single-thread rivers. These long-term alterations in habitat composition may have far-reaching consequences for the functioning of floodplain systems. Vegetated islands, for example, exhibited the highest SR rates of all habitats investigated; therefore, they play a pivotal role in the carbon flux in riverine floodplains. They not only serve as "hot spots" in SR, as demonstrated in the present study, they may also function as key producers of organic matter that might fuel SR rates in adjacent less productive habitats (e.g., exposed gravel fields; Langhans 2006). However, vegetated islands are among the first landscape elements that disappear as a consequence of flow regulation and channel modification.

Implications

Humans have modified floodplain systems dramatically (Abramovitz 1996, Tockner and Stanford 2002, Meybeck 2003, Revenga and Kura 2003) resulting in a loss of environmental heterogeneity and fluvial dynamics. On the global scale air temperatures are expected to increase between 0.5 and 4 °C by 2100 (Intergovernmental Panel on Climate Change 2001). Both circumstances have severe consequences for ecosystem functioning such as SR as demonstrated in this study. Our simple heuristic model allows us to address different "what if" scenarios to predict the behavior of highly dynamic floodplain systems with respect to organic matter dynamics. We were able to demonstrate how alterations in habitat type, temperature, and inundation regime may affect SR, although our data primarily showed the trajectory of change rather than accurate quantities (see also Ryan and Law 2005). In addition, we lack data from floodplain systems especially in very cold or very warm regions that are expected to comprise most of the C storage (Burke et al. 2003). Thus, further research of underlying processes determining SR in different floodplains is needed to validate our modeling results. Large scale manipulation experiments (e.g. experimental floods), in combination with investigation of different carbon pools, and the availability of highly accurate data on morphological and hydrological changes (e.g. by using LIDAR radar) could contribute to a better and more accurate understanding of the close interactions between environmental heterogeneity and ecosystem processes along riparian corridors.

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Synopsis

Riverine floodplains are complex ecosystems whose physical structure changes dramatically in space and time. To cope with this complexity several ecological concepts have been developed during the past decades. In the early 70s, Hawkes (1975) attempted to deal with this complexity by dividing lotic ecosystems into characteristic longitudinally ordered zones. In 1980, Vannote et al. developed the River Continuum Concept (RCC). They argued that a river's biological and chemical processes correspond to its physical attributes, and that the nature of biological communities changes in a downstream direction just as the river itself does. Today river networks are viewed as a complex of hydrogeomorphic patches, which are repeatable along rivers and only partially predictable in position (Thorp et al. 2006). Their composition and configuration change in time, and has been referred to as the shifting habitat mosaic (Arscott et al. 2002, Stanford et al. 2005).

Understanding the causes and consequences of spatial heterogeneity affecting ecosystem functioning has been considered as the "final frontier" in ecology. Further, there is a need for spatially explicit models that allow us to make predictions about the future behaviour of such highly complex and dynamic ecosystems (Canham et al. 2003, Dole and Niemi 2004), which again is a prerequisite for successful river management.

We investigated the linkage between ecosystem structure and function in the Tagliamento River. The Tagliamento is a model ecosystem of European importance that provides insight into the structural and functional complexity that must have characterized many Alpine rivers before regulation.

The dynamic and heterogeneous nature of floodplain ecosystems

Our results reflected the dynamic and heterogeneous nature of a natural floodplain ecosystem. The highly variable flow regime caused extensive expansion and contraction dynamics along longitudinal, vertical, and lateral dimensions. Along a 41.5 km braided section, for example, we identified a 29 km losing zone characterized by massive infiltration of surface water and a 12.5 km gaining zone. Up to 23 km of the losing zone lacked surface flow and even small changes in water level caused major increases or decreases in aquatic and terrestrial ecosystem size.

The floodplain consisted of a mosaic of contrasting aquatic, semi-aquatic, and terrestrial landscape elements including the riparian forest, vegetated islands, large wood accumulations, exposed gravel sediments, channel and pond habitats. We found that these landscape elements differed widely in their structural properties (e.g., organic matter and water content, and local climatic conditions; Figure 1) and therefore in their functional performance.

Structural properties and functional performance

The results clearly underpinned the importance of structural habitat properties for the functional performance of floodplain habitats. The direction of vertical hydrologic exchange provided the habitat template, which again influenced hyporheic respiration and periphyton density in the large-scale losing and gaining zones. The effect of surface inundation of prevalent terrestrial habitats, using laboratory experiments, led to a decrease in soil and sediment respiration. The structural properties of different habitat types were reflected by the rate of soil and sediment respiration and thereby spanned the whole range of rates reported for aquatic and terrestrial soil and sediment environments world wide. However, the influence of structural habitat properties was not limited to respiration. Comparative results from various sources along the Tagliamento clearly demonstrated that structural habitat properties determine various ecosystem processes in different ways (Figure 1). Overall, vegetated islands were identified as key habitats that exhibited high processes rates and that were, in particular, very sensitive to changes in temperature.

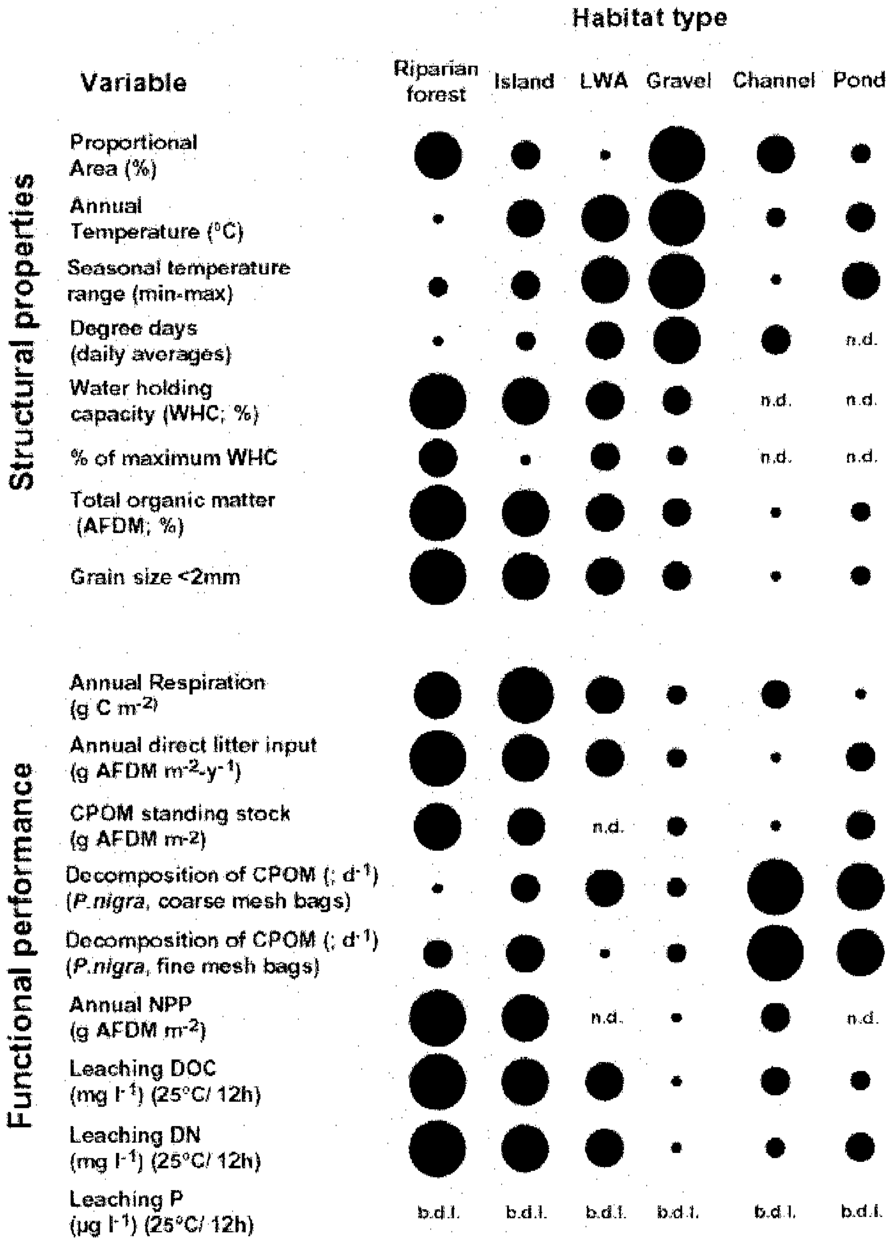

Figure 1: Ranked contribution of structural properties and functional performance of the dominant aquatic and terrestrial habitat types in the island-braided floodplain of the Tagliamento River. The size of bubbles represents the magnitude of process rates and of structural properties. LWA = Large wood accumulation. NPP = Net Primary Productivity. AFDM = Ash Free Dry Mass. n.d. = not determined. b.d.l. = below detection limit.

From the habitat to the landscape scale

Given the size, complexity and dynamics of most floodplains, it is difficult to investigate large-scale ecosystem processes empirically or experimentally, and modeling approaches are essential to understand how floodplain ecosystems function at various scales. Using a spatially explicit heuristic model to quantify the effect of temperature, inundation and landscape composition, on soil and sediment respiration at the landscape scale showed that respiration was extremely sensitive to temperature variation. Although inundation had a strong impact on soil and sediment respiration at the habitat level, its impact at the landscape level was much lower and underpinned the importance of viewing ecosystem processes at different spatial scales. In contrast, simulated changes in habitat composition severely affected soil and sediment respiration.

Outlook

The results of this thesis provided new insights to the linkage of habitat heterogeneity and ecosystem functioning in a complex and dynamic floodplain system. However, our knowledge on the linkage between patterns and processes in floodplains is far from being complete or definitive. The following topics would require future attention: (i) understanding the underlying mechanisms of temperature sensitivity of different floodplain habitats; (ii) quantifying the functional linkage among individual floodplain habitats and how the performance of a habitat depends on the performance of an adjacent habitat, (iii) comparing the behavior of floodplains of different geomorphic types (meandering, anastomosing) to changes in temperature and inundation regime, (iv) testing the effect of environmental heterogeneity on ecosystem functioning at different scales, and (v) developing a mechanistic and spatially explicit river network model on ecosystem processes; to name only a few challenges for research.

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