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The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy)

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Abstract Despite growing recognition of the importance of a natural flow regime in river-floodplain systems, researchers struggle to quantify ecosystem responses to altered hydrological regimes. How do frequency, timing, and duration of inundation affect fundamental ecosystem processes such as leaf litter decomposition? Along the semi-natural Tagliamento River corridor, located in northeastern Italy, we employed in situ experiments to separate effects of different inundation components on breakdown rates of black poplar (*Populus nigra*). We used a litter-bag method with two different mesh sizes to investigate how fungi and macroinvertebrates influence leaf breakdown rates. Ten treatments, each representing a specific combination of duration and frequency of inundation, were deployed in two seasons (summer, winter) to mimic complex inundation patterns. After 30 days of exposure, mean percentage of remaining leaf litter (ash free dry mass) ranged between 51% (permanent wet) and 88% (permanent dry). Leaf breakdown was significantly faster in winter than in summer. Duration of inundation was the main inundation component that controlled leaf breakdown rates. Leaf-shredding macroinvertebrates played only a role in the permanent wet treatment. Fungal parameters explained the faster leaf breakdown in winter. Our study suggests that modifications of the inundation regime will directly modify established decomposition processes. Factors reducing duration of inundation will decelerate leaf breakdown rates, whereas a decrease in flow variation will reduce leaf breakdown heterogeneity.

Keywords Ecosystem process · Flow regime · Hydrology · Leaf breakdown · Tagliamento

Introduction

A natural inundation regime is regarded as the key driver of river-floodplain ecosystems (Junk et al. 1989; Poff et al. 1997; Tiegs and Pohl 2005). The magnitude, frequency, duration, and timing of the inundation regime influence biotic communities and ecosystem processes, either directly or indirectly through their effects on other primary regulators (Hart and Finelli 1999; Hession et al. 2000; Tockner et al. 2000; Robertson et al. 2001). Modification of the inundation regime thus has cascading effects on the ecological integrity of river-floodplain systems (Bunn et al. 2002).

In a wide range of aquatic and terrestrial environments, decomposition of plant litter is a very important process in ecosystem metabolism and a driving force in nutrient cycling (Wallace et al. 1997; Webster et al. 1999; Cleveland et al. 2004). Much research has been conducted to identify the controlling factors and underlying mechanisms of decomposition (e.g. Robinson and Gessner 2000; Shaw and Harte 2001; Austin 2002; Hieber and Gessner 2002). In wetlands (marshes, swamps, floodplains), the flow regime has been identified as the primary driver of decomposition processes (Molles et al. 1995; Glazebrook and Robertson 1999; Andersen et al. 2003). Drying and wetting define the physical nature of the decomposition environment (Tockner et al. 2000), alter litter quality (Harner and Stanford 2003), and change nutrient conditions (Robertson et al. 1999; Heffernan and Sponseller 2004).

However, major inconsistencies exist in inundation–decomposition relationships. Decomposition can be hindered by anoxic conditions due to standing-water conditions or sediment deposition (Cuffney and Wallace 1987; Chauvet 1988) or enhanced by physical (i.e. leaching or fragmentation by stream flow or alternating dry/wet cycles) and biological processes (i.e. microbial

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activity or invertebrate consumption) (Ryder and Horwitz 1975; Brinson 1977; Molles et al. 1995; Lockaby et al. 1996; Battle and Golladay 2001). Most field studies have used a gradient or a correlative approach (e.g. comparing leaf mass loss with flood duration), which limits the ability to elucidate causal mechanisms (e.g. Brinson 1977; Shure et al. 1986; Graça et al. 2001; Austin 2002). However, hydrologic manipulation experiments are often difficult to interpret because the duration, frequency, and timing of inundation are poorly defined (Lockaby et al. 1996). Microcosm experiments in the laboratory offer limited value because they do not reflect natural conditions (Day 1983; Hagvar 1988).

In the present study, we designed intensive in situ experiments to mimic complex inundation patterns that were once characteristic for many temperate floodplain rivers (Poff et al. 1997; Tockner et al. 2003). We asked two key questions: first, to what extent does duration, frequency, and timing (season) of inundation influence leaf mass loss? Second, what is the role of microbes (i.e. aquatic fungi) and aquatic and terrestrial macroinvertebrates in controlling rates of leaf litter decomposition under different inundation regimes? We hypothesize that a complex inundation regime maintains high heterogeneity in leaf litter decomposition at the river-floodplain scale.

Methods

Study site

In situ experiments were carried out in summer 2003 and winter 2004 along the braided reach of the Fiume Tagliamento, a seventh-order gravel-bed river in NE Italy (46°N, 12°30'E) with a total catchment area of 2,580 km². The corridor is fringed by continuous riparian woodland. Despite local water abstraction and a channelized downstream section, the river retains essentially pristine morphological and hydrological characteristics. The flow regime is highly dynamic with

frequent flow pulses (sensu Tockner et al. 2000) throughout the year (Arscott et al. 2002; Van der Nat et al. 2002).

Our study was conducted in an island-braided reach (river-km 79.8–80.8; 135 m a.s.l.) where lateral riparian forests and vegetated islands supply the floodplain with allochthonous organic material. *Populus nigra* and five species of *Salix* dominate the vegetation (Karrenberg et al. 2003). Average standing stocks of deposited CPOM (mainly leaves) across different floodplain strata ranged from < 1 g m⁻² ash free dry mass (AFDM) on bare gravel surface to > 1,000 g m⁻² AFDM on vegetated islands and riparian forests. In aquatic habitats, average annual CPOM standing stock was 10 g m⁻² AFDM (Van der Nat 2002). Detailed information on the catchment, the main study reach, and the water chemistry is provided by Ward et al. (1999), Tockner et al. (2003), and Kaiser et al. (2004). Water chemistry, air temperature, and relative humidity at the study site, measured during the experiments, are summarized in Table 1.

Experimental treatment

The experiment was conducted in a 200 m long riffle-run section of a 20-m wide braided channel (detailed description: Paetzold et al. 2005). We used a random-block design in which four blocks (ten treatments each) were established along the riffle-run section (Fig. 1). Each treatment represented a specific combination of duration and frequency of inundation. Therefore, the effect of duration and frequency could be analysed separately. To simulate wet/dry cycles, leaves enclosed in nylon bags were transferred manually from instream to terrestrial (wet to dry) positions and vice versa. To partition the effects of shredders and microorganisms, breakdown of leaves enclosed in fine mesh bags, which preclude shredder access, was compared with leaf breakdown in coarse mesh bags. The experiment was designed for 30 days to have a trade-off between considerable leaf breakdown and reduced flood risk

Table 1 Physico-chemical characterization of the study site in summer and winter (n = number of measurements, mean \pm 1 SD)

Environmental parameter	Summer		Winter	
	n	Mean	n	Mean
Air temperature (daytime)	360	32.8 \pm 6.0	380	5.9 \pm 6.0
Air temperature (nighttime)	360	19.0 \pm 2.8	380	0.0 \pm 3.1
Relative humidity (%)	30	55.9 \pm 6.2	30	66.6 \pm 12.5
Water temperature (°C)	730	16.5 \pm 2.4	730	9.0 \pm 0.7
Flow velocity (m s ⁻¹)	5	0.49 \pm 0.11	7	1.05 \pm 0.11
Specific conductance (μ S cm ⁻¹)	5	492.0 \pm 1.6	3	649.7 \pm 5.4
pH	5	8.0 \pm 0.0	3	8.2 \pm 0.1
Oxygen (%)	5	72.7 \pm 11.4	3	132.5 \pm 22.8
Total inorganic carbon (mg l ⁻¹)	4	28.5 \pm 4.0	4	33.5 \pm 2.2
Total organic carbon (mg l ⁻¹)	4	1.6 \pm 0.2	4	0.5 \pm 0.2
NH ₄ -N (μ g l ⁻¹)	4	ND	4	4.0 \pm 2.0
NO ₃ -N (μ g l ⁻¹)	4	531.2 \pm 54.3	4	837.0 \pm 126.3
NO ₂ -N (μ g l ⁻¹)	4	1.9 \pm 1.7	4	10.0 \pm 1.5
PO ₄ -P (μ g l ⁻¹)	4	ND	4	ND

ND not detectable

T	D	F	
1	30	0	30
2	20	15	3 2 3 1 2 1 2 1 2 1 2 1 3 1 3 2
3	20	10	4 2 3 2 3 2 3 2 3 2 4
4	20	5	7 3 6 4 7 3
5	20	1	20 10
6	10	15	2 3 1 3 1 2 1 2 1 2 1 2 1 3 2 3
7	10	10	2 4 2 4 1 4 1 4 2 4 2
8	10	5	3 7 4 6 3 7
9	10	1	10 20
10	0	0	30

Fig. 1 Experimental design: ten treatments (*T*) with different inundation regimes (*white* wet; *grey* dry conditions). *N* number days, *D* duration of inundation (days), *F* number of dry/wet cycles (frequency)

(Arcsott et al. 2002). Water chemistry (nitrogen, phosphorus, and carbon species) and environmental parameters (temperature, conductivity, oxygen, vegetation cover, and gravel size) were similar among blocks.

Sampling procedures

Experiments were carried out in summer 2003 (28 July–27 August) and winter 2004 (8 January–7 February). Leaves of *Populus nigra* (black poplar) were collected during senescence in autumn 2002 (summer experiment) and 2003 (winter experiment) directly from trees adjacent to the study site. Leaves were air-dried and stored under dry conditions. Portions of 5 ± 0.25 g were weighed, moistened and packed in fine mesh (0.5 mm mesh size) and coarse mesh (10 mm mesh size) nylon bags (Boulton and Boon 1991). Pairs of fine and coarse mesh bags were tied to iron bars and exposed in the stream bed and along the terrestrial shore corresponding to the experimental design (treatment). During the summer experiment, one coarse mesh bag out of 80 was lost because of vandalism. In both experiments, bags were retrieved after 30 days, placed individually in polyethylene bags and returned to the laboratory in cooling boxes.

Laboratory procedures

Leaves were carefully removed from the bags and gently rinsed with tap water to remove adhering debris and invertebrates. The remaining slurry was filtered through a 500- μ m mesh and the retained invertebrates were preserved in 70% ethanol. Fifteen leaf discs (diameter, 12 mm) were cut from five different leaves (three discs per leaf) from each bag using a cork borer. Two sets of five discs were placed in a small polyethylene bag and frozen at -20°C for ergosterol

analyses. The ergosterol content of decaying litter, an indicator of fungal biomass, was estimated according to Gessner and Schmitt (1996). The third set of five leaf discs was put in a separate aluminium pan, and dried to constant mass at 60°C for 48 h together with the remaining decomposed leaves, before weighing to the nearest 0.1 g. Total dry mass was determined by adding the dry mass of the leaf discs (times three) to the main bulk of leaves. Ground 0.5 g subsamples were ashed (500°C , 6 h) to determine AFDM. Subsamples of initial leaves were processed in the same way to develop air dry mass to AFDM conversion factors.

The preserved invertebrates were sorted, identified to the lowest possible taxon, and counted. Taxa were assigned to functional feeding groups according to Tachet et al. (2000).

Statistical analysis

We used analyses of variance (ANOVA) with subsequent Scheffé's post-hoc tests to test for differences among treatment means (expressed as percentage of remaining AFDM; Wieder and Lang 1982), with block, season, duration, frequency, and mesh size as independent variables. If season and mesh size had significant influences on treatment means, we performed an ANOVA for each season and mesh size separately. Data were square root-arcsine transformed to meet ANOVA assumptions. The same ANOVA model was applied to analyse differences among mean fungal biomass (expressed as ergosterol).

Leaf breakdown rates (k , day^{-1}) were calculated using an exponential decay model (Webster and Benfield 1986). We applied the ANOVA model as described above with k -values as dependent variable. As both analyses provided the same results, only data from percentage of remaining AFDM were presented.

Differences in macroinvertebrate abundance and shredder abundance among treatments 1, 3, and 7 were calculated using a MANOVA model. Wilks' λ test statistics was used to assess treatment effects. Prior to the analyses, data were square root transformed to meet ANOVA assumptions.

The relationship between fungal biomass and remaining AFDM was determined by Spearman rank correlation.

All statistical analyses were performed using SPSS (ver. 11.0/SPSS Inc., IL, USA) with significance levels set at $P \leq 0.05$.

Our sampling design allowed us to statistically separate the effects of duration and frequency on leaf breakdown based on the calculation of partial residual plots (Ryan 1997). Depending on the treatment combination (duration/frequency), the parameter estimate value for the specific duration was subtracted to evaluate the effect of the corresponding frequency treatment, and vice versa.

Results

Effect of timing (season)

Leaf breakdown (expressed as percent remaining AFDM after 30 days of exposure) was significantly higher in winter than in summer (ANOVA: $F_{1,147}=124.16$; $P<0.001$). In the summer experiment, mean percentage of remaining AFDM ranged 51.4–80.5% in coarse mesh bags and from 57.3 to 83.3% in fine mesh bags. In the winter experiment, 41.3 to 82.3% AFDM remained in coarse mesh bags and 49.2 to 88.4% in fine ones (Fig. 2).

Effects of duration and frequency

In the summer and winter experiment, leaf breakdown was fastest in permanently inundated and slowest in permanently dry treatments (both mesh sizes) (Table 2). In both seasons, duration had significant effects on remaining AFDM, while frequency was only significant in the summer experiment (Table 3). Subsequent post-hoc tests showed that all duration treatments differed significantly from each other, whereas leaves inundated for 30 days broke down fastest, followed by leaves inundated for 20, 10 and 0 days. In summer, leaf breakdown from treatments with 1 dry/wet cycle was fastest differing significantly from treatments with 5 and with 0 dry/wet cycles. Leaves which were exposed to 10 and 15 dry/wet cycles broke down significantly faster than leaves, which underwent 0 changes (Scheffé's post-hoc test). In summer, we also found a significant two-way interaction between duration and frequency (Table 3). Leaves from treatments with 1 or 15 dry/wet cycles broke down significantly faster when they were inundated 20 instead of 10 days, whereas leaves from treatments with 5 or 10 dry/wet cycles decomposed only slightly faster when inundated 20 days.

Analysing coarse mesh bags for both seasons separately, we found significant effects for duration but not for frequency (Table 4). Subsequent post hoc tests

revealed that leaf breakdown differed significantly among all duration treatments with fastest rates during permanent inundation. Leaf breakdown in fine mesh bags was significantly influenced by duration and frequency in summer and by duration in winter (Table 4). In summer, leaves which were inundated 30 days decomposed fastest, those inundated 0 days slowest. Leaf breakdown in treatments with 10 and 20 days of

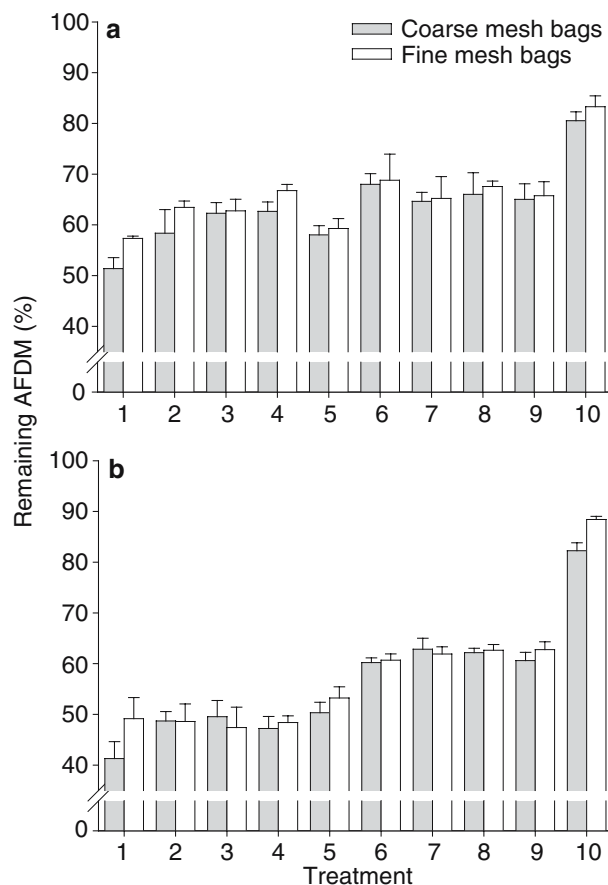


Fig. 2 Mass loss (mean \pm 1 SE) of black poplar leaves in coarse and fine mesh bags with different hydrologic regimes in **a** summer and in **b** winter. (Treatments see Fig. 1; $n=3-4$)

Table 2 Summary of breakdown coefficients ($k \text{ day}^{-1}$) for summer and winter experiments in coarse and fine mesh bags ($n=4$, mean \pm 1 SE)

Treatment	Summer		Winter	
	Coarse mesh	Fine mesh	Coarse mesh	Fine mesh
1	0.0222 \pm 0.0010	0.0185 \pm 0.0000	0.0296 \pm 0.0014	0.0238 \pm 0.0015
2	0.0181 \pm 0.0012	0.0152 \pm 0.0005	0.0240 \pm 0.0006	0.0241 \pm 0.0012
3	0.0158 \pm 0.0005	0.0155 \pm 0.0014	0.0235 \pm 0.0011	0.0250 \pm 0.0014
4	0.0156 \pm 0.0004	0.0135 \pm 0.0001	0.0251 \pm 0.0008	0.0242 \pm 0.0005
5	0.0182 \pm 0.0005	0.0174 \pm 0.0003	0.0229 \pm 0.0007	0.0210 \pm 0.0007
6	0.0129 \pm 0.0004	0.0126 \pm 0.0010	0.0169 \pm 0.0003	0.0167 \pm 0.0003
7	0.0146 \pm 0.0002	0.0143 \pm 0.0014	0.0155 \pm 0.0006	0.0160 \pm 0.0004
8	0.0139 \pm 0.0006	0.0131 \pm 0.0002	0.0158 \pm 0.0002	0.0156 \pm 0.0003
9	0.0143 \pm 0.0009	0.0140 \pm 0.0006	0.0167 \pm 0.0005	0.0155 \pm 0.0004
10	0.0072 \pm 0.0004	0.0061 \pm 0.0001	0.0065 \pm 0.0003	0.0041 \pm 0.0001

Table 3 Values of *F* from two-way analyses of variance (ANOVA) with percentage of remaining AFDM as dependent variable and block, mesh size, frequency, and duration as independent factors for summer and winter experiments ($n = 79\text{--}80$ per season). Degrees of freedom for each effect are given in parentheses

Effect	Remaining AFDM (%)	
	Summer	Winter
Block (3)	3.56*	0.87
Mesh size (1)	8.41**	8.71**
Frequency (3)	4.67**	1.42
Duration (2)	210.31***	530.98***
Frequency \times Duration (3)	3.16*	1.87

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

inundation duration was similar to each other. Frequency affected leaf decomposition as follows: leaves from treatments with 0 dry/wet cycles decomposed significantly slower than leaves from treatments with 1, 10, and 15 dry/wet cycles. In winter, 30 and 20 days of inundation caused fastest leaf breakdown differing significantly from 10 and 0 days of inundation.

Effects of macroinvertebrates and fungi

In both seasons, leaf breakdown was significantly faster in coarse than in fine mesh bags (Table 3). Differences between coarse and fine mesh bags were greatest under permanent wet (5.97% of remaining AFDM in summer and 7.86% in winter) and permanent dry conditions (2.75% in summer and 6.15% in winter). Mesh size was only found to have significant effects on leaf breakdown if permanent wet and dry treatments were included in statistical analyses. In both seasons, numbers of

macroinvertebrates were high, when, at the end of the experiment, bags were retrieved from wet conditions (treatments 1, 3 and 7) (Table 5). Where bags were retrieved from dry conditions (all other treatments), the number of macroinvertebrates was low (< 2 ind. bag⁻¹). In summer, total macroinvertebrate and shredder abundance were similar in treatments 1, 3, and 7 (MANOVA: Wilks' $\lambda = 0.952$, $F_{4,16} = 0.10$, $P = 0.981$). In winter, total macroinvertebrate and shredder abundance were higher in treatments 1 and 3 than in treatment 7, although not significantly different (MANOVA: Wilks' $\lambda = 0.348$, $F_{4,16} = 2.78$, $P = 0.063$).

Initial fungal biomass (0.011 mg ergosterol per g AFDM) indicated minor fungal colonization of freshly collected leaves. The ANOVA model showed that the ergosterol content of leaves was significantly higher in winter than in summer (ANOVA: $F_{1,148} = 9.58$; $P = 0.002$). In summer, mesh size (ANOVA: $F_{1,69} = 26.31$; $P < 0.001$) and duration (ANOVA: $F_{2,69} = 6.38$; $P = 0.003$) had significant effects on the ergosterol content of leaves, whereas frequency was only marginally significant (ANOVA: $F_{3,69} = 2.60$; $P = 0.059$). Fungal biomass was higher in coarse mesh bags, and treatments with permanent inundation were significantly different from all other treatments (Fig. 3a). However in winter, duration (ANOVA: $F_{2,66} = 254.99$; $P < 0.001$), frequency (ANOVA: $F_{3,66} = 7.86$; $P < 0.001$), and the interaction term of both (ANOVA: $F_{1,69} = 3.50$; $P = 0.002$), but not mesh size (ANOVA: $F_{1,66} = 0.002$; $P = 0.968$) significantly influenced fungal biomass. Leaves inundated for 20 and 30 days showed significantly higher fungal biomass than leaves which were inundated for 10 days. Permanent dry leaves showed lowest fungal biomass. Treatments with 5 dry/wet cycles showed highest ergosterol values, significantly different

Table 4 Values of *F* from two-way analyses of variance (ANOVA) with percent of remaining AFDM as dependent variable and block, frequency, and duration as independent factors for summer and

winter experiments, with coarse and fine mesh bags separated ($n = 39\text{--}40$ per season and mesh size). Degrees of freedom for each effect are given in parentheses

Effect	Summer experiment		Winter experiment	
	Coarse mesh	Fine mesh	Coarse mesh	Fine mesh
Block (3)	1.64	2.02	0.78	0.87
Frequency (3)	1.45	3.82*	0.77	2.49
Duration (2)	113.53***	96.71***	385.58***	320.69***
Frequency \times Duration (3)	2.27	1.44	1.29	1.29

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 5 Total macroinvertebrate abundance (N bag⁻¹) and shredder abundance (N bag⁻¹) in coarse mesh bags for summer and winter experiments ($n = 4$, mean \pm 1 SE)

	Summer		Winter	
	Total abundance	Shredder abundance	Total abundance	Shredder abundance
Treatment 1	37.8 \pm 10.8	20.8 \pm 8.2	243.8 \pm 64.0	23.0 \pm 2.7
Treatment 3	37.8 \pm 4.6	17.8 \pm 3.9	149.3 \pm 31.1	19.3 \pm 3.2
Treatment 7	33.5 \pm 5.9	16.5 \pm 5.2	42.0 \pm 8.3	8.8 \pm 1.7

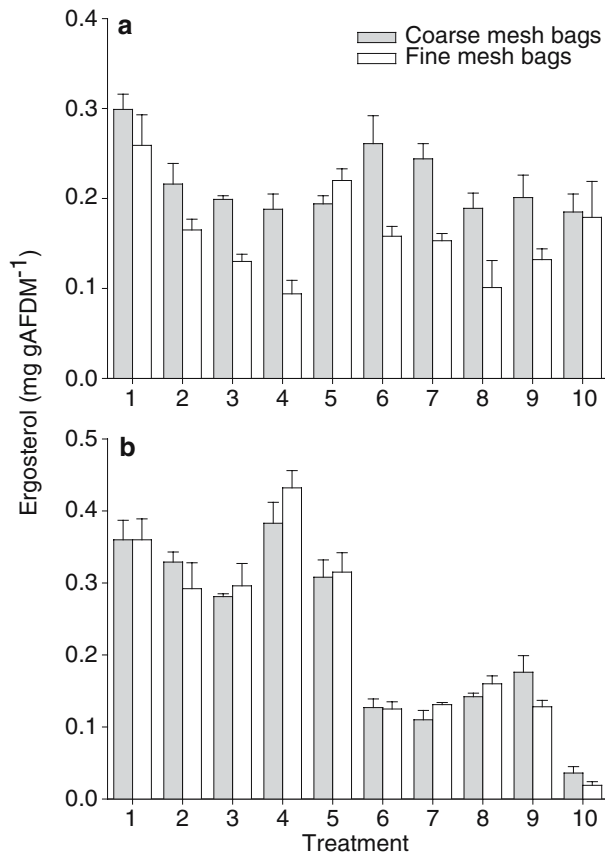


Fig. 3 Ergosterol content of leaves (mg gAFDM⁻¹) in coarse and fine mesh bags with different hydrologic regimes in **a** summer and in **b** winter. (Treatments see Fig. 1; $n=4$)

from treatments with 0, 10, and 15 dry/wet cycles (Fig. 3b). The significant interaction between duration and frequency resulted from the fact that the increase of fungal biomass observed from 10 to 20 days of inundation was greater in treatments with 1 or 10 dry/wet cycles than in treatments with 5 or 15 dry/wet cycles.

In both seasons, leaf litter breakdown rate (percent of remaining AFDM) was significantly correlated with ergosterol concentration (Spearman rank correlation; summer, $r = -0.335$, $P = 0.003$; winter, $r = -0.849$, $P < 0.001$).

Discussion

Effects of season and inundation regime

In our study, leaf litter breakdown varied considerably between seasons and among treatments. Leaves broke down faster during the winter experiment. Leaves under permanent inundated conditions lost almost 50% of its organic matter within 30 days, indicating a high decomposition rate compared to estimates from other temperate regions (e.g. Baldy et al. 1995; Pereira et al. 1998; Menéndez et al. 2003). Under dry conditions, leaf breakdown was similar to previously observed winter

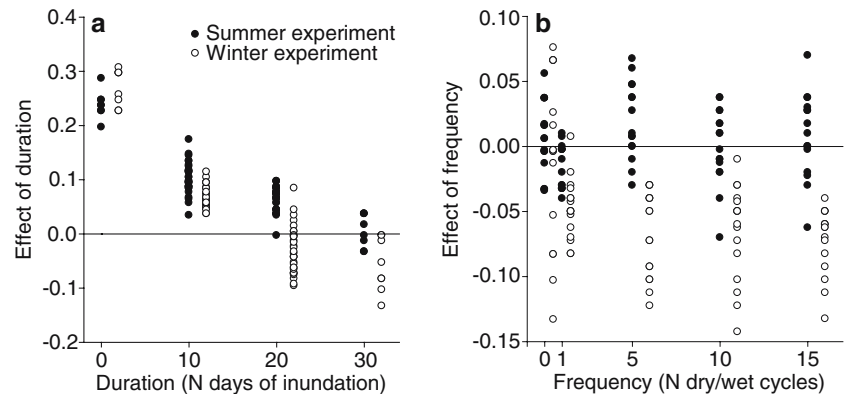
rates in the Tagliamento system (S.D. Langhans, unpublished data).

Leaf litter processing in aquatic and terrestrial habitats is the result of factors such as leaf-litter quality (Shaw and Harte 2001), temperature (Irons et al. 1994), relative humidity (Kuehn et al. 2004), dissolved oxygen (Chergui and Pattee 1988), dissolved nutrient concentrations (Robinson and Gessner 2000), and abundance and diversity of organisms responsible for decomposition (Dangles and Malmqvist 2004). In our study, oxygen, nutrient concentrations, velocity, and relative humidity were higher, and temperatures were lower in the winter experiment. Increased oxygen and relative humidity levels favour aerobic microbial respiration, and high concentrations of dissolved nutrients accelerate the processing of leaf litter (Robinson and Gessner 2000). Current velocity, ranging from 0.02–1.20 m/s, was found not to alter leaf breakdown rates (V.J.L. Ferreira et al., unpublished data). The effect of differing thermal regimes on leaf litter decomposition shows a clear tendency towards faster breakdown rates with increasing temperatures (e.g. Carreiro and Koske 1992; Menéndez et al. 2003). Apparently, in our experiments, the effect of temperature was most likely masked by other factors such as increased humidity and nutrient concentrations in winter.

Generally, mass loss from decaying leaf litter is faster in aquatic than in terrestrial systems because of enhanced leaching and microbial metabolisms (Molles et al. 1995). Similarly in our experiments, duration of inundation rather than frequency was the “master variable” controlling leaf breakdown in both seasons and mesh sizes. Our results correspond to those of Herbst and Reice (1982), who also found faster leaf breakdown rates in a permanent stream relative to a temporary and an intermittent stream (Tanninim and Daliya River, Israel). However, Battle and Golladay (2001) observed greatest decomposition under the most fluctuating hydrologic regime (Dougherty Plain, GA, USA). Their study was conducted under standing water conditions, where oxygen depletion may be a controlling factor. Oxygen was never a limiting factor and fine sediment deposition is not prevalent in the braided section of the Tagliamento River where we worked.

In both seasons, the effect of duration on percentage of remaining AFDM was particularly high if leaves were inundated only for few days. With increasing inundation time, the effect of duration decreased to zero. Frequency showed no correlation with percentage of remaining AFDM (Fig. 4). Our winter results are comparable with those of Lockaby et al. (1996) who suggested fastest decomposition under single inundation events. Mitsch and Gosselink (1993) stated that decomposition rates are most rapid under aerobic but moist conditions. These conditions existed in the hibernal humid climate in NE Italy, and intensified the effects we have found for 1 dry/wet cycle. During the hot and dry summer, only frequent dry/wet cycles could enhance decomposition.

Fig. 4 The effect of **a** duration (days) and **b** frequency (dry/wet cycles) of inundation on percentage of remaining AFDM in summer ($n=79$) and in winter ($n=80$) experiments calculated on the basis of remaining AFDM(%)



Effects of macroinvertebrates and fungi

Our second research question focused on the role of fungi and aquatic and terrestrial macroinvertebrates in controlling leaf litter decomposition under different inundation regimes. Shredding macroinvertebrates significantly increased leaf breakdown only during permanent wet conditions (on average by 3.3 to 16.0%). Under permanent dry conditions, faster leaf breakdown in coarse mesh bags might have been caused by leaching because shredders were absent in these bags. Leaves in fine mesh bags seemed to be protected from heavy leaching by the mesh coverage. The minimal difference between coarse and fine mesh bags in all other treatments and both seasons suggested that dry/wet cycles were too frequent to establish feeding effects by macroinvertebrates on leaves. Physical abrasion must have played a minor role in the permanent wet treatment, otherwise, leaves in coarse mesh bags inundated for 20 and 10 days would have shown significantly faster breakdown rates than leaves in fine mesh bags.

In many aquatic ecosystems, fungi (hyphomycetes) play the predominant role in the microbial decomposition of leaves (Hieber and Gessner 2002). In contrast to bacteria, fungal assemblages are able to respond immediately to rewetting (Fierer et al. 2003). Therefore, alternating dry/wet cycles have only a small influence on the activity of fungal decomposers which might explain why duration was most important in our experiments. In a recent study, Kuehn et al. (2004) demonstrated that microbial activity on *Phragmites australis* leaves exhibited a diel periodicity with highest activity during night when relative humidity peaked. This finding suggests, why, in our case, fungal biomass was higher in winter than in summer. Even under terrestrial conditions, the humid winter climate in NE-Italy provided enough moisture for microbial activity. Therefore, increased microbial activity accounted for higher leaf breakdown rates during the winter. However, hot and dry summers (as in 2003) may reduce microbial activity, because leaching of polyphenols via rainfall and dew might be necessary before litter can be broken down (Boulton 1991). This explanation agrees with our finding that, if we considered leaf breakdown without feeding effects

(fine mesh bags), significant duration effects in the moist season (winter), and significant duration and frequency effects in the dry season (summer) were found. Additionally, fungal biomass explained the effect of duration of inundation on leaf breakdown. However in winter, leaf breakdown behaved differently under the frequency treatments than fungal biomass. We suggest that frequency effects on fungal biomass are too small to influence leaf litter breakdown.

The relationship between hydrology and the decomposition process

In headwater streams, leaf litter enters the wetted channel during the autumnal litter fall period, thus input and processing overlap spatially and temporally. In floodplains, however, areas of production, storage and processing of leaves are spatially and temporally separated. Across a river-floodplain transect, standing stock of leaf litter biomass can change over four-orders of magnitude, from <1 (bare gravel surface) to about 1,000 g (vegetated islands) AFDM per m^2 (Van der Nat 2002). While vegetated islands and the fringing riparian forest are the primary input and storage areas, aquatic habitats, in particular channels are the fastest processing areas. In such habitats, breakdown rates are several times faster compared to terrestrial areas. Most leaf litter is transferred from input/storage areas to river channels (fast processing areas) during periods with over bank flow. A human-regulated hydrologic regime often changes the duration, frequency, and magnitude of flow and flood pulses (Richter et al. 1997; Poff and Hart 2002). In flow-controlled systems, not only the amount of conveyed organic matter but also the transport distance and the breakdown dynamics are restricted.

Concluding remarks

Most attention on altered flow regimes has focused on their effects upon water quality and biota. There are only a few studies that rigorously tested for their impacts on ecosystem functioning (e.g. leaf litter decomposition)

(Bunn et al. 2002). Results from our study showed that riverine floodplains display a remarkable heterogeneity in their ability to process organic matter, similar (albeit more complex) to riparian margins in small headwater streams (Hutchens and Wallace 2002).

Modifications of the inundation regime will directly (as shown in this study) and indirectly (i.e. by changing litter composition and quality) influence decomposition processes. Factors reducing duration of inundation will decelerate breakdown rates, whereas, a decrease in flow variation will reduce breakdown heterogeneity. If floodplain inundation changes the riparian vegetation will alter too (e.g. Busch 1995; Tiegs et al. 2005). This can result in dramatic consequences for leaf litter quality and quantity. In addition, the complex mosaic of terrestrial (e.g. bare gravel, islands, riparian forest) and aquatic (e.g. ponds, backwaters, channels) habitats, which ensure large spatial and temporal variation in litter dynamics, might be reduced to a less heterogeneous habitat composition. This decline in heterogeneity will weaken aquatic-terrestrial linkages by reducing the exchange of water, nutrients, and leaf litter among adjacent ecosystems (Gurnell et al. 2005).

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