

## Research Article

# Leaf-decomposition heterogeneity across a riverine floodplain mosaic

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**Abstract.** Riverine floodplains are a mosaic of aquatic, semi-aquatic and terrestrial habitats. While spatially distinct, these habitats are well connected by flows of carbon and nutrients, often in the form of leaf litter, and thus the ecological processes occurring in one habitat have ramifications for others. The aim of this study was to compare leaf decomposition, a key process in riverine ecosystems, across diverse floodplain-habitat types and to assess the role of leaf-shredding detritivores and fungi. Black poplar, *Populus nigra* L., leaves were exposed in seven contrasting habitat types (total of 28 sites) on the floodplain of the Tagliamento River (NE-Italy). Three distinct classes of decomposition rates emerged, corresponding to sites in the river channel (fast), terrestrial sites (slow), and ponds (intermediate). In the river channel and in ponds, leaf decomposition was driven by both microbial and detritivore activity, as evidenced by differences in coarse- and fine-mesh bags, which respec-

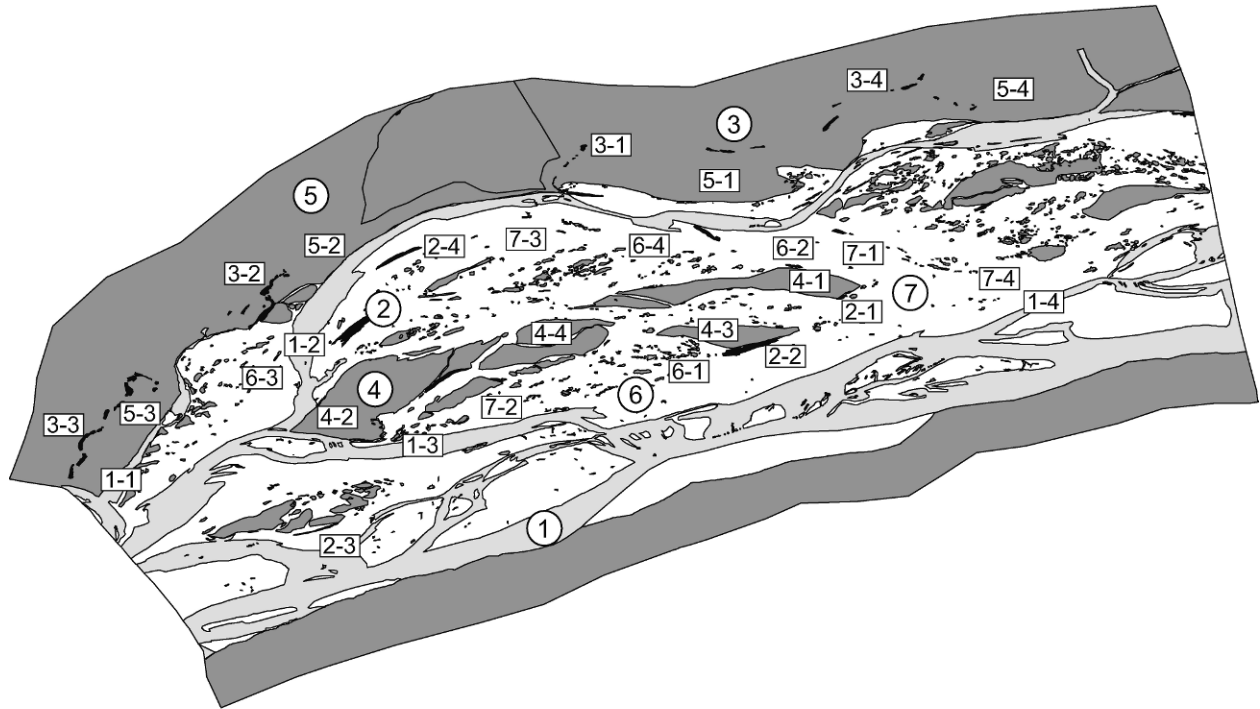
tively allowed and prevented access to the leaves by leaf-consuming detritivores. Additionally, we cannot rule out that decomposition in the channel was also promoted by physical abrasion and/or fragmentation. In terrestrial floodplain habitats, very little plant litter was utilized, and leaching of soluble compounds appeared to be the primary process responsible for leaf-mass loss. Our results demonstrate that the wide range of habitats of braided floodplain rivers can have diverse decomposition potentials, creating spatial variability in both the rates of decomposition and its causes. Alterations to the natural flow regime (e.g., water abstraction, or retention by dams) and morphological changes (e.g., channelization) strongly reduce habitat diversity. These impacts will likely reduce the heterogeneity in decomposition rates across floodplains of braided rivers, with unknown consequences for overall functioning of floodplain ecosystems.

**Key words.** Habitat complexity; ecosystem process; braided river; litter breakdown; Tagliamento River.

## Introduction

Natural riverine floodplains are ecosystems of global importance (Tockner and Stanford, 2002), and typically consist of a complex mosaic of aquatic and

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Habitat type	Description	Habitat category
□ 1 River channel	Riffle habitats characterized by flowing water	River channel
■ 2 Parafluvial pond	Isolated still-water habitats located in the active floodplain	Pond
■ 3 Orthofluvial pond	Isolated still-water habitats located in the riparian forest	Pond
■ 4 Island	Forest floor of vegetated islands	Terrestrial
■ 5 Riparian forest	Forest floor of riparian zone	Terrestrial
■ 6 Large wood	Accumulations of large wood located on the active floodplain	Terrestrial
□ 7 Exposed gravel	Areas of non-vegetated gravel located on the active floodplain	Terrestrial

**Figure 1.** Map of the main study area during base flow, with descriptions of the seven different habitat types (1 to 7), and locations of the 4 sites per habitat type (e.g., 1–1 to 1–4). Adapted from Tiegs et al. (2007).

terrestrial habitats (Ward et al., 2002; Naiman et al., 2005). Interaction between hydrologic and geomorphic processes produces a continually changing spatial pattern of these habitats, which has been conceptualized as the Shifting Habitat Mosaic (Arscott et al., 2002; van der Nat et al., 2003a; Lorang et al., 2005; Stanford et al., 2006). Periodic flooding, erosion and deposition of inorganic sediments, recruitment of large wood, vegetation development, and ground water-surface water exchange processes determine the dynamic character of riverine floodplains (Richter et al., 1997; Tockner and Stanford, 2002; Tiegs and Pohl, 2005; Stanford et al., 2006). Typical floodplain habitats include lotic channels, lentic water bodies in the active plain (parafluvial ponds) and in the riparian forest (orthofluvial ponds), areas of exposed sediment, vegetated islands, and riparian forests (Fig. 1). Juxtaposition of these landscape elements creates

highly heterogeneous floodplain structure and function (Tockner et al., 2008).

Riparian zones and aquatic-terrestrial interfaces (e.g., shorelines) function as transition zones and control the exchange of nutrients and energy between adjacent habitats (Malanson, 1993; Risser, 1995; Naiman and Décamps, 1997; Ward et al. 1999). Floodplain forests are often highly productive (Naiman and Décamps, 1997) resulting in large inputs of leaf litter to the riparian forest floor and adjacent open floodplain habitats (Chauvet and Jean-Louis, 1988). Exchange of organic material among floodplain habitats can be extensive and is driven by flow and flood pulses (Tockner et al., 2000; Neatroux et al., 2004; Valett et al., 2005). During lower flow periods, organic material accumulates on floodplain surfaces where it is temporarily stored. Here, it is colonized by microbes and partly decomposed before entering aquatic and other

habitats during subsequent high-flow (Merritt and Lawson, 1992).

Decomposition of plant litter is an important ecosystem process (Aerts, 1997; Webster and Benfield, 1986; Gessner et al., 1999) and a controlling force in nutrient cycling (Cleveland et al., 2004) across a wide range of aquatic and terrestrial environments. It is influenced by the physico-chemical environment (Aerts, 1997; Webster and Benfield, 1986), composition and abundance of the decomposer community (Petersen and Luxton, 1982; Hieber and Gessner, 2002), leaf-litter quality (Melillo et al., 1982; Gessner and Chauvet, 1994) and, in aquatic environments, the hydrological regime (Ellis et al., 1999; Langhans and Tockner, 2006).

While leaf decomposition has been widely studied in both aquatic and terrestrial environments (Webster and Benfield, 1986; Aerts, 1997), very few studies have examined leaf decomposition across the numerous and diverse habitats that are commonly encountered on riverine floodplains (Chauvet, 1988; Chergui and Pattee, 1988a). This information is necessary, however, if the controls of decomposition are to be understood at the landscape scale. Here, we examine leaf decomposition and the potential roles of macroinvertebrates and fungi as decomposers across a range of aquatic and terrestrial floodplain habitats characteristic of braided river reaches. Specifically, we hypothesized that leaf decomposition rates will vary widely among different floodplain habitats, with fastest rates in aquatic and slowest rates in terrestrial sites. We also expected that leaf-consuming detritivores (shredders) would be important drivers of leaf decomposition in aquatic habitats, whereas in terrestrial habitats microbial decomposition would predominate.

## Material and methods

### Site description

The study was conducted in the island-braided reach of the Tagliamento River, a 7<sup>th</sup> order gravel-bed river (catchment area of 2580 km<sup>2</sup>) located in NE-Italy (46°N, 12°30'E; Ward et al., 1999; Tockner et al., 2003). The active channel (parafluvial floodplain) is fringed by continuous riparian forest dominated by black poplar (*Populus nigra* L.) and five willow species (*Salix* spp.) (Karrenberg et al., 2003). Despite local water abstraction and channelization of the most downstream section, the Tagliamento River retains an essentially pristine morphological and hydrological character (Ward et al., 1999). It is characterized by a flow regime driven by intense rainfall events in fall, and snowmelt runoff in spring (Arscott et al., 2002).

Long-term average discharge in the study reach is 90 m<sup>3</sup> s<sup>-1</sup>, with floods of 1100, 1500, and 2150 m<sup>3</sup> s<sup>-1</sup> having estimated return intervals of 2, 5, and 10 years, respectively (Gurnell et al., 2001). During high flow, large amounts of organic matter, including large wood (van der Nat, 2003b) and leaf litter (personal observation) are redistributed among floodplain habitats.

During base flow, the 1-km<sup>2</sup> study reach consists of 42 % exposed gravel, 35 % riparian forest, 15 % river channels, 7 % islands and each 0.5 % ponds and large wood (Fig. 1). The areal extent of these habitats changes in response to the water level, and while high discharge events rearrange them regularly, the relative area of each remains approximately constant (van der Nat et al., 2003a). Average standing stocks of coarse particulate organic matter (CPOM; primarily leaves and large wood) across the floodplain range from < 1 g m<sup>-2</sup> ash free dry mass (AFDM) on exposed gravel to 1000 g m<sup>-2</sup> AFDM on vegetated islands and in the riparian forest. In aquatic habitats, average annual CPOM standing stock ranges from 5 g m<sup>-2</sup> AFDM in ponds to 50 g m<sup>-2</sup> AFDM in river channels (van der Nat, 2002).

Detailed information on the catchment, main study reach, and water chemistry is provided by Ward et al. (1999), Tockner et al. (2003), and Kaiser et al. (2004). Physical and chemical variables of the different habitats were measured during the experiment and are summarized in Table 1.

### Field methods

Decomposition dynamics were studied across seven floodplain-habitat types: river channels, parafluvial ponds, orthofluvial ponds, exposed gravel, large wood accumulations, vegetated islands, and riparian forest (Tiegs et al., 2007; Fig. 1). Both fine- and coarse-mesh bags were used as an approach to respectively deter and allow access by macroinvertebrates to experimentally introduced leaves and thus approximately separate the influence of microbes, and invertebrates/physical factors (Boulton and Boon, 1991). A factorial experiment was designed with habitat type (seven levels), and mesh size (two levels) as factors and leaf decomposition (expressed as percentage of litter dry mass remaining) as the dependent variable. Four replicate sites of each habitat type were randomly selected on the floodplain (28 sites total) (Fig. 1).

The experiment was initiated in December 2002, shortly after peak leaf fall in the area. It was designed to run during base flow conditions until the end of March (Fig. 2), when leaf decomposition in the investigated area is usually disrupted by spring floods (Arscott et al., 2002). Senescent leaves of black poplar (*Populus nigra* L.) were collected from trees near the study site in the fall of 2002. Leaves were air-dried to

**Table 1.** Physical and chemical characteristics of a) aquatic and b) terrestrial habitat types in the Tagliamento River floodplain during the leaf decomposition experiment (mean  $\pm$  1 SD, n = 20, \*continuously recorded).

## a) Aquatic habitats

Parameter	River channel	Parafluvial pond	Orthofluvial pond
Water temperature ( $^{\circ}$ C)*	9.3 $\pm$ 1.1	8.0 $\pm$ 1.8	7.4 $\pm$ 1.8
Current velocity (m/s)	0.24 $\pm$ 0.29	0	0
Conductivity ( $\mu$ S/cm at 20 $^{\circ}$ C)	445 $\pm$ 127	451 $\pm$ 131	465 $\pm$ 158
pH	8.2 $\pm$ 0.3	8.1 $\pm$ 0.3	7.8 $\pm$ 0.1
O <sub>2</sub> (mg/L)	12.4 $\pm$ 2.3	12.5 $\pm$ 4.8	11.5 $\pm$ 4.3
NH <sub>4</sub> -N (mg/L)	< 0.01	< 0.01	0.01
NO <sub>3</sub> -N ( $\mu$ g/L)	656 $\pm$ 77	395 $\pm$ 118	580 $\pm$ 325
Soluble reactive phosphorus ( $\mu$ g/L)	< 5	< 5	< 5

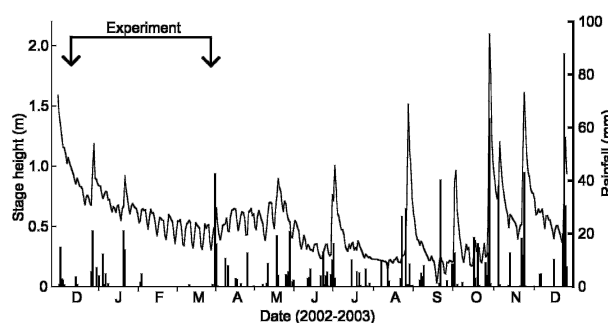
## b) Terrestrial habitats

Parameter	Exposed gravel	Large wood	Island	Riparian forest
Air temperature ( $^{\circ}$ C)*	3.5 $\pm$ 7.7	3.7 $\pm$ 7.0	4.1 $\pm$ 6.1	3.3 $\pm$ 5.5

constant weight and stored. Portions of  $5.00 \pm 0.25$  g were weighed, re-moistened and packed in fine-mesh (0.5 mm mesh size) and coarse-mesh (10 mm mesh size) nylon bags (Boulton and Boon, 1991). Five coarse- and fine-mesh bags were tied in pairs to individual iron bars which were hammered into the ground. The five pairs of litter bags were randomly placed in each of the 28 sites on 16 December 2002. In aquatic habitats, the cords attaching the litter bags to iron bars were weighed down to fix litter bags on the bottom of river channels and ponds. Litter bags in terrestrial sites were placed on the respective substrate, such as pebbles in the exposed gravel habitat, and the litter layer in the riparian forest and on islands. In the large wood habitat, litter bags were fixed in the upper area of the accumulation on miscellaneous material including sand, gravel, litter, small twigs and roots. One litter bag pair was randomly retrieved from each replicated habitat type after 18, 32, 50, 62, and 80 days (river channels), and after 18, 32, 62, 80, and 102 days (all other habitat types) (Fig. 2). Litter bags were placed in polyethylene bags, transported to a field research station near the site, and immediately processed.

**Laboratory procedures**

Following incubation in the field, leaves were removed from bags, individually rinsed with water, and carefully cleaned with a brush to remove macro-invertebrates and adhering debris. The resulting slurry was passed over a 100- $\mu$ m mesh screen and captured invertebrates were preserved in 80% ethanol. Individuals were identified under a dissecting microscope, counted, and sorted into functional feeding groups according to Tachet et al. (2000), Freude et al. (2004a; 2004b; 2004c), and Kerney et al. (1983). Fungal biomass in all sites was examined on only one occasion

**Figure 2.** Changes in rainfall and water level near the study reach from December 2002 to 2003. Black bars represent total daily rainfall.

near the end of the experiment to account for the dissimilarity that fungal activity in aquatic habitats typically peaks 4–10 weeks after initial leaf incubation (Gessner and Chauvet, 1994; Baldy et al., 2002), whereas fungal colonization on leaves in terrestrial sites increases over the first two months (Ormeno et al. 2006). Immediately following the cleaning of leaf material, 10 leaf discs (diameter: 12 mm) were cut from 5 different leaves (2 discs per leaf) from each litter bag, using a cork borer. One set of 5 discs was placed in a small polyethylene bag and frozen at  $-20^{\circ}$ C for ergosterol analysis to provide an estimate of fungal biomass. Ergosterol content of decaying litter was quantified according to Gessner and Schmitt (1996) and converted to fungal biomass based on an average ergosterol content of 5.5 mg per g fungal dry mass (Gessner and Chauvet, 1993). The second set of leaf discs was placed in a separate aluminum pan, and dried to constant mass at  $60^{\circ}$ C for 48 h together with the remaining leaves, before weighing to the nearest 0.1 mg. Total leaf dry mass was determined by adding the bulk leaf mass and two times the disc mass.

Subsamples of leaves not placed in the field were processed in an identical fashion to establish an air-dry to oven-dry mass relationship.

### Data analysis

Leaf-decomposition rates ( $k$ ) were estimated for comparative purposes only using linear regression of  $\ln(x)$ -transformed data. Differences in leaf decomposition (% remaining leaf dry mass) among habitat types and mesh sizes were analyzed using repeated measures ANOVA with habitat types (seven levels), and mesh size (two levels) as independent variables, and exposure time (18, 32, 62, and 80 days) as the repeated-measures factor. Subsequently, weighted contrasts were used to test for differences between pairs of the three habitat categories (i.e., river channel vs ponds, ponds vs terrestrial sites, and river channel vs terrestrial sites) with weights based on the number of habitat types within each habitat category (Lindman, 1974).

Total abundance of macroinvertebrates and shredders in different habitat types and mesh bags were also analyzed using repeated-measures ANOVA. Differences in fungal biomass (mg/g leaf dry mass) among habitat types and mesh size were analyzed using two-way ANOVA. When significant habitat type effects were detected, weighted contrasts were performed. One-way ANOVA was used to test for differences in environmental parameters among habitat types.

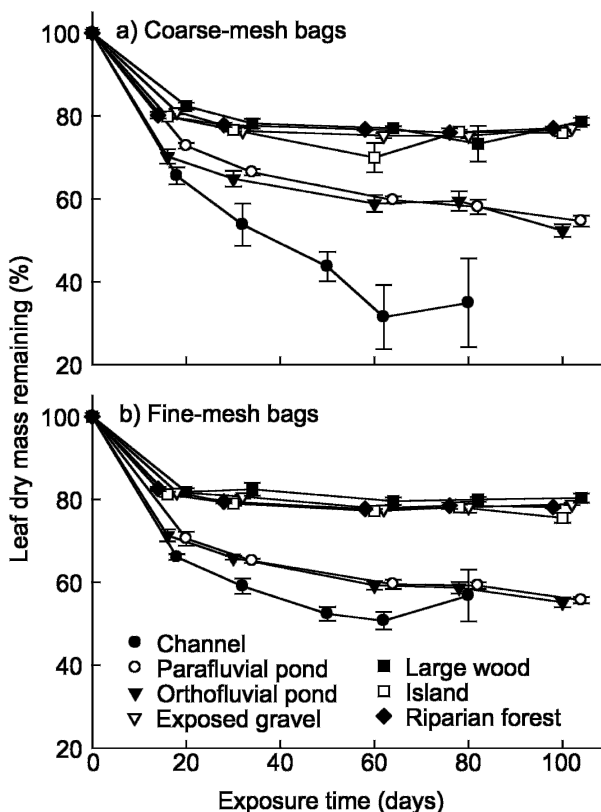
Prior to analyses, % leaf dry mass data were arcsine-square root transformed, and invertebrate abundance and environmental data were  $\log_{10}(x+1)$ -transformed to meet ANOVA assumptions. All analyses were performed using SPSS (version 11.0/SPSS Inc., Illinois, USA). For all tests, an  $\alpha$ -value of 0.05 was set to assess statistical significance.

## Results

### Leaf mass loss

Leaf decomposition rates were highly variable across floodplain-habitat types, ranging 10-fold in coarse-mesh bags and 4-fold in fine-mesh bags (Table 2). Leaf dry mass significantly decreased over time (Wilks'  $\lambda$ :  $F_{3,40} = 71.6$ ,  $P \leq 0.001$ ) differing among habitat types ( $F_{6,42} = 45.0$ ,  $P < 0.001$ ) and mesh sizes ( $F_{1,42} = 8.2$ ,  $P = 0.006$ ), whereas significant differences in leaf dry mass between mesh sizes resulted mainly from river channel samples (Fig. 3, Table 2). In all habitat types, leaves decomposed faster in coarse-mesh than in fine-mesh bags, although the difference was most pronounced in the river channel. Weighted contrasts revealed three distinct categories of decomposition rates for coarse- and fine-mesh bags: fast rates in the

river channel, intermediate rates in ponds, and slow rates in terrestrial habitats.

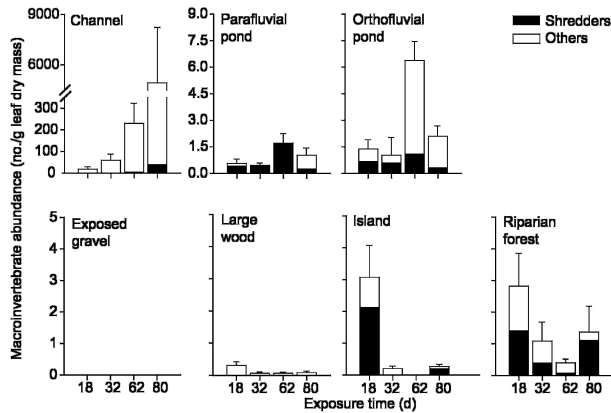


**Figure 3.** Dry mass remaining of poplar leaves decomposing in litter bags with two different mesh sizes in seven habitat types on the Tagliamento floodplain (mean  $\pm$  1 SE,  $n = 4$  sites per habitat type).

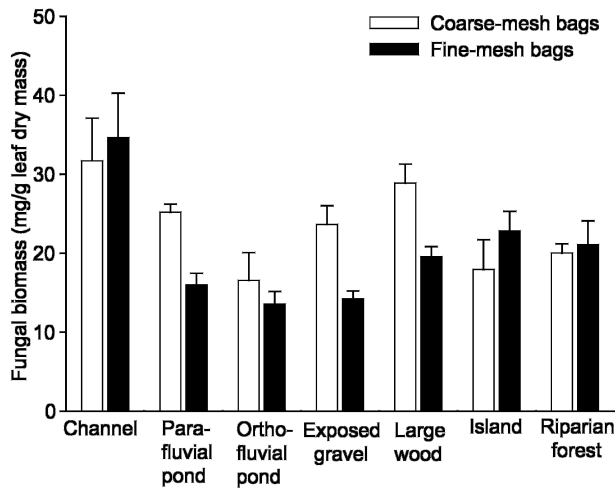
### Macroinvertebrate abundance and community composition

Total abundance of macroinvertebrates in coarse-mesh bags increased significantly over time (Wilks'  $\lambda$ :  $F_{3,19} = 5.0$ ,  $P = 0.010$ ) and varied among habitat types ( $F_{6,21} = 24.7$ ,  $P < 0.001$ ) (Fig. 4). Leaf bags in river channel sites had the highest number of macroinvertebrates, an effect largely due to numerous chironomids. Weighted contrasts indicated significant differences in macroinvertebrate numbers among the three habitat categories with the highest abundance in river channel sites, intermediate abundance in ponds, and lowest abundance in terrestrial habitats (river channel vs ponds:  $F_{1,21} = 82.3$ ,  $P < 0.001$ ; river channel vs terrestrial habitats:  $F_{1,21} = 141.0$ ,  $P < 0.001$ ; ponds vs terrestrial habitats:  $F_{1,21} = 6.22$ ,  $P = 0.020$ ). Total numbers of macroinvertebrates peaked on day 62 in para- and orthofluvial ponds, but continued to rise in river channel sites (Fig. 4).

Abundance of shredders did not change over time (Wilks'  $\lambda$ :  $F_{3,19} = 1.99$ ,  $P = 0.15$ ), but differed



**Figure 4.** Abundance of shredders and other macroinvertebrates (no./g leaf dry mass) associated with coarse-mesh bags in the seven different habitat types (mean  $\pm$  1 SE,  $n$  = 4 sites per habitat type). Note differences in scale of the y-axes.



**Figure 5.** Fungal biomass (mg/g leaf dry mass) after 80 days of poplar leaf decomposition in coarse-mesh and fine-mesh bags in seven different habitat types (mean  $\pm$  1 SE,  $n$  = 4 sites per habitat type).

significantly among habitat types ( $F_{6,21} = 6.16$ ,  $P = 0.001$ ). Weighted contrasts revealed: significantly more shredders in the river channel than in ponds ( $F_{1,21} = 10.3$ ,  $P = 0.004$ ); higher abundance in the river channel relative to terrestrial habitats ( $F_{1,21} = 26.6$ ,  $P < 0.001$ ); and slightly higher abundance in ponds than in terrestrial habitats ( $F_{1,21} = 4.47$ ,  $P = 0.05$ ). Although fine-mesh bags in river channel sites were colonized by a small number of early instar chironomid larvae, the fine mesh effectively excluded all other groups of macroinvertebrates.

### Fungi

Fungal biomass significantly differed among habitat types after 80 days of decomposition ( $F_{6,41} = 4.82$ ,  $P =$

0.001), but not between mesh sizes ( $F_{1,41} = 3.4$ ,  $P = 0.073$ ). Weighted contrasts indicated higher fungal biomass in the river channel than in ponds ( $F_{1,41} = 12.3$ ,  $P = 0.001$ ) and greater abundance in river channel sites relative to terrestrial habitats ( $F_{1,41} = 20.7$ ,  $P < 0.001$ ). Fungal biomass did not differ between ponds and terrestrial habitats. Separate analyses performed on fungal biomass in coarse- and fine-mesh bags showed significant variation among habitat categories in fine-mesh bags (river channel vs ponds:  $F_{1,21} = 24.0$ ,  $P < 0.001$ ; river channel vs terrestrial habitats:  $F_{1,21} = 13.4$ ,  $P = 0.001$ ; ponds vs terrestrial habitats:  $F_{1,21} = 4.9$ ,  $P = 0.04$ ), whereas no differences were observed in coarse-mesh bags ( $P = 0.062$  to 0.47).

### Physical and chemical characteristics of habitats

Based on our 20 observations, pH ( $F_{2,45} = 13.8$ ,  $P < 0.001$ ), nitrate concentration ( $F_{2,57} = 3.6$ ,  $P = 0.035$ ), and current velocity ( $F_{2,57} = 22.4$ ,  $P < 0.001$ ) differed among aquatic habitat types (Table 1a). The pH was higher in parafluvial ponds and in river channel sites than in orthofluvial ponds, and nitrate concentrations were lower in parafluvial ponds than in river channel sites. There was no current in ponds. All other physical and chemical characteristics were similar among aquatic habitats. Mean temperature (air temperature for terrestrial sites, and water temperature for aquatic sites) differed significantly among habitat types ( $F_{6,21} = 6.6$ ,  $P = 0.002$ ). Weighted contrasts showed higher temperatures in the river channel and ponds than in terrestrial habitats (river channel vs terrestrial habitats:  $F_{1,14} = 28.2$ ,  $P < 0.001$ ; ponds vs terrestrial habitats:  $F_{1,14} = 19.0$ ,  $P = 0.001$ ) (Table 1b).

### Discussion

#### Patterns of leaf decomposition across floodplain habitats

Decomposition throughout winter and spring varied widely across the seven floodplain habitats we examined. Leaves decomposed rapidly in the river channel, at intermediate rates in ponds, and most slowly in terrestrial habitats. These results are consistent with previous studies conducted in much smaller stream systems that compared river channels and adjacent terrestrial habitats (Gurtz and Tate, 1988), ponds and terrestrial floodplain sites (McArthur et al., 1994), and riffle, pond, floodplain and forest floor habitats (Nakajima et al., 2006). While studies conducted in the alluvial corridor of the Garonne River, a human-impacted 7<sup>th</sup> order river in south-western France, showed that *Salix alba* leaves decomposed at a wide

**Table 2.** Summary of decomposition rates ( $k$ , mean  $\pm$  1 SE,  $n = 4$ ,  $p \leq 0.001$  in all cases) of black poplar leaves in seven floodplain-habitat types and litter bags with two different mesh sizes as estimated by linear regression of  $\ln(x)$ -transformed data; day 80 for coarse-mesh bags in channels was removed for the analysis.

Habitat type	Mesh	$k$ ( $d^{-1}$ ) $\pm$ SE	$r^2$	N
Channel	Coarse	$-0.0188 \pm 0.0030$	0.68	20
Parafluvial pond	Coarse	$-0.0051 \pm 0.0006$	0.79	24
Orthofluvial pond	Coarse	$-0.0051 \pm 0.0007$	0.73	24
Exposed gravel	Coarse	$-0.0020 \pm 0.0004$	0.49	24
Large wood	Coarse	$-0.0021 \pm 0.0005$	0.42	24
Island	Coarse	$-0.0021 \pm 0.0006$	0.40	24
Riparian forest	Coarse	$-0.0019 \pm 0.0004$	0.50	24
Channel	Fine	$-0.0083 \pm 0.0010$	0.76	23
Parafluvial pond	Fine	$-0.0047 \pm 0.0006$	0.73	24
Orthofluvial pond	Fine	$-0.0048 \pm 0.0006$	0.76	24
Exposed gravel	Fine	$-0.0018 \pm 0.0004$	0.51	24
Large wood	Fine	$-0.0016 \pm 0.0004$	0.45	24
Island	Fine	$-0.0020 \pm 0.0004$	0.57	24
Riparian forest	Fine	$-0.0018 \pm 0.0004$	0.54	24

range of rates in some aquatic and terrestrial sites (Chauvet, 1988), decomposition of *Populus gr. nigra* leaves was similar in the mainstem and a parafluvial pond on the same floodplain (Baldy et al., 2002).

Rapid leaf decomposition in aquatic habitats is the result of physical, chemical and biological ecosystem properties associated with water (Hutchens and Wallace, 2002). In our study, faster decomposition in river channels relative to ponds could not be explained by the chemical characteristics of the water alone. However, leaching (Petersen and Cummins, 1974) and fragmentation (Heard et al., 1999; but see Ferreira et al., 2006), which are promoted by current velocity in river channels, may have interacted to result in rapid mass loss. The fact that decomposition rates in para- and orthofluvial ponds did not differ is likely due to similar physical, chemical and biological conditions.

More rapid leaf decomposition in aquatic habitats may have been promoted by higher temperatures, whereas lower temperatures in terrestrial habitats (Table 1b) were associated with slower decomposition. In all terrestrial habitats, leaves decomposed at similar rates with extremely small within-habitat variability. As warmer and particularly wetter conditions are known to promote decomposition rates (Meentemeyer, 1978; Aerts, 1997; Cortez, 1998), we expected leaf decomposition to be faster in shaded, more mesic habitats, such as in the riparian forest or on islands, relative to more xeric sites such as bare gravel. However, after a rapid initial mass loss, presumably due to leaching of water-soluble material (Anderson, 1973), only negligible decomposition occurred. This suggests that leaves in terrestrial floodplain habitats may start to measurably decompose only after spring floods when higher temperatures together with increased humidity (primarily through floodplain inundation) promote microbial degradation and invertebrate colonization.

### Leaf decomposition and invertebrates

Differences in total macroinvertebrate and shredder abundance in litter bags may partly account for the observed differences in leaf decomposition among habitat types. Although numbers of shredders in litter bags were generally low (Fig. 4) compared to values reported in the literature (Chergui and Pattee, 1988a; Chauvet et al., 1993), they were significantly greater in the river channel relative to ponds, and greater in ponds compared to terrestrial habitats. In addition, decomposition in coarse-mesh bags was faster than in fine-mesh bags at sites (Table 2, Fig. 3) where shredders were most abundant (Fig. 4). Collectively, these results suggest that macroinvertebrates contributed significantly to decomposition in the river channel and to a lesser extent in ponds. Physical effects were unlikely to be important under base flow (Ferreira et al., 2006) as experienced during our experiment, given the low concentration of suspended sediments (personal observation) and low current velocities that accompany this hydrologic condition. However, as the effects of shredding invertebrates vs abrasion and fragmentation can not be clearly separated in the present study, faster decomposition in the river channel might have been a combination of both factors.

In temperate zones, the major period of leaf decomposition by stream invertebrates is typically in fall and winter (cf. Merritt and Lawson, 1992). The activity of microbial decomposers and shredders in terrestrial habitats is also strongly constrained by seasonal climatic patterns (Heneghan et al., 1999), with high microarthropod numbers being associated with elevated soil moisture (Crossley and Hoglund, 1962). However in the ecosystem we investigated, leaf decomposition in terrestrial habitats is time-constrained by spring floods during which large amounts of leaves are removed from the sites where litter

originated. The implication of the slow decomposition we observed during the months before the typical flooding in spring is that very little plant litter is utilized in the terrestrial floodplain habitats.

### Leaf decomposition and fungi

Fungi play an eminent role in leaf decomposition in both terrestrial systems (Swift et al., 1979) and flowing waters (Gessner et al., 2007), even in larger rivers where direct input of leaf litter is limited (Baldy et al., 1995; 2002; Chergui and Pattee, 1988b). We observed the highest fungal biomass in the river channel, intermediate biomass in terrestrial habitats, and lowest biomass in ponds. This is consistent with the findings of Baldy et al. (2002), who found significantly lower fungal biomass in a parafluvial pond compared to the river channel of the Garonne River. Chergui and Pattee (1988b) studied the spatial distribution of aquatic fungi associated with decomposing black poplar leaves on the Rhone River floodplain in France and found faster leaf-decomposition rates in the river channel where aquatic fungi were active, compared to still-water habitats where very few species were found. The water flow in river channels supplies a continuous source of fungal inoculum to leaves (e.g., Bärlocher, 1987), which in ponds is greatly restricted. More important may be the fact that the fungi most efficient at degrading leaves in streams and rivers (i.e., aquatic hyphomycetes) are much less prevalent in standing waters (Bärlocher, 1992), including floodplain ponds (Baldy et al., 2002). Consistent with the higher fungal biomass in the river channel compared to ponds and terrestrial habitats, decomposition rates in both coarse-mesh and fine-mesh litter bags were also greatest in the river channel suggesting that faster decomposition in flowing water is attributable to fungal activity, in addition to abrasion/fragmentation and invertebrate feeding.

### Implications at the river landscape scale

Our results demonstrate that natural floodplain habitats within a river system provide a wide range of decomposition potentials. Both microbes and invertebrates contributed to leaf decomposition in the river channel and ponds, whereas in terrestrial habitats leaching of water-soluble compounds appeared to be the only major factor causing leaf mass loss during the first five months after leaf fall. During winter and early spring, river channels are clearly "hot spots" for leaf decomposition (*sensu* McClain et al., 2003). Although the habitat types we investigated are spatially distinct during baseflow conditions in winter, they become connected during periods of high flow later in spring. As a consequence, pre-conditioned litter and decomposition products stor-

ed on the floodplain are redistributed among habitats by high discharge events. A dynamic natural flow regime can therefore be seen as an important component of organic matter dynamics at the river floodplain scale (Langhans and Tockner, 2006). A dynamic natural flow regime, together with morphologically intact floodplains, redistributes organic matter and the products resulting from decomposition on a large spatial scale, thus providing physical connectivity within river corridors and affecting overall ecosystem functioning (Valett et al., 2005). However, through severe river regulation, floodplains habitats are often disconnected from adjacent rivers (hydrologically regulated systems) or totally lost (morphologically modified systems). In both cases, riverine habitat heterogeneity decreases and spatially-complex organic matter cycles, including litter decomposition, are altered, with potentially important consequences for the functioning of riverine ecosystems.

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