

Environmental heterogeneity affects input, storage, and transformation of coarse particulate organic matter in a floodplain mosaic

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Abstract Quantifying spatial and temporal dynamics of organic matter (OM) is critical both for understanding ecosystem functioning and for predicting impacts of landscape change. To determine the influence of different habitats and coarse particulate OM (CPOM) types upon floodplain OM dynamics, we quantified aerial input, lateral surface transfer, and surface storage of CPOM over an annual cycle on the near-natural floodplain of the River Tagliamento in NE-Italy. Using these data, we modelled floodplain leaf dynamics, taking account of the spatial distribution and hydrologic connectivity of habitats, and using leaf storage as a response variable. Mean aerial CPOM input to the floodplain was similar from riparian forest and islands, but surface transfer was greater from islands, supporting the suggestion that these habitats act as “islands of fertility” along braided rivers. Leaves were the lateral conveyor of energy to more open parts of the floodplain, whereas CPOM was mainly

stored as small wood in vegetated islands and riparian forest. Simulating the loss of habitat diversity (islands, ponds) decreased leaf storage on the whole floodplain, on exposed gravel and in large wood accumulations. In contrast, damming (loss of islands, ponds and floods plus floodplain overgrowth) greatly increased storage on exposed gravel. A random shuffle of habitats led to a storage increase on exposed gravel, while that in large wood accumulations and ponds declined. These results disentangle some of the complexities of CPOM dynamics in floodplain ecosystems, illustrate the value of models in understanding ecosystem functioning at a landscape level, and directly inform river management practice.

Keywords Tagliamento · Leaf decomposition · Ecosystem modelling · Flood pulse · Hydrological connectivity · Organic matter dynamics

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Introduction

In their natural state, river floodplains are amongst the world's most diverse, complex and dynamic ecosystems (Tockner et al. 2010a). They are composed of a shifting mosaic of aquatic, semi-aquatic and terrestrial habitats, which vary widely in sediment composition, nutrient and organic matter (OM) content, and thermal and flow regimes (Junk et al. 1989; Naiman et al. 2005; Tonolla et al. 2010). They also encompass a wide range of successional stages, with populations, communities and ecosystems in a state of continuous adjustment to changes in the habitat mosaic (Stanford et al. 2005; Winemiller et al. 2010). The functioning of any patch in this mosaic is determined not only by its own habitat properties, but by its spatial relationship and connectivity to neighbouring habitats (Tockner et al. 2010b). For example, a close linkage between water bodies and highly productive vegetated islands may increase the capacity of overall OM transformation capacity of the entire floodplain (Langhans et al. 2006; Tockner et al. 2010b). Thus, disentangling the effects of the composition and the spatial arrangement of habitats is critical to understand the functioning of floodplain ecosystems.

The input, transfer, storage and transformation of OM are key ecosystem processes on floodplains that are strongly affected by linkages across habitats (Tank et al. 2010). Many aspects of OM dynamics in headwater streams have been well studied, including direct aerial input and lateral transport (Fisher and Likens 1973; Benfield 1997; Pozo et al. 1997), lateral transport of deposited OM by wind (Teeri and Barrett 1975; Benson and Pearson 1993), input of OM by bank erosion (Zah 2001), and import and export of OM by hydrological processes (Dance et al. 1979; Maamri et al. 1994). However, the OM dynamics of floodplains is more complex (Thoms et al. 2005; Valett et al. 2005; Tockner et al. 2010a), as these areas can serve as both sources and sinks for OM, depending upon (among others) flow regime, degree of connectivity of habitat patches, floodplain topography, and sediment load (Cuffney 1988; Tockner et al. 1999; Naiman et al. 2005). Floodplains can be important storage areas (Noe and Hupp 2009), where OM is 'pre-processed' and the resulting particles are entrained to the channel during high flows (Smock 1990), thereby driving in-stream food webs (together with local autochthonous production; Thorp and Delong 1994; Hedges et al. 1994).

Hydrologic connectivity, in the sense of water-mediated transfer of matter or energy within and between longitudinal, lateral, and vertical dimensions of riverine landscapes (Ward and Stanford 1989; Pringle 2003), is a key property influencing OM dynamics. In hydrologically connected floodplains, lateral exchange of OM among habitats can be considerable (Junk et al. 1989; Ward and

Stanford 1995; Neatrou et al. 2004), especially if material is also transported by wind (Teeri and Barrett 1975; Benson and Pearson 1993). In both cases, leaf litter is an important medium for transferring energy and nutrients from terrestrial to aquatic habitats (Fisher and Likens 1973; Cummins 1974; Webster et al. 1995; Xiong and Nilsson 1997), and also among terrestrial habitat patches. However, if flow is regulated or the channel is modified, the hydrological connectivity amongst habitats may be disrupted. More OM is then retained within the terrestrial areas (where it may decompose slowly because of dry conditions; Ellis et al. 1998; Tockner et al. 1999), and the quantity entering the aquatic system is greatly reduced.

Quantifying the various processes involved in OM dynamics is a complex undertaking, which has rarely been attempted for large temperate river floodplain ecosystems (but see Zah and Uehlinger 2001; Hein et al. 2003). Such studies conducted in near-natural systems can greatly increase our understanding of how hydrologic connectivity and habitat complexity interact to control ecosystem processes. This information is important because of the significant role floodplains are assumed to have in the global carbon cycle (Battin et al. 2009). Additionally, they provide valuable data for managing river ecosystems by revealing the main transfer and transformation pathways of OM and nutrients (Karlsson et al. 2005).

The work described here is among the first attempts to quantify the various CPOM processes at a floodplain scale. Our two main goals were: (1) to determine the role of different habitats and types of CPOM (leaves, small wood, grass, and miscellaneous material) by quantifying the spatial and temporal dynamics of aerial input, lateral transport and storage of CPOM, and (2) to apply these data—in combination with previously published data on decomposition rates from the same habitat types—in a spatially and temporally explicit floodplain model to simulate the consequences of altered habitat composition, lack of floodplain flooding and spatial configuration on leaf litter dynamics under contemporary flow conditions.

Materials and methods

Study site

Located in NE Italy (46°N, 12°30'E), the Tagliamento is a 7th order gravel-bed river with a catchment area of 2,580 km². Despite local water and gravel abstractions and a channelized downstream section, the river retains its essentially pristine morphological and hydrological characteristics (Fig. 1). The river has a flashy flow regime ($Q_{80} = 72 \text{ m}^3 \text{ s}^{-1}$; Ward et al. 1999) with frequent flow and flood pulses (sensu Tockner et al. 2003).

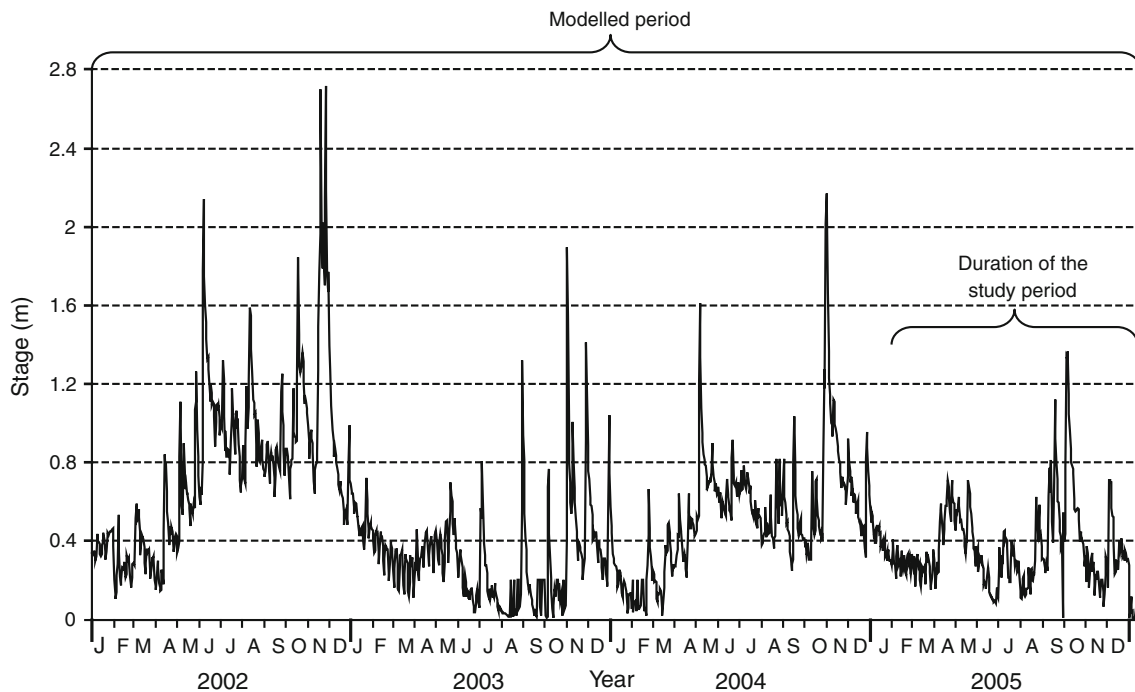


Fig. 1 Water level (m; measured at Villuzza) at the study site during the study period (2005) and the model period

Fig. 2 The island-braided reach of the Tagliamento River. Three transect types were established to investigate aerial input and lateral transfer: perpendicular island transects (isl.per), parallel island transects (isl.para), and perpendicular forest transects (for). Flow is from *right to left*



The floodplain segment we investigated has a broad floodplain that forms a complex mosaic of aquatic, semi-aquatic, and terrestrial habitats, fringed by continuous riparian woodland (Gurnell et al. 2001; Langhans et al. 2006; Fig. 2). At base flow (about $20 \text{ m}^3 \text{ s}^{-1}$), the study area consists of exposed gravel habitats (60.3 ha, 51.8 % of total area), vegetated islands (10.4 ha, 8.9 %), accumulations of large wood (0.4 ha, 0.4 %), the channel network (18.2 ha, 15.6 %), numerous ponds in the riparian forest (orthofluvial ponds) and the active tract (parafluvial ponds) (0.6 ha, 0.6 %), and fringing riparian forest (26.5 ha, 22.8 %). The dominant riparian tree in the investigated floodplain segment is *Populus nigra* (Karrenberg et al. 2003). Detailed information on the Tagliamento catchment and the main study area can be found in Ward et al. (1999), Gurnell et al. (2001), Tockner et al. (2003) and Doering et al. (2011).

Aerial CPOM input and lateral surface transfer

We quantified the aerial input and the lateral surface transfer of CPOM along 12 transects. Four of these extended perpendicularly from the fringing riparian forest (i.e. perpendicularly to the longitudinal axis of the river corridor; in the following referred to as perpendicular forest transects), four extended from islands parallel to the islands' main axis (i.e. along the longitudinal axis of the river corridor; aka parallel island transects), and four extended perpendicularly from islands (i.e. perpendicularly to the longitudinal axis of the river corridor; aka perpendicular island transects) (Fig. 2). This design made it possible to test for the role of wind, which usually blows along the longitudinal axis of the river corridor (unpublished data), and therefore, might have promoted aerial CPOM input and transport along parallel island transects.

Two kinds of traps were set out to collect CPOM along all transects. The aerial traps captured material falling from above, and consisted of buckets (0.049 m²) fixed to the floodplain surface. The lateral traps (buckets, 25 cm diameter) captured CPOM driven laterally over the floodplain surface by wind and gravity. Buckets were separated in two equal parts by a flat piece of wood to distinguish between lateral transfer from the vegetation and from the open tract, respectively. Pieces of wood (30 × 10 cm) on each side of the bucket prevented input from other directions. Buckets were dug into the ground with the rim flush to the sediment surface, and the top covered to avoid aerial input. Traps contained four holes at the bottom of the bucket, covered with 1.0 mm mesh, to avoid slack flow. Along all transects, we deployed 96 pairs of these traps (i.e. one aerial and one lateral trap).

The first trap pair was located 5 m inside the vegetation, and the remaining pairs were positioned on the floodplain at 1, 5, 10, 20, 35 and 70 m distance from the vegetation edge. The exact trap locations were determined with a differential global positioning system (dGPS; TCS1, Trimble, Sunnyvale, California, USA; accuracy <1 m). The traps were installed in February 2005 and sampled at monthly intervals from March to October and bi-weekly in November and December 2005.

CPOM storage

On five occasions during 2005 (in April, May, September, October, and November), we collected by hand all CPOM of ≤0.1 m diameter from plots of 0.25 m² from exposed gravel and shore zones or 0.0225 m² plots from islands and riparian forest habitats. We chose these specific habitats to complement storage data from van der Nat (2002) needed for the leaf dynamics model, and as we considered them to be most important for explaining floodplain CPOM dynamics: Islands and the riparian forest as production areas, exposed gravel as the largest habitat in the floodplain, and shore zones as they most closely depend on hydrology. For each habitat type, we sampled 12 randomly replicated sites (n = 48 per sampling date).

All CPOM samples were rinsed on a 1-mm sieve and separated into four types: leaves, small wood, grass and miscellaneous material (mainly fruits, roots, and catkins). The CPOM types were dried to constant weight (60 °C for 48 h), weighed, ashed (500 °C for 6 h), and reweighed to calculate ash-free dry mass (AFDM).

Leaf litter decomposition

During a previous study in the same floodplain segment (Langhans et al. 2008), leaf litter decomposition of black poplar (*P. nigra* L.) was quantified in river channels,

Table 1 Summary of decomposition coefficients (k , mean ± 1 SE, $n = 4$, $p \leq 0.001$ in all cases) of black poplar leaves in seven floodplain habitat types and coarse-mesh litter bags as estimated by linear regression (Langhans et al. 2008)

Habitat type	k (d ⁻¹) ± 1 SE	R ²	n
Channel	-0.0188 ± 0.0030	0.68	20
Parafluvial ponds	-0.0051 ± 0.0006	0.79	24
Orthofluvial ponds	-0.0051 ± 0.0007	0.73	24
Large wood accumulations	-0.0021 ± 0.0005	0.42	24
Islands	-0.0021 ± 0.0006	0.40	24
Exposed gravel	-0.0020 ± 0.0004	0.49	24
Riparian forest	-0.0019 ± 0.0004	0.50	24

parafluvial and orthofluvial ponds, on exposed gravel, in large wood accumulations, on vegetated islands and in the riparian forest. This work was carried out in four replicate sites of each habitat type during a period of base-flow conditions between December 2002 and March 2003. Habitat-specific leaf-decomposition coefficients were estimated using linear regression of ln(x)-transformed data of % remaining leaf dry mass (Table 1). For the model presented here, we used data from leaves enclosed in coarse-mesh litter-bags (mesh size = 10 mm), which allow access to macroinvertebrates and therefore reflect natural decomposition conditions.

Data analysis

Aerial CPOM input was expressed as gAFDM m⁻² day⁻¹, and lateral surface transfer as gAFDM m⁻¹ day⁻¹ (Zah 2001). Lateral CPOM transfer was calculated from the amount of CPOM crossing the trap opening (0.25 m) per day. To estimate values for January and February 2005, which were not measured, we assumed that input and transport declined linearly between December and March, and that rates in December 2004 were the same as those in December 2005. For November and December, means of aerial input and lateral transport from the two sampling dates were used for further analyses.

Variation in aerial input and lateral transfer along the three transect types over time were analysed using repeated measures analysis of variance (rmANOVA) with transect type (three levels) and CPOM type (four levels) as independent variables, and month (ten levels) as a repeated measures factor followed by Scheffé's post-hoc tests for unequal samples sizes. Differences among means of CPOM storage (expressed as gAFDM m⁻²) were analysed in the same way, with habitat type (four levels) and CPOM type (four levels) as independent variables, and month (six levels) as the repeated measures factor. Only significant interactions are reported and discussed here. As sphericity was violated (Mauchly's test ≤0.05) in all analyses, the

degrees of freedom were corrected using Greenhouse-Geisser estimates. Additionally, results from rmANOVA models were compared to mixed models, which accounted for missing values (Krueger 2004), with autoregressive variance–covariance structures for aerial input and compound symmetry structures for lateral transport. There were no differences between the two models, and only results from the rmANOVA are discussed here. We performed a separate Mann–Whitney-test to test whether lateral CPOM transport between the two directions (from the vegetation and from the open tract) differed. This information was needed for the model.

Input, transport, and storage data were $\log(x + 1)$ -transformed before rmANOVAs were performed. Although data did not perfectly meet assumptions of homoscedasticity and normality (Kolmogorov–Smirnov test), ANOVA was deemed to be an acceptable method due to its robustness to moderate violations of test assumptions (Box 1954).

All statistical analyses were performed using SPSS (vers. 17.0/SPSS Inc., IL, USA) with significance levels set at $P \leq 0.05$.

Developing a spatially and temporally explicit floodplain leaf dynamics model

We developed a GIS-based leaf dynamics model that took account of the spatial configuration and hydrologic connectivity of the floodplain. Leaf storage (gAFDM m^{-2}) was used as a summary response variable representing the net outcome of all the important processes affecting leaf litter—deposition (aerial leaf input), transport (lateral surface transfer of leaves), transformation (leaf decomposition) and erosion (through flooding). The model applied a one-dimensional, empirical floodplain leaf model to a three-dimensional raster application that simulated floodplain inundation (implemented using ArcGIS 9.2; ESRI, Redlands, California, USA; Doering 2007).

The 3D GIS-raster application

Major components of the GIS-raster application included a digital elevation model (DEM; Doering 2007), a raster layer defining the extent and spatial distribution of individual habitat types, distance raster layers of island and riparian forest vegetation, and continuous stage records to simulate inundation patterns. The DEM was represented by a map of grid cells (3×3 m) storing the height of each individual cell. Further raster layers (3×3 m) for the definition of habitat types and distance to vegetated habitats (distance raster layer) were derived from a detailed habitat mapping using dGPS in January 2005. The inundated floodplain area was calculated at different water

levels, and the duration of inundation at each time step (daily intervals) was stored in each single cell. Water level data, required to simulate the timing and magnitude of flood dynamics within the GIS-raster application, were continuously recorded from 2002 through 2005 at a gauging station 1.5 km downstream of the study reach (at location S. Pietro).

The empirical floodplain leaf model

The leaf model comprised aerial leaf input and decomposition rates of *P. nigra* leaves and air and water temperature data. *Populus nigra* is the most abundant leaf species at the study site (>90 %, Karrenberg et al. 2003), and decomposition rates of this species were therefore used as a proxy for leaf decomposition generally. Spatially explicit information on *P. nigra* decomposition is provided by Langhans et al. (2008). We, first, developed the empirical floodplain leaf model including aerial and lateral input. As lateral leaf transfer did not have a significant impact on leaf storage in each cell (for explanations see discussion section) it was omitted from the final model.

Changes in leaf storage for different habitats—riparian forest, vegetated islands, lentic water bodies in the riparian forest (orthofluvial ponds) and in the active tract (parafluvial ponds), large wood accumulations and channels—were calculated using Eq. (1),

$$\frac{dM_i}{dt} = -k_i(T)M_i \quad (1)$$

where M is the actual biomass (storage, gAFDM m^{-2} ; data from this paper and from van der Nat 2002), t is time, i the habitat type, k the leaf decomposition coefficient, T temperature ($^{\circ}C$) and $k_i(T)$ the habitat-specific leaf decomposition coefficient as a function of temperature. To be able to include temperature as a determining factor of habitat-specific leaf decomposition rates, air and water temperatures were monitored in aquatic (channel, orthofluvial and parafluvial ponds) and terrestrial (on the surface of exposed gravel, within the decomposing litter on vegetated islands and in the riparian forest, and in accumulations of large wood) habitats using VEMCO Minilog temperature loggers (Langhans et al. 2008). It was assumed that the temperature optimum for leaf decomposition was $35^{\circ}C$ and the upper limit was $45^{\circ}C$ (Ise and Moorcroft 2006).

As aerial input of leaves (J , gAFDM $m^{-2} \text{ day}^{-1}$) was similar along all transect types (see results section), it was described by a single exponential decay function for input from island and riparian forest vegetation (Eq. 2) with distance from the edge of islands or riparian forest vegetation indicated by x . We estimated the function parameters separately for each month by applying non-linear

Table 2 Model parameters (*a*, *b*) of the negative exponential functions (Eq. 2) describing the aerial input of leaves from forest (*n* = 28, mean ± 1 SE) and island vegetation (*n* = 56, mean ± 1 SE) over an annual cycle

Year 2005 Month	Forest vegetation			Island vegetation		
	<i>a_t</i>	<i>b_t</i>	<i>R</i> ²	<i>a_t</i>	<i>b_t</i>	<i>R</i> ²
April	0.395 ± 0.10	1.791 ± 1.54	0.33	0.014 ± 0.003	1.66 ± 1.17	0.25
May	0.703 ± 0.15	1.397 ± 0.86	0.43	0.967 ± 0.3	1.48 ± 1.40	0.14
June	2.669 ± 0.57	0.258 ± 0.16	0.41	1.799 ± 0.4	1.21 ± 0.78	0.27
July	3.510 ± 0.73	0.522 ± 0.34	0.45	1.892 ± 0.35	1.53 ± 0.87	0.31
August	9.070 ± 2.49	1.013 ± 0.8	0.31	3.173 ± 0.99	0.35 ± 0.32	0.14
September	24.140 ± 6.07	1.110 ± 0.8	0.31	8.823 ± 1.97	1.86 ± 1.44	0.25
October	96.72 ± 28.15	1.508 ± 1.35	0.27	45.460 ± 14.1	0.28 ± 0.26	0.14
November	21.08 ± 3.74	0.7324 ± 0.43	0.53	11.300 ± 3.69	1.31 ± 1.25	0.13
December	9.9 ± 1.7	1.034 ± 0.51	0.53	16.420 ± 5.53	3.17 ± 8.00	0.12

regression to empirical data for April to December 2005. Aerial inputs in January, February and March were too small to be parameterized and were assumed to be zero. Constants *a* and *b* of the function, including their standard errors, as well as *R*² are given in Table 2.

$$J(x) = a_t e^{-b_t x} \tag{2}$$

The final model equation (Eq. 3) resulted from combining Eqs. 1 and 2, with *J_{DIRF}* and *J_{DIVI}* being aerial inputs from riparian forest and island vegetation, respectively, over time (*t*) at a specific location (*x*).

$$\frac{dM_i}{dt} = J_{DIRF}(t, x) + J_{DIVI}(t, x) - k_i(T)M_i \tag{3}$$

To implement the continuous differential Eq. 3. in our three dimensional GIS-raster application, it first had to be discretized (Riddaway and Hortal 2002) into Eq. 4, where *j* and *m* are coordinates of the raster cell and *n* the count of time steps.

$$M_{ij,m}^{n+1} = \left(J_{DIRF}^n_{j,m} + J_{DIVI}^n_{j,m} - b_i M_{ij,m}^n \right) \Delta t + M_{ij,m}^n \tag{4}$$

Assessment of model uncertainty

To estimate the uncertainty in model results due to parameter uncertainty (*a*, *b*, *k*), we used a linearized approximation according to Eq. 5, neglecting parameter correlation (Reichert 1994).

$$\sigma_y = \sqrt{\sum_{i=1}^m \left(\frac{\partial y}{\partial p_i} \right)^2 \sigma_{p_i}^2} \tag{5}$$

p_i are the uncertain model parameters, *σ_{p_i}* are their standard deviations, *y(p₁, ..., p_m)* is the solution of the model equations for a given variable at a given location and time, and *σ_y* is the approximate standard deviation of the model result.

Encompassing hydrology in the floodplain leaf model

The influence of hydrology on leaf storage was encompassed implicitly in our model. On the one hand, it was represented by the implementation of decomposition rates differing among habitats due to habitat-specific wetting–drying cycles (Langhans et al. 2008). On the other hand, spatially and temporally explicit floodplain inundation patterns were reproduced by the three dimensional GIS-raster application. Leaves in flooded habitats were assumed to be exported from the study reach and decomposed downstream (Tockner et al. 1999; Neatrou et al. 2004). Hence, we subtracted them from our model.

Simulated response of leaf dynamics to habitat changes

To simulate and evaluate the effects of leaf dynamics to changes in habitat composition and configuration under the hydrological regime of the years 2002–2005, we considered three scenarios. The base scenario simulated the natural development of leaf dynamics with the measured parameters, i.e., with no changes in habitat composition or configuration. Scenario 1 simulated the effect of the loss of vegetated islands and parafluvial ponds. We chose this scenario because vegetated islands and isolated ponds contribute greatly to floodplain biocomplexity (Gurnell et al. 2005), but are among the first habitats to disappear as a consequence of flow and channel regulation (Gurnell et al. 2001; Karaus et al. 2005). Additionally to the loss of vegetated islands and parafluvial ponds, we simulated the loss of floods (by setting the maximum stage level at 0.7 m), and successive overgrowth of the active floodplain with riparian forest vegetation in scenario 2. All of these effects are commonly associated with upstream damming and ceasing floodplain inundation, which are prominent threats for rivers especially in mountainous areas such as

the Tagliamento. The total overgrowth was simulated in three steps. We assumed that each year one additional third of the initial area of the active floodplain, from the riparian forest inwards, was covered with vegetation. After each step, we let the model run until an equilibrium was reached. In scenario 3, vegetated islands, parafluvial ponds, large wood accumulations and exposed gravel were randomly shuffled in the active tract of the floodplain, but in the same proportion as for the base scenario, to simulate the effect of a change in habitat configuration. Such random changes are characteristic of riverine floodplains driven by hydro-geomorphological processes (Lorang et al. 2005; Stanford et al. 2005; Lorang and Hauer 2006). Large wood accumulations and parafluvial ponds, for instance, can form at almost any location within the floodplain triggered by deposited tree trunks (Gurnell et al. 2005). A change in the location of vegetated islands, however, would take more than one big flood event.

Results

Aerial CPOM input

Aerial CPOM input ($\text{AFDM m}^{-2} \text{ year}^{-1}$) decreased exponentially from the edge of the riparian forest and vegetated islands towards the open tract (Fig. 3). At the forest edge, total annual aerial input averaged $213.8 \pm 150.0 \text{ g}$, while at the edges of islands it was $323.5 \pm 119.5 \text{ g}$ (perpendicular island transects) and $175.2 \pm 82.0 \text{ g}$ (parallel island transects). In the open tract (1 to 70 m distance from vegetation edge) average aerial CPOM inputs ($\text{AFDM m}^{-2} \text{ year}^{-1}$) were 15.4 ± 10.9 , 27.8 ± 21.4 and $17.3 \pm 14.2 \text{ g}$ for the perpendicular forest transects and the perpendicular and

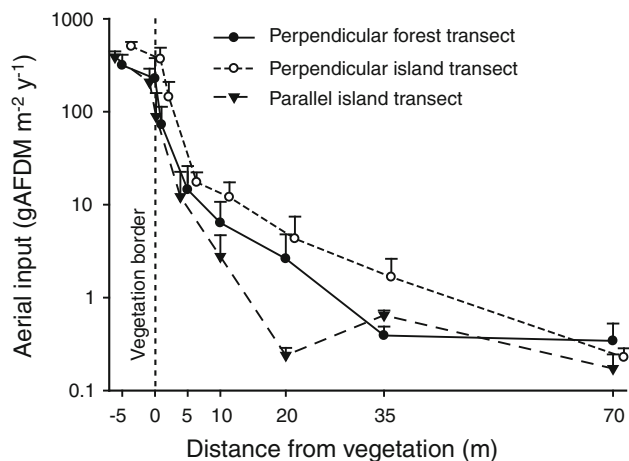


Fig. 3 Decrease in total annual aerial input of CPOM ($\text{g AFDM m}^{-2} \text{ year}^{-1}$; log-scale) with increasing distance from the vegetation (m) ($n = 4$, mean + 1 SE)

parallel island transects, respectively. Aerial input was dominated by leaves, especially at distances of 5–20 m from the vegetation edge, whereas miscellaneous material was the most prominent type at 35–70 m.

Aerial input varied significantly over time (season) ($F_{4,1213} = 33.1$, $P \leq 0.001$), being one-order-of-magnitude higher in autumn ($1.6 \pm 1.0 \text{ g AFDM m}^{-2} \text{ day}^{-1}$) than during the rest of the year, and among CPOM types ($F_{3,318} = 26.0$, $P \leq 0.001$), but did not differ significantly among transect types ($F_{2,318} = 1.7$, $P = 0.057$). Along the individual transects, the mean aerial CPOM input ($\text{g AFDM m}^{-2} \text{ month}^{-1}$) ranged from $0.1 \text{ g} \pm 0.1 \text{ g}$ (perpendicular island transects in March) to $49.9 \pm 28.7 \text{ g}$ (perpendicular island transects in October). Leaves were the dominant CPOM type (average: 78.8 %), and miscellaneous material was more abundant than small wood and grass. CPOM composition changed seasonally from miscellaneous material (predominant from March to May) to leaves (July to December), this being reflected in a significant interaction between time and CPOM type ($F_{11,1213} = 34.2$, $P \leq 0.001$).

Lateral surface CPOM transfer

Lateral CPOM transfer also decreased significantly with distance from the vegetation edge (Fig. 4a, b). At the vegetation margin, lateral transfer ($\text{AFDM m}^{-1} \text{ year}^{-1}$, mean of both opening directions) ranged from $10.3 \pm 4.74 \text{ g}$ (perpendicular island transects) to $21.0 \pm 5.3 \text{ g}$ (perpendicular forest transects) and declined along transects to minimum average values of $5.0 \pm 3.7 \text{ g}$ (perpendicular forest transects) and $16.3 \pm 4.2 \text{ g}$ (perpendicular island transects). Independently of distance and transect type, CPOM was dominated by leaves.

Mean lateral CPOM transfer along transects ($\text{g AFDM m}^{-1} \text{ month}^{-1}$) ranged seasonally (Fig. 5a–d; $F_{6,3504} = 46.6$, $P \leq 0.001$) from $0.2 \text{ g} \pm 0.1 \text{ g}$ (perpendicular forest transects in March) to $9.0 \pm 2.9 \text{ g}$ (parallel island transects in December), with highest amounts in autumn. Mean lateral transfer varied among transect types ($F_{2,597} = 4.7$, $P = 0.009$) and CPOM types ($F_{3,597} = 169.4$, $P = 0.009$), but not between trap opening directions ($U = 4,871,788$, $Z = -1.6$, $P = 0.121$). Lateral transfer did not differ among the two different island transect types, but was significantly higher along perpendicular island transects than to the riparian forest. CPOM composition varied with time (season) ($F_{18,3504} = 95.7$, $P \leq 0.001$), being dominated by miscellaneous material from March to August and by leaves from September to December. Another significant interaction between season and transect types ($F_{12,3504} = 3.3$, $P \leq 0.001$) arose from the fact that the highest lateral transfer in June and December was along perpendicular forest transects and not island transects.

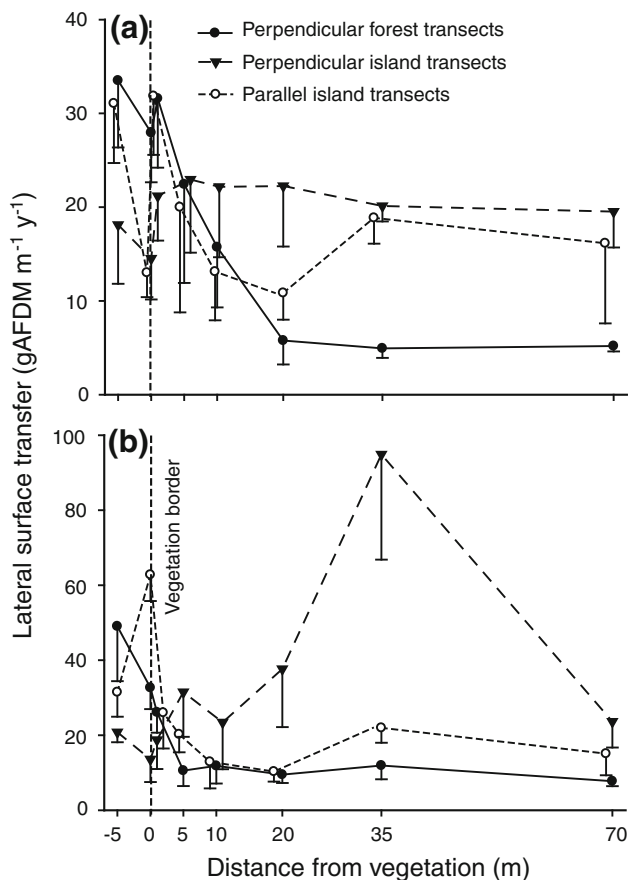


Fig. 4 Decreasing total annual lateral transfer of CPOM ($\text{g AFDM m}^{-1} \text{ year}^{-1}$) with increasing distance from the vegetation boundary (m) ($n = 40$, mean ± 1 SE). **a** Traps open towards the open tract, **b** traps open towards the vegetation

CPOM storage

Mean CPOM storage (AFDM m^{-2}) ranged from 2.8 ± 0.8 g (on exposed gravel in November) to 562.4 ± 119.6 g (in the riparian forest in April) (Fig. 6a, b), with an area-weighted mean for the entire floodplain of 154.6 ± 40.5 g. CPOM storage changed with season ($F_{4,650} = 7.2$, $P \leq 0.001$) and varied among habitats ($F_{3,176} = 211.4$, $P \leq 0.001$), with peak amounts in the riparian forest being significantly higher than on vegetated islands, exposed gravel and along the shore (Fig. 6a, b). In vegetated habitats, storage decreased from spring to summer, and increased again in autumn. In spring, storage in the riparian forest was twice as high as on vegetated islands. In autumn, CPOM storage on islands increased to levels similar to those in the riparian forest. There were no clear seasonal patterns of CPOM storage on either exposed gravel or along the shore, leading to a significant season-habitat interaction ($F_{11,650} = 5.8$, $P \leq 0.001$).

CPOM was significantly dominated by small wood and leaves ($F_{3,176} = 107.4$, $P \leq 0.001$) throughout the year.

However, a steeper increase in leaf than in small wood storage in autumn led to a significant interaction between season and CPOM types ($F_{11,650} = 15.1$, $P \leq 0.001$). Leaves were the dominant CPOM type on islands, whereas small wood was prominent in all other habitats, leading to a significant interaction between habitats and CPOM composition ($F_{9,176} = 17.1$, $P \leq 0.001$).

Habitat change effects on leaf litter dynamics

With the base scenario, we simulated a net increase in leaf storage in all habitats following an initial decrease in 2003 on exposed gravel and large wood accumulations (Fig. 7). In comparison to this scenario, leaf storage in the total floodplain declined by $20.3 \% \pm 1.4$ (mean ± 1 SE, $n = 1,466$) over 4 years under scenario 1—representing the loss of vegetated islands (at present 8.9 % of total area) and parafluvial ponds—with particularly high losses in some habitats ($98.2 \% \pm 2.7$ in large wood accumulations; $66.4 \% \pm 15.6$ on exposed gravel, Fig. 8). An additional absence of floods and successive overgrowth of the floodplain in scenario 2 resulted in a decline of total floodplain leaf storage ($38.2 \% \pm 0.8$), comprising a loss in the riparian forest (5.4 ± 0.9) and a significant increase of leaf storage on exposed gravel (245.0 ± 104.0 , Fig. 8).

The random redistribution of habitat types in scenario 3 (i.e., islands, large wood accumulations and parafluvial ponds) did not affect overall floodplain storage. However, storage increased by $147.5 \% \pm 91.4$ on exposed gravel, and decreased by $98.2 \% \pm 1.8$ in large wood accumulation and by $98.3 \% \pm 1.4$ in parafluvial ponds (Fig. 8). In all scenarios, model uncertainty for the different parameters (i.e., standard errors) was low.

Discussion

Quantifying spatial and temporal CPOM distribution and transport processes is vitally important to floodplain ecosystem functions, and river carbon cycling and storage in general. To better understand the role of habitat and CPOM diversity for floodplain CPOM dynamics, we measured spatiotemporally explicit aerial input, lateral transfer, and surface storage of CPOM. Very few studies, with the exception of those conducted on the pro-glacial Val Roseg floodplain, Switzerland (Zah 2001) and on the subtropical Ogeechee River, USA (Cuffney 1988) have made an attempt to measure these complicated transport fluxes.

Aerial CPOM input

Overall, mean area-specific aerial CPOM input ($\text{g AFDM m}^{-2} \text{ year}^{-1}$) into the riparian forest and on vegetated

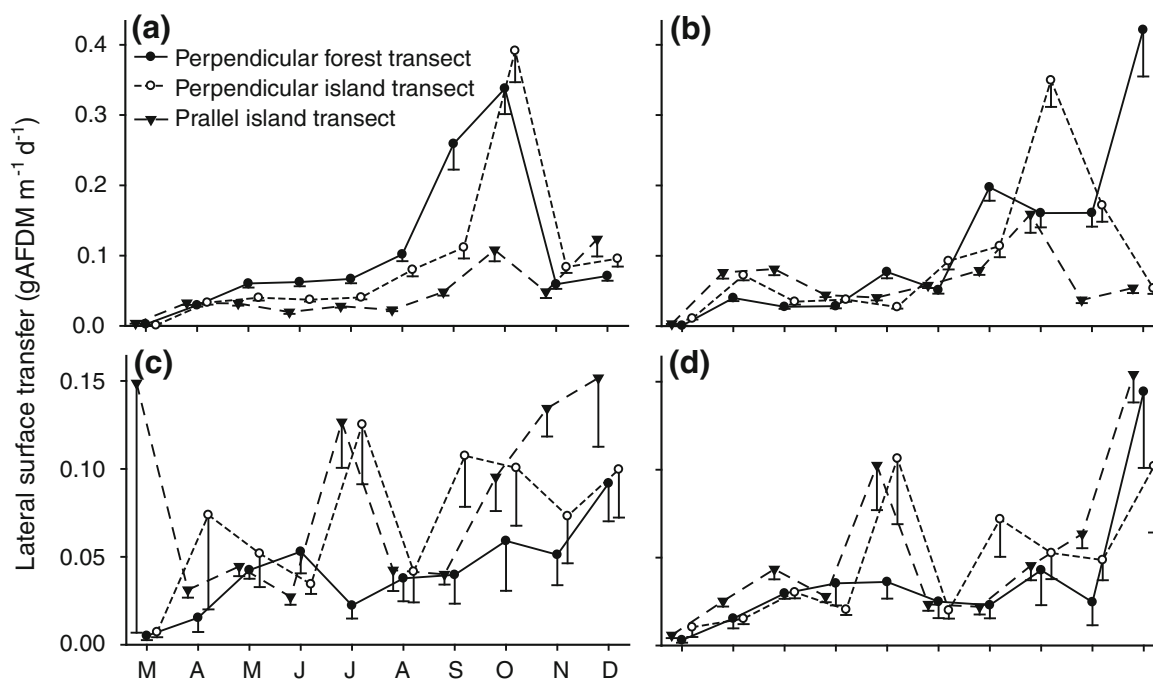


Fig. 5 Lateral CPOM transfer rates ($\text{g AFDM m}^{-1} \text{ day}^{-1}$) within the vegetation (*upper panels*) and in the open tract (*lower panels*) over an annual cycle in 2005. **a** Open towards the open tract, and

b open towards the vegetation (mean \pm 1 SE, $n = 4$), **c** open towards the open tract, **d** and open towards the vegetation (mean \pm 1 SE, $n = 28$)

islands was similar to those reported from other temperate deciduous forests (Weigelhofer and Waringer 1994; Pozo et al. 1997). However, input to the total floodplain was much lower than inputs measured along headwater streams and in meandering temperate floodplains (Bell et al. 1978; Neatrou et al. 2004). This result is not surprising considering that the investigated reach, in contrast to other studied floodplains, comprises an extensive area of unvegetated exposed gravel (Fig. 2). Consistent with that finding, aerial inputs to the open tract were mostly restricted to areas close to vegetation (Fig. 4; see also Zah and Uehlinger 2001), with leaves being the dominant type close to the vegetation edge (0–20 m) and miscellaneous material at distances >20 m. These results suggest that natural vegetation, including both riparian forest and vegetated islands, is probably the most determinant factor for overall floodplain CPOM dynamics in the reach that we studied.

Braided river floodplains such as the Tagliamento are composed of a complex mosaic of habitats (Fig. 2) that differ greatly in their characteristics. In our study, CPOM input varied among habitats by a factor of 40 ranging from $0.03 \text{ g m}^{-2} \text{ day}^{-1}$ on exposed gravel (AFDM, averaged over the year) to $1.22 \text{ g m}^{-2} \text{ d}^{-1}$ in vegetated islands. Doering et al. (2011) demonstrated that mean sediment respiration in the same floodplain reach, differed by more than 2-orders-of-magnitude from $0.04 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ on exposed gravel (January) to $8.22 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in

vegetated islands (July). Differences in these respiration rates may have mostly evolved from habitat-specific OM contents. This hypothesis is supported by Bodmer (2011), who found that the variation in floodplain respiration along a braided Swiss gravel-bed river was largely driven by differences in OM supply to specific habitats. Hence, aerial CPOM input is important for shaping habitat characteristics and defining various ecosystem processes.

Because properties of contrasting habitats are so different, OM dynamics of the entire floodplain are strongly influenced not only by the composition of the various habitats but also by their spatial configuration. Our study showed that exposed gravel and aquatic habitats derive most of their OM from adjacent vegetated islands and the riparian forest. Hence, we conclude that the length of the riparian ecotone together with the distance to the nearest vegetation mainly defines the contribution of allochthonous CPOM input to the active tract of our study reach. Thus, a natural, continuous riparian cover along floodplains should be considered when managing these ecosystems.

Lateral surface CPOM transfer

Lateral transfer of CPOM declined less steeply with distance from vegetation than did aerial input, indicating that the former is the more important pathway for CPOM over most of the open floodplain. Interestingly, the floodplain leaf dynamics model showed only a minor influence of

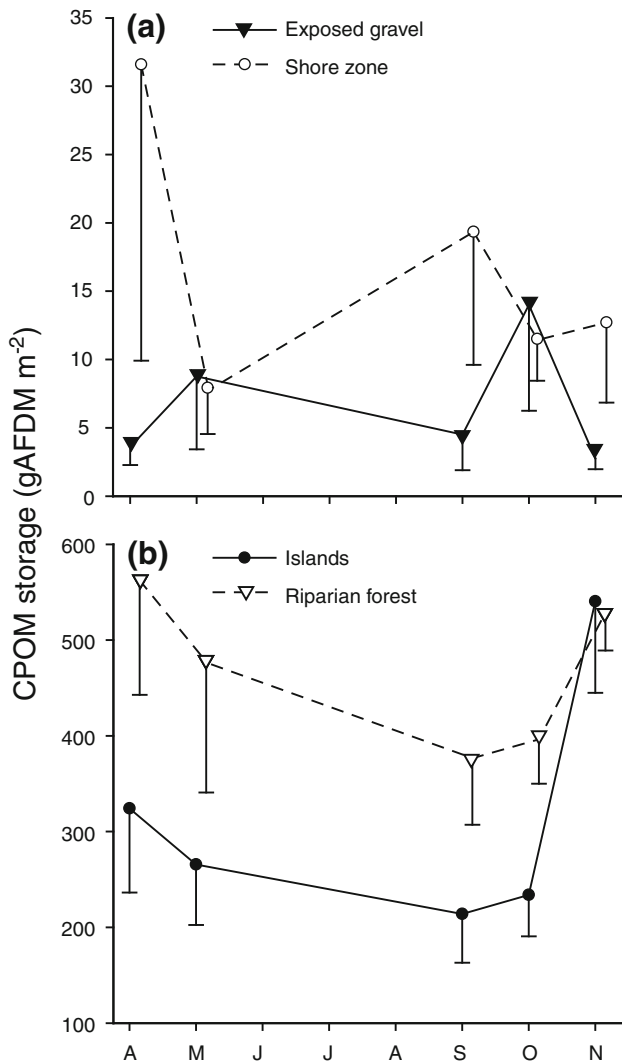


Fig. 6 CPOM storage (g AFDM m⁻², n = 12, mean - 1 SE) on **a** exposed gravel and along shorelines, and **b** in vegetated habitats

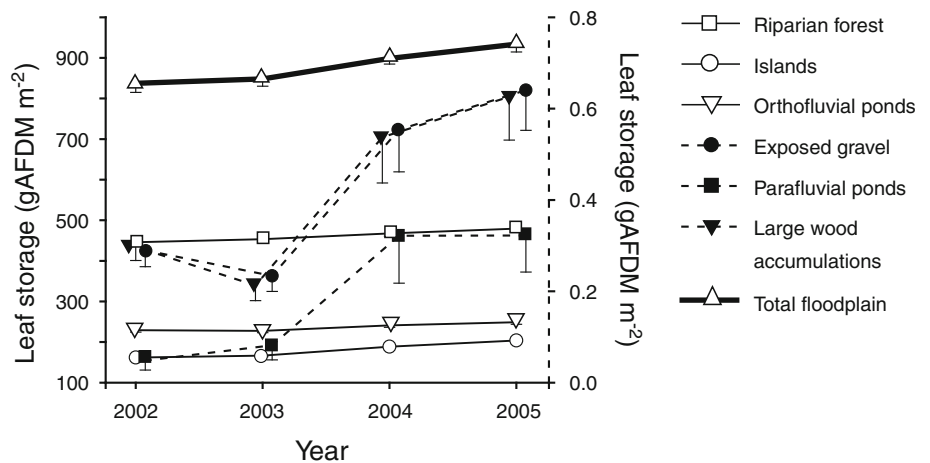
lateral transfer on leaf storage (and was therefore omitted from the model), which suggests that habitat-specific inputs and outputs to individual model cells were similar. Although unexpected, this suggestion is supported by the absence of any significant difference between lateral transfer from the vegetation and the open tract. We argue that lateral transfer of leaves from the vegetation towards the open tract may be promoted by wind and gravity, but is counterbalanced by water movement in the other direction. Such a back transfer was implicitly included in the leaf dynamics model through the implementation of current stage records. Higher lateral transfer from islands than from riparian forest may be explained by their greater exposure to wind and flooding, and perhaps also to higher productivity. Indeed, CPOM storage on islands increased twice as much as in riparian forest during the period of leaf fall (October to November).

Leaves dominated the laterally transferred CPOM at all distances. Hence, leaves not only provided the main energy source in their habitat of origin (i.e., island and riparian forest) but were also the main medium for energy transfer across the open floodplain. This material is often pre-processed before being transferred by wind or water, and provides a high-quality resource in less productive aquatic (ponds, channels) and terrestrial habitats (exposed gravel surface or large wood accumulations). However, CPOM is not evenly distributed within the open tract: structures that provide roughness, such as large wood and coarse gravel deposits, strongly influence patterns of deposition by retaining a larger than average proportion of material.

CPOM storage

CPOM storage in vegetated habitats was similar to that in other floodplains such as that of the Ogeechee River, USA

Fig. 7 Simulation of the natural development of leaf storage (g AFDM m⁻², n = 365, mean - 1SE) in the study reach with the measured parameters for the years 2002–2005 (base scenario). Error bars represent results from model uncertainty. Dashed line curves refer to the Y-axis on the right, solid line curves to the Y-axis on the left. Data points are slightly shifted to the left or right for better graphical representation



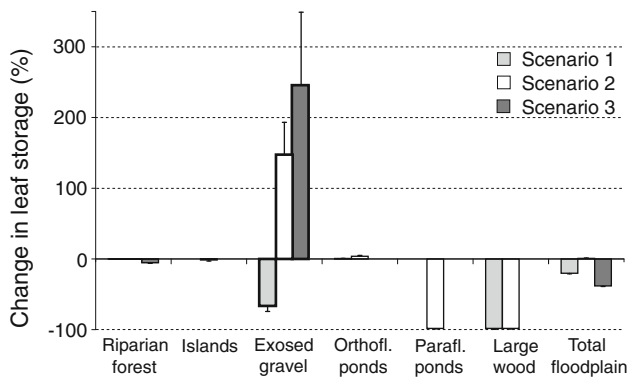


Fig. 8 Simulated change in habitat-specific leaf storage averaged over the years 2002–2005 compared to the base scenario (%; $n = 1,466$, mean + 1 SE) under the loss of habitat diversity (islands and paraffluvial ponds, scenario 1), the loss of habitat diversity, floodplain flooding and overgrowth of the floodplain (scenario 2), and random redistribution of habitats within the active tract (scenario 3). Error bars represent results from model uncertainty

(Cuffney 1988), and was approximately two orders of magnitude higher than in non-vegetated habitats. Although CPOM storage on islands was 1.5 times lower than in the riparian forest in spring, levels were similar in autumn. This dynamism probably arose not only from the higher rates of leaf production and decomposition on islands than in the riparian forest but also higher rates of export (Langhans et al. 2008). Islands are particularly productive when influenced by groundwater (Harner and Stanford 2003; Morris et al. 2010) or water-level fluctuations that deliver nutrients (Junk et al. 1989; Tockner et al. 2000), and both these conditions applied to the islands we studied (Doering 2007; Bertoldi et al. 2009). In return, islands may not only export OM to surrounding surface habitats, but also nutrients to subsurface habitats due to leaching. Thus, islands along braided rivers increase the availability of OM and nutrients to the open tract of the river floodplain (van der Nat et al. 2003) and, like patches of vegetation in deserts, can be considered as “islands of fertility” (sensu Schade and Hobbie 2005).

Compared to vegetated habitats, CPOM storage along shore zones and on exposed gravel was low and unaffected by leaf abscission, being driven by floodplain hydrology. Thus, CPOM was washed ashore during higher flow in April and September 2005 (Fig. 1), while CPOM storage on exposed gravel peaked in October, after the main flood in that year had receded (Fig. 6).

In all habitats, the majority of transported CPOM (aerial and lateral) consisted of leaves, while CPOM was stored in the form of small wood on exposed sediment and as small wood and leaves in vegetated habitats. From these findings, together with data on CPOM storage and decomposition from former studies (van der Nat 2002; Langhans et al. 2008), we infer that leaves represent reactive elements in

floodplain environments, while small and large wood are more refractory.

Habitat change effects on leaf litter dynamics

Modelling approaches are essential to understand how ecosystems function at various scales (Canham et al. 2003; Turner et al. 2004; Zobitz et al. 2008). Given the size, complexity and dynamics of most floodplains, it is difficult to investigate large-scale ecosystem processes empirically or experimentally. Here, we used a simple heuristic model that combines a one-dimensional empirical model based on data from extensive in situ experiments (this paper and Langhans et al. 2008) with a three-dimensional spatial model to simulate the effects of surface inundation and habitat composition and configuration on leaf dynamics. The model proved to be useful in predicting habitat-related effects on leaf storage and can, therefore, help in formulating hypotheses for future research.

In a simulation based upon the base scenario, considerable amounts of CPOM were exported from the studied reach by a large flood in November 2002 (Fig. 1), which led to reduced leaf storage in 2003 in habitats within the active tract (Fig. 7). Subsequently, with no flood of a similar magnitude in the following years, leaf storage increased greatly. There was even a slight but steady increase of leaf storage in habitats protected from floods (such as the riparian forest, vegetated islands and orthofluvial ponds), indicating that leaf input was outstripping decomposition. Thus, these habitats served as important storage areas for CPOM as well as sources for the adjacent habitats.

The loss of habitat diversity (scenario 1, Fig. 8) greatly reduced total floodplain leaf storage mainly because of the missing island vegetation. More importantly, however, storage was reduced by an average of 66 % on exposed gravel and by 98 % in large wood accumulations. In these naturally energy-poor ecosystems, such changes would certainly significantly reduce rates of decomposition (Langhans et al. 2008) and soil and sediment respiration in the affected habitats (Doering et al. 2011).

In contrast to scenario 1, the loss of islands and ponds plus missing floods and consequential floodplain overgrowth (scenario 2, Fig. 8) massively increased leaf storage on exposed gravel. We argue that this is a consequence of missing floodplain flooding and consequential export of OM from the study reach. Consequently, the combination of decreased habitat and hydrograph diversity likely affects decomposition and respiration rates on exposed gravel reversely to habitat loss only.

As expected, the simulated change of habitat configuration (scenario 3, Fig. 8) did not alter overall leaf storage on the floodplain. However, it had severe implications for

particular habitats, notably exposed gravel, large wood accumulations and parafluvial ponds. These ponds are often located along the margins of vegetated islands (Karaus et al. 2005), where they receive high aerial and lateral CPOM inputs. Leaf storage decreases significantly, however, if these habitats are lost or displaced; in these cases, leaves that would otherwise be trapped in the ponds are distributed across the active tract, increasing storage on exposed gravel. Consequently, our results highlight that a change in habitat configuration can produce a shift of hot spots, in this particular case from parafluvial ponds to exposed gravel surfaces. Other habitat configurations may promote different hot spots within the investigated area. However, we argue that all of them would have far-reaching consequences for the floodplain as a system (Tockner et al. 2010a), including changes in the location and amount of available N and C and related processes.

All scenarios underpin the importance of a natural flow regime for maintaining the original character of CPOM dynamics in the studied floodplain reach. Flow, though, should be managed in a way that allows the floodplain to flood, habitats to shuffle and vegetated islands to grow.

Implications of contemporary flow conditions for study results

In their natural state, Mediterranean rivers are hydrologically dynamic; they experience regular and predictable periods of drought, but flooding may occur at any time of the year and is less predictable (Acuna et al. 2007; Bertoldi et al. 2009). Depending on their extent and timing, such floods may export large amounts of CPOM stored in the active tract (Acuña and Tockner 2010) and strongly influence the dynamics of CPOM, especially leaf litter. In 2005, the Tagliamento experienced no major flood (defined as ≥ 300 cm stage at Villuzza; Bertoldi et al. 2009). But, as sediment transport in this system starts at relatively low flow stages of ca. 75–100 cm (Bertoldi et al. 2009), several flow pulses of up to 140 cm stage height may already have induced channel change; i.e., an increase in the number of flowing channel segments or sediment turnover on low bars (Bertoldi et al. 2009). However, some of our results—for example, the high transfer of CPOM from island vegetation to unproductive habitats—might have been less pronounced if major floods in spring and autumn had exported large amounts of CPOM from the floodplain.

Conclusions

Quantifying ecosystem processes within large, heterogeneous landscapes with the aim of predicting the impacts of landscape change (Valett et al. 2005; Malard et al. 2006) has

been recognized as a fundamental challenge in ecology (Tockner et al. 2010a; Doering et al. 2011). To meet this challenge, we distinguished the roles of different habitats and CPOM types in the cycling of OM. Vegetated habitats were sources and storage areas for CPOM, while open tracts were receivers and transfer areas of CPOM; aquatic habitats, in particular channels, were ‘hot spots’ of C decomposition (sensu Tockner et al. 2010a, Table 1). Leaves, as reactive elements, were particularly important for conveying energy among habitats, while small and large wood represented a more refractory element in floodplain CPOM dynamics. Implementing this information in the spatial dynamics model confirmed the importance of island vegetation as a source of OM to less productive habitats. Additionally, it demonstrated the possible influence of floodplain flooding on ecosystem processes in exposed gravel habitats. Finally, it showed how the spatial context of habitats affects ecosystem function, and therewith highlighted the role of a natural flow regime for the functioning of CPOM dynamics in floodplain ecosystems.

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