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Mesh size and site effects on leaf litter decomposition in a side arm of the River Danube on the Gemenc floodplain (Danube-Dráva National Park, Hungary)

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Abstract

In forested floodplain ecosystems, leaf litter represents an important energy source for aquatic organisms, and its decomposition is a key ecosystem process. In this paper, we investigate the decomposition dynamics of *Salix alba*, *Populus* hybrids in the depositional zone of a side arm of the River Danube, and of *Fraxinus angustifolia*, *Ulmus laevis, Quercus robur* in the erosional zone. To estimate the effect of small-sized invertebrates we used litter bags with two mesh sizes (0.04 mm and 1 mm) and to evaluate the site effects the *F. angustifolia* leaves were exposed in both sites. Willow and poplar leaf litter decomposed at an intermediate rate, ash and elm quickly and the oak slowly. The faunal exclusion experiments revealed the importance of Chironomidae larvae, which formed the dominant macroinvertebrate taxon in the medium mesh bags. The initial quality of the leaf litter, especially the N:P ratio, affected

the activity of microorganisms, the density of chironomids, and was positively correlated with the breakdown rates. The site conditions had a significant effect on the decay rate and nutrient dynamics. We concluded that the leaf litter decomposition processes and the associated nutrient dynamics are affected by nutrient availability, consumer activity and site conditions.

Keywords: litter quality, nutrients, ETS-activity, fungal biomass, chironomid larvae, site effect

Introduction

In large river floodplain ecosystems, the main driving force of the processes is the flood pulses, which accelerate the exchange of organic matter and nutrients through the enhancement of the lateral hydrological connectivity of side arms. These latter are important sites of organic matter processing and sources of energy to the main arm (Junk et al., 1989; Riedl et al., 2013; Ágoston-Szabó et al., 2013; Tiegs et al., 2007; Tank et al. 2010). The quantity, identity, timing and mechanism of the entry of allochthonous organic matter into the floodplain waters is largely influenced by the composition and structure of the surrounding forest and by the channel-floodplain hydro-geomorphology (Junk et al., 1989; Langhans & Tockner, 2006; Ágoston-Szabó et al., 2014). Rivers meandering across floodplains erode sediment from the outer bend with fast flowing water - the erosional zone - and deposit it further down the stream near the inner bend, where the water flows more slowly, in the depositional zone. Hydro-geomorphological alterations and meander cut-offs can have an impact on the structure and functioning of these ecosystems, also including on the decomposition processes (Sheldon & Thoms, 2006; Mendoza-Lera et al., 2012).

Leaf litter-originated organic matter represents an important energy base and a potentially limiting nutrient source to aquatic decomposer communities, increases the stability of food webs, and provides a habitat and shelter for the associated invertebrates (Chauvet & Decamps, 1989; Graça et al., 2001; Callisto et al., 2007; Swan & Kominoski, 2012).

Leaf litter decomposition involves the chemical leaching of soluble compounds, physical and biological fragmentation and the microbial mineralization of structural components, which is achieved mainly via aquatic hyphomycetes (Gulis & Suberkropp, 2003). Fungi increase the palatability and facilitate the consumption of leaf litter by detritivorous macroinvertebrates, which in turn indirectly influence the microbial activity by controlling nutrient availability via consumer nutrient recycling (Langhans et al., 2008; Gessner & Chauvet, 1994; Cheever &

Webster, 2014). The important role of macroinvertebrates in the fragmentation, consumption, increase in the nutritional content and accelerated decomposition of leaf litter has been elucidated in several previous studies (Graça et al., 2001; Wright & Covich, 2005; Ferreira et al., 2006; Gaudes et al., 2009; Ligeiro et al., 2010 etc.). There is, however less information concerning the contribution of small-sized invertebrates to decomposition processes (Callisto et al., 2007; Gaudes et al., 2009; Jabiol & Chauvet, 2015).

The breakdown of leaf litter is regulated by several factors, among which are numbered the quantity and quality of the substrate, the physicochemical properties of the leaves and their habitat, the colonization and activity of microbial and invertebrate decomposer communities, and the hydrological regime, etc. (Thompson & Bärlocher, 1989; Gessner & Chauvet, 1994; Bärlocher et al., 1995; Baldy et al., 1995; Chauvet, 1997; Graça et al., 2001; Langhans & Tockner, 2006).

Studying the factors influencing decomposition assists in the understanding and evaluation of the effects of naturally and anthropogenically originating changes in the ecosystem's structure and functioning (Andersen & Nelson, 2006).

Leaf litter is an important element in nutrient spiralling, flood pulse and river continuum concept (Junk et al., 1989; Vannote et al., 1980; Webster & Meyer, 1997). The river continuum concept focuses on the importance of litter input and the changes in composition of the organisms along the river continuum, whilst the flood pulse concept emphasizes the role of hydrogeomorphology and of lateral habitats in the control of biological communities and biogeochemical processes and suggests that river food webs are more dependent on allochthonous detritus input than upon organic matter transported from upstream reaches (Vannote et al., 1980; Junk, 1989; Chauvet, 1997).

A number of litter decomposition studies exist on stream and lake ecosystems, while rather fewer are to be found on riverine floodplain ecosystems (Langhans & Tockner, 2006; Langhans et al., 2008; Tiegs et al., 2007; Baldy et al 1995).

Our hypotheses were that 1) the breakdown rates and the activity of decomposer communities vary within species in the function of litter quality 2) small-bodied detritivorous invertebrates have a significant effect on litter breakdown processes 3) the decomposition rates are different between the erosional and depositional zones of the side-arm.

In the present study, we aimed to examine the decomposition dynamics of five native litter species in a side arm of the River Danube using the litter-bag method, with an emphasis on 1) the effect of litter identity and availability on decomposer microbial and invertebrate communities, 2) the influence of small-sized invertebrate consumers on litter breakdown processes by enclosing litter in bags with intermediate and small meshes, which allow or restrict the feeding of small sized detritivorous invertebrates, and 3) the site effects by pairing measurements in medium mesh bags exposed at the depositional and erosional zones.

Material and Methods

Study area

The sampling sites were situated in the depositional and erosional zones of the Rezéti-Holt-Duna (RDU), which is a permanently flowing side arm on the right bank of the River Danube in the active floodplain with an upstream junction at river kilometre (rkm) 1488 and its mouth at rkm 1485.

The Gemenc forested floodplain (46º15'N 018º51'E) along the River Danube has an area of 180 km^2 and includes a variety of tree species and habitats. It is protected under the European Union's Natura 2000 network, and is listed under the Ramsar Convention on Wetlands. In the

higher floodplain elevations, the dominant forest type and detritus sources are the hardwood Fraxinus-Ulmus-Quercus and on the lower elevations, softwood Populus-Salix groves.

Water column characteristics

The temperature, pH, and electrical conductivity of the water surrounding the litter bags were determined *in situ* using a WTW 340i Multi instrument (Germany). The total carbon (TC), total organic carbon (TOC) and total nitrogen (TN) were determined from unfiltered water, the dissolved organic (DOC), dissolved inorganic carbon (DIC), and total dissolved nitrogen (TDN) concentrations were determined from filtered water samples by a TOC analyser (Elementar-liqui-TOC). The chlorophyll-a (Chl-a), suspended matter (SPM), ammonium (NH_4^+-N), phosphate (PO_4^{3-}-P), nitrate (NO_3^--N), total phosphorus (TP), and total dissolved phosphorus (TDP) concentrations of the water were determined in the laboratory with standard analytical methods (Golterman et al., 1978). The dissolved inorganic nitrogen (DIN) was calculated as the sum of the NH_4^+-N, NO_3^--N concentrations. The DON was calculated from TDN by the subtraction of DIN. The particulate organic carbon (POC) and the particulate nitrogen (PN) were calculated as the differences between TOC and DOC and TN and TDN, respectively. The dissolved organic phosphorus (DOP) was calculated as the difference between TDP and PO_4^{3-}-P. The daily water level and water discharge data, which were measured at the official gauge at Baja (rkm 1478.70) were obtained from www.hydroinfo.hu.

Litter-bag Experiment

The decomposing litter mass and its chemistry, the associated microbial activity, the macroinvertebrate density, and the chemical characteristics of the surrounding water were determined at two sampling sites and at four sampling times.

Leaf decomposition was measured by using the litter-bag method. Senescent leaves were collected for decomposition studies in October 2007, before their natural abscission by gently shaking, and then they were transported to the laboratory. The leaves were air dried and stored in open paper bags at room temperature until their exposition. 8 g of air dried leaves were put in litter bags of 1 mm (which allowed medium-sized invertebrates, excluded larger invertebrates, and prevented the loss of large fragments of material through the mesh), and of 0.04 mm mesh size (which excluded macro- and meiofauna, but allowed entry of most microbial decomposers). Litter-bags were exposed in the water column of the RDU side arm on 12 March 2008.

Leaves of *S. alba, P. hybrids* were placed at site 1 (S1) in the depositional zone (46°13'23.98"N 18°52'4.96"E), and of *Q. robur*, *U. laevis* and *F. angustifolia* at site 2 (S2) in the erosional zone (46°13'24.72"N 18°51'57.92"E) of the side arm. *F. angustifolia* leaves in 1 mm mesh bags were exposed at both sites in order to evaluate the site effects. Three bags from each type of leaf litter and mesh size were retrieved altogether at 4 sampling times (the 12th and 14th of March, 15th of April, and 13th of May, 2008) for laboratory analyses. Leaf bags on 0 day (12th March) were immersed in water *in situ* then retrieved. The invertebrates were removed from the medium-mesh bags and preserved. The leaf material from both types of mesh-bags was carefully washed with tap water in order to remove the accumulated silt. At each site, all data for all leaf species are presented up to the point at which the litter species exposed in medium-mesh bags lost about 38-79 % of its initial mass, which was 62 d.

The dry mass of the remaining leaf material was determined at 105 °C and the ash content at 550 °C. The ash free dry mass (AFDM), which is an index of the organic matter content, was calculated as the difference between the dry weight and ash content. The dried leaf material was ground in a motor mill to determine its ash and nutrient contents on aliquots. The total C and N concentrations were determined using an NCS analyser (NA-1500, Fisons Instruments,

153 Italy) and the total P concentrations with the spectrophotometric molybdenum blue method,
154 after digestion with concentrated sulphuric acid (Rûžička & Stewart, 1975).
155
156 **Small-sized invertebrates, microbial activity and biochemical assay**
157 The potential microbial respiratory activity was determined spectrophotometrically from fresh
158 subsamples (20-40 mg) by using the tetrazolium reduction test-based ETS (electron transport
159 system) assay (Packard et al., 1971). The litter-associated fungal biomass was estimated by
160 extracting and quantifying the ergosterol (Gessner & Newel, 1997), which was extracted from
161 fresh subsamples through saponification (2-4 g samples were put in 25 ml absolute ethanol
162 then 5 ml 4% alcoholic potassium-hydroxide was added, followed by reflux boiling, 80 °C for
163 30 min), and partitioning from the saponified samples with n-hexan extraction, using a
164 separatory funnel. The resultant ergosterol extract was evaporated to dryness (under a stream
165 of N_2 gas and stored in a deep freezer until the analysis, when it was redissolved in 4 ml
166 ethanol in an ultrasound bath, filtered (using a 2µm filter pore) and quantified by HPLC
167 (Thermo Separation UV150, P200 high pressure, Column LiChospher 100 RP-18, 5 µm.
168 250x4 mm).
169 The small-sized invertebrates were represented entirely by chironomid larvae, which were
170 identified to the family level and a comparison was made between their densities on different
171 leaf litter species and on the same leaf species at both sites.
172
173 **Data analysis**
174 The C, N, P amounts were calculated by multiplying the concentrations (mg g^{-1}) by the
175 remaining dry mass (g). The remaining amounts of AFDM and C, N, P were calculated as
176 follows: $X=(X_t/X_0)\cdot 100$, where X is the percentage of mass or nutrient remaining, X_t is the
177 amount of AFDM or C, N and P, at time t, X_0 is the initial amount of AFDM or C, N and P.

178 The single exponential model $X_t=X_0\exp(-kt)$ was applied to the AFDM data from whole study
179 period (Olson, 1963), in which k is the exponential breakdown rate (k_{AFDM}). The Nonlinear
180 Estimation method was used for function fitting, which uses the method of Levenberg-
181 Marquardt (Marquardt, 1963). The data were analysed by Pearson product moment
182 correlation analyses, one-, two- and three-way ANOVA models and t-tests for independent
183 samples for variables. The significance level was assigned a value of 0.05 in all cases.
184 Statistical analyses were carried out with Statistica 6, PAST and Real Statistics (StatSoft, Inc.,
185 2001; Hammer et al. 2001; Zaiontz, 2015).
186

187 **Results**

188 **Water characteristics**

189 The mean water level of the River Danube was 394 cm, with a minimum of 290 cm and
190 maximum of 510 cm, and the main physical and chemical parameters of the water column did
191 not differ significantly between the sampling sites during the investigation period (Table 1).
192

193 **Litter decay**

194 The initial litter quality indices varied widely between the five litter species. *F. angustifolia*
195 had the highest C and N concentration, N:P ratio and the lowest C:N ratio; *Q. robur* the
196 highest P concentration and the lowest N:P ratio, *P.* hybrids the highest C:N, C:P, while the *S.*
197 *alba* the lowest C:P ratio (Table 2).
198 The amounts of AFDM, N and P remaining were significantly influenced by species, mesh
199 size, site, and time and as also by the interaction of these factors (Table 5).
200 There were no significant differences in the AFDM leached out in the first 48 h between the
201 examined litter species; neither mesh sizes, nor site effects had any significant effect on the
202 leaching.

Significant mesh size effects were found to exist on the remaining AFDM in the middle of decomposition (34 d) in the case of *P.* hybrids*, S. alba, F. angustifolia* and at the end of decomposition (62 d) in the case of *S. alba* and in the erosional zone. The percentage (%) of AFDM remaining in the 1 mm mesh bags was significantly lower than in the 0.04 mm at 62 d, while at 34 d was significantly higher. The remaining amount of AFDM was higher at S1 than at S2 starting from the 34 d, significant site differences were found only in the middle of the decomposition (Figure 1). The two-way Anova analyses of %AFDM remaining reflected significant time and site x time interaction effects (Table 5), while in the case of nutrients (%N and %P remaining), the site effect was also significant.

Similar to the case of the AFDM, there were no significant differences between litter types, mesh sizes, and sampling sites in N and P leached out, while significant mesh size, species and site effects were found on the N and P remaining at the end of the decomposition (Figure 2). In those cases where the mesh size effects were significant on N at 62 d the % of N remaining in 1 mm mesh bags was lower (Figure 2). The % of P remaining was higher in each case in 1 mm than in 0.04 mm mesh bags, and the mesh size effect on the percentage of P remaining on 62 d was significant only in the case of *P.* hybrids. The site effect was significant at 62 d, when the remaining amount of P was higher at S1 than at S2 (Figure 2).

A significant correlation was found between the initial N:P ratio and the C, N and P leached out (Table 3).

The litter breakdown rate (k_{AFDM}) was influenced by mesh size and litter species (Table 5) and site effects (Table 4b; Fraxinus: one-way ANOVA $F(1, 4) = 7.72$, $p=0.0498$). The mesh size effect was significant only in the erosional zone of the side arm (Table 4a). The k_{AFDM} from among the initial litter quality parameters positively correlated to a significant degree with the initial N:P ratio (Table 3) and could be ranked in an order similar to this ratio Fraxinus>Ulmus>Salix>Populus>Quercus (Tables 2, 4).

228

229 **Macroinvertebrates and microbial activities associated with litter decomposition**

230 The dominant macroinvertebrate taxon was the Chironomidae in its larval stage. Their relative
231 abundance was 100% at 62 d. The densities of chironomid larvae showed significant
232 differences between leaf species, but not between S1 and S2 (Figure 3). Among leaf species
233 *F. angustifolia* and *U. laevis* showed significantly high densities g_{AFDM}^{-1}. The chironomid
234 densities showed significant positive correlation with k_{AFDM}, the total loss of N, AFDM, the
235 initial N:P ratio and a negative correlation with the initial C:N ratio (Table 6).
236 The effect of mesh size on the potential respiratory activity and fungal biomass was
237 significant only in the depositional zone of the side arm (Figure 4, 5). A significant site effect
238 was found on the ETS-activity in the case of *P.* hybrids and *S. alba* at 34 and 62 d, while the
239 ETS was higher at S2 than at S1, and on fungal biomass at 62 d, while at S1 was higher than
240 at S2.
241 The initial ETS on the second day negatively correlated with the N:P ratio (Table 7) and
242 showed a significant negative correlation with AFDM leached out. The ergosterol on the
243 second day positively correlated with the initial C:P ratio and at 62 d negatively correlated
244 with k_{AFDM} and total loss of AFDM and N (Table 7).

245

246 **Discussion**

247 The results of this study show statistically significant differences in the decomposition of leaf
248 litter in a side arm of a large river. The intermediate decomposing *P.* hybrids and *S. alba*, the
249 fast decomposing *U. laevis* and *F. angustifolia,* and the slow decomposing *Q. robur* leaf litter
250 contributed to differing degrees to organic matter and nutrient dynamics in the side arm
251 during their breakdown. The differences in decomposition across species within a certain zone
252 of the side arm were mainly due to the quality of leaf litter.

253

254 **Initial litter quality**

255 The quality of leaf litter, particularly its nutrient concentration significantly influenced the
256 activity of microorganisms and density of macroinvertebrate consumers (Table 6, 7).
257 The initial litter quality showed a large variation between the examined five species. The
258 ranges of the C:N ratio in this study (Table 2) were similar to the ranges (20-60) reported by
259 Chauvet (1997) for deciduous forest tree species. The correlations of the initial quality indices
260 with the breakdown rate confirmed that these parameters significantly influence the
261 decomposition of organic matter originating in leaf litter (Table 3). Several studies have
262 shown that within a certain climatic region, and on a local scale, litter chemistry and quality
263 are the best predictors of k-values and of the differences in decomposition rates between litter
264 types (Jabiol et al., 2013). In our study the N:P molar ratio proved to be the most important
265 influencing factor of decomposition from among the examined initial quality indices (C:N,
266 C:P, N:P ratio), which is consistent with the results of Güsewell & Gessner (2009).

267

268 **Mass and nutrient loss**

269 The leaching losses varied between species, and according to our results, may account for less
270 than 27% of the loss of the initial ash free dry mass, which is consistent with the results of
271 other studies (Table 8). The percentage of N released from *Populus* leaf litter (17%) was
272 similar to the results of Andersen & Nelson (2006), who found that poplar leaves lost 20% of
273 their N content through leaching and have an important role in the floodplain N dynamics.
274 The significant correlation of AFDM leached with the initial N:P ratio suggests that the
275 intensity of leaching was affected by the intrinsic factors, such as the initial litter quality
276 (Berg & Mc Claugherty, 2008; Park & Cho, 2003). The lack of significant differences
277 between the fine and medium mesh bags in the amount of AFDM and nutrients leached,

suggests that the applied exclusion technique did not significantly influence the chemical processes in the leaching phase of decomposition. Previous comparative studies performed in aquatic or terrestrial environments using litter bags with different mesh sizes showed no effect of mesh size, in the absence of invertebrates (Bokhorst & Wardle, 2013); in other studies, however, it has been assumed that coarser mesh bags are more exposed to the leaching, abrasion fragmentation and loss of particles than fine mesh bags (Webster & Benfield, 1986; Bradford et al., 2002).

The decomposition rates of *S. alba* and *P.* hybrids observed in this study were consistent with the majority of the data to be found in the literature (Table 9), but differed from some of them, which can be explained by the differences at species-level and/or in the environmental and experimental conditions.

The loss of mass and nutrients in fine mesh bags can be attributed to leaching and microbial breakdown, while in the case of medium sized mesh bags, the consumption and a possible comminution of leaf litter by feeding activity of small-sized invertebrates to a particle size lower than the mesh size and the movement of meiofauna may also contribute to the loss of fragmented litter. The significant differences between the two mesh sizes in the remaining amount of AFDM, N, which at 34 d was significantly lower in fine than in medium mesh bags might be due the deposition and accumulation of fine particulate matter and associated nutrients in litter bags with medium mesh size. The differences in the remaining AFDM, N and P between the medium- and fine-mesh bags at 62 d may be assigned to small sized invertebrates which accelerated the decomposition of leaf litter.

Small-sized invertebrates

The colonization of leaf detritus by decomposer organisms is influenced by several intrinsic factors as leaf chemistry and toughness, and extrinsic factors, such as the abiotic

environmental conditions (Graça et al., 2001). Small-sized invertebrates intervene later in the process of decomposition following the increase in palatability of leaf litter brought by the action of microorganisms. Chironomidae larvae, which were the numerically dominant macroinvertebrate taxon on all of the examined leaf species, were macroscopically observed only at the end of decomposition. The dominance of Chironomidae larvae was in accordance with other work carried out in lotic ecosystems (Ligeiro et al., 2010; Mathuriau & Chauvet, 2002). Leaf litter serves as a source of food, a surface for the formation and deposition of fine particulate organic matter, and a refuge for these larvae (Maltby & Barker, 2009). The fine particulate organic matter from decaying litter has a high nutritional quality, and is the predominant food source of chironomids associated with decomposing leaves (Grubbs et al., 1995; Casas et al., 2000). A large proportion of these larvae are classified as shredders or gatherer-collectors, but most of them are not restricted to a single feeding mode; the flexibility in their mode of feeding in the presence of leaf litter has been described by Armitage et al. (1995) and Hodkinson & Williams (1980).

The significantly higher chironomid densities found on the species with the highest N:P ratio, i.e. *F. angustifolia* and *U. laevis*, as compared to other species, suggested that the higher-quality organic matter (with greater N content) supports higher larval densities. Insects have been shown to have higher body N content and N:P ratios than molluscs and crustaceans; these differences in elemental composition could result in large differences in nutrient (i. e. N) demand, retention, and cycling between these taxonomic groups (Evans-White et al., 2005; Cheever & Webster, 2014).

The significant positive correlations of the larval densities with the N:P, and the negative with the C:N ratio indicated that the limiting nutrient of the chironomids was the nitrogen. The quality of leaf litter (in our study, especially the N:P ratio) remarkably influenced the chironomid densities, which coincides with other studies (Brennan et al., 1978; Armitage et

al., 1995). The positive correlations of the larval densities with k_{AFDM}, the total loss of N and AFDM suggested the role of chironomids in the breakdown of organic matter and nutrient retention, and recycling. The detritus attached microorganisms serve as a direct food source for the leaf litter associated chironomid larvae; previous studies have revealed that the most commonly ingested food of chironomids was detritus, which accounted for 50-70% of their gut content (Armitage et al., 1995, Sanseverino & Nessimian, 2008). Callisto et al. (2007) also found that some chironomids can use the well-conditioned leaf litter as a complementary food source. Chironomids may also indirectly affect the decomposition and the activity of microorganisms by modifying the abiotic microenvironment and resource availability (i. e. through their moulted integument, faecal pellets, and dwelling-tubes exerting a feedback on the microbial activity), and by their possible role in litter comminution (Armitage et al., 1995; Hodkinson & Williams, 1980).

The effect of macroinvertebrate and meiofauna exclusion varied within leaf types and sampling sites consistent with the results of other studies (Wright & Covich, 2005). Although the non-exclusion bags had a higher count and density of chironomid larvae in the depositional than in the erosional zone of the side arm, these differences were not statistically significant. Our experiments with medium and fine-mesh litter-bags, which allowed or restricted the access of macro- and meiofauna, demonstrated that these faunal size classes increase the breakdown rates.

Microorganisms

Heterotrophic microorganisms, particularly aquatic hyphomycetes, are largely responsible for the process of decomposition by catabolising organic macromolecules, in this way playing an important role in the mineralization of leaf litter originated organic matter (Gulis & Suberkropp, 2003). The initial fungal biomass in our decomposition experiment can be

353 explained by the previous colonization of leaf material by terrestrial fungi. In some studies on
354 microbial colonization of plant detritus in aquatic environment bacteria have been found to be
355 the primary colonizers (Ágoston-Szabó et al., 2006), while in other studies fungi found to be
356 and in the advanced stages of decomposition, bacteria also complemented fungi (Baldy et al.,
357 1995; Suberkropp et al., 1976).
358 The negative correlation of ETS-activity with the amount of AFDM, N, and P leached out
359 leads us to assume that leaching could have an inhibitory effect on the potential microbial
360 respiratory activity, probably due to the antimicrobial substances released. Salix and Populus
361 species contain a wide range of toxic phenolic glycosides, e. g. salicin, which, transformed
362 into salycilic acid by hydrolysis, uncouples oxidative phosphorylation, while Quercus species
363 contain defensive phenolics, i.e. tannins (Lambers et al., 2008). This could be an explanation
364 for the highest ETS-activity occurring in case of *Q. robur*, from which the highest amount of
365 P also leached out, whilst in the case of *S. alba* and *P.* hybrids, despite of the high amount of
366 P leached, the ETS-activity values remained low. Further complementary laboratory and field
367 studies are needed to test our assumptions.
368 The positive correlation of fungal biomass with the C leached and initial C concentration
369 suggested a stimulatory effect of the soluble C compounds on fungal colonization. The
370 microbial decomposers preferentially metabolize soluble C compounds leached from the more
371 labile litters, with no enzymatic breakdown prior to uptake (Rinkes et al., 2013). On the labile
372 organic matter, microorganisms have a high rates of metabolic activity and growth, which
373 requires high concentrations of ribosomes (the most phosphorus rich cell organelles, due to
374 their high r-RNA content) (Fontaine et al., 2003; Elser et al., 2003; Güsewel & Gessner,
375 2009). Contrary to the chironomid larval density, the ergosterol on 62 d negatively correlated
376 with k_{AFDM} and total loss of AFDM and N, which suggested the higher role of chironomids in
377 the regulation of litter mass and nitrogen loss as compared with aquatic fungi.

In fine mesh bags, which excluded both macro- and meiofauna, the breakdown could be caused only by leaching and the activity of microorganisms. The differences in microbial respiratory activity and fungal biomass between the fine and medium mesh bags at 62 d suggested that the activity of the microbial decomposer community was affected by the action of the invertebrate decomposer community, which decreases the microbial metabolism and fungal biomass, but the effect was only significant for the ETS activity associated with leaf litter of *P*. hybrids and *S. alba* decomposing in the depositional zone of the side arm.

The higher were the chironomid densities, the lower were the microbial activities, which suggests the top-down effect of chironomid larvae on microbial respiratory activity and fungal biomass.

Conclusions

The identity and initial chemical quality of leaf litter notably influenced the activity associated with the decomposition process. The differences in site conditions between the erosional and depositional zones of the side arm significantly affected the decomposition rate of *F. angustifolia* leaf litter and the associated nutrients dynamics.

The exclusion experiments demonstrated the significant role of small sized invertebrate decomposers in the breakdown of leaf litter-originated organic matter and the associated nutrient dynamics and suggest that the lack of lotic chironomid communities would alter the processing of detrital carbon dynamics. The microbial metabolism associated with decomposing leaf litter was influenced by both litter quality and small sized invertebrate activity.

According to our results, microbial activity and the Chironomidae larvae fulfil an important role in the decomposition of allochthonous organic matter and consequently in the functioning of large river-floodplain ecosystems.

In general, we may conclude that leaf litter breakdown rates and the associated nutrient dynamics are affected by the nutrient availability, consumer activity and hydrogeomorphic site conditions.

Our results support the idea that the tree species composition of floodplain forests affects terrestrial-aquatic linkages through the quality of leaf litter entering aquatic detritus based food webs and the notion that taking these factors into account may contribute to a better understanding of the nutrient dynamics of river-floodplain ecosystems.

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586

587 Table 1 Water chemistry of the sites (mean±1SE, n=3) and Anova results

		Site 1		Site 2		one-way Anova		
Site		Mean	*SD*	Mean	*SD*	D.F.	F	p value
T	°C	13.9	*4.8*	14.0	*4.8*	1, 4	0.000	p>0.05
pH		8.2	*0.7*	8.2	*0.7*	1, 4	0.000	p>0.05
Cond.	µS cm^{-1}	387.3	*61.3*	402.3	*64.9*	1, 4	0.786	p>0.05
NO_3N	mg l^{-1}	1.8	*0.6*	1.9	*0.8*	1, 4	0.823	p>0.05
DON	mg l^{-1}	0.5	*0.6*	0.3	*0.9*	1, 4	0.013	p>0.05
PN	mg l^{-1}	0.2	*0.1*	0.2	*0.1*	1, 4	1.000	p>0.05
TN	mg l^{-1}	2.6	*0.2*	2.4	*0.4*	1, 4	0.543	p>0.05
PO_4P	µg l^{-1}	10.1	*10.8*	10.3	*8.4*	1, 4	0.279	p>0.05
DOP	µg l^{-1}	21.2	*6.0*	13.8	*1.4*	1, 4	1.519	p>0.05
TP	µg l^{-1}	132.1	*81.9*	97.5	*13.4*	1, 4	0.651	p>0.05
DIC	mg l^{-1}	33.0	*5.5*	33.0	*5.4*	1, 4	0.000	p>0.05
DOC	mg l^{-1}	6.5	*1.4*	7.0	*1.7*	1, 4	0.206	p>0.05
POC	mg l^{-1}	1.0	*0.1*	0.7	*0.3*	1, 4	3.226	p>0.05
TC	mg l^{-1}	41.3	*6.4*	41.7	*6.8*	1, 4	0.007	p>0.05
SPM	mg l^{-1}	34.8	*28.5*	19.1	*8.8*	1, 4	0.832	p>0.05
Chl-a	µg l^{-1}	56.8	*42.2*	42.0	*28.3*	1, 4	1.710	p>0.05

588

589

590 Table 2 Initial quality indices of leaf litter (mean±1SE, n=3; significant differences ($p<0.05$)
591 are indicated by different letters), the C, N, P concentrations are given in mg g^{-1} and the ratios
592 are molar ratios

		Site 1			Site 2		
		Fraxinus	Populus	Salix	Fraxinus	Ulmus	Quercus
C	Mean	475.50 ^{ab}	472.72 ^{ab}	475.66 ^{ab}	491.14 ^{b}	463.08 ^{a}	478.79 ^{ab}
	SE	3.76	3.19	11.55	24.34	1.95	4.99
N	Mean	23.67 ^{bc}	8.52 ^{a}	19.75 ^{b}	26.59 ^{c}	12.13 ^{a}	13.98 ^{a}
	SE	0.36	0.20	1.09	5.31	0.15	0.30
P	Mean	1.18 ^{b}	0.57 ^{a}	1.24 ^{b}	1.16 ^{b}	0.71 ^{a}	1.62 ^{c}
	SE	0.01	0.03	0.03	0.00	0.04	0.17
C:N	Mean	23.4 ^{a}	64.8 ^{d}	28.1 ^{b}	21.9 ^{a}	44.6 ^{c}	40.0 ^{c}
	SE	0.5	1.1	0.8	3.0	0.5	0.6
C:P	Mean	1045.9 ^{a}	2168.5 ^{b}	997.9 ^{a}	1095.4 ^{a}	1729.0 ^{b}	777.3 ^{a}
	SE	47.9	303.7	111.4	66.2	375.8	123.4
N:P	Mean	44.6 ^{bc}	33.5 ^{b}	35.5 ^{bc}	50.8 ^{c}	38.7 ^{bc}	19.5 ^{a}
	SE	1.2	4.7	4.7	10.1	8.0	3.2

593

Table 3 Pearson's correlations of initial litter quality parameters (symbol meanings: $p<0.05$ *, $p<0.001$ ***, ns - non significant, leach - the amount of AFDM or nutrients leached)

	$C:N_{initial}$		$C:P_{initial}$		$N:P_{initial}$	
k_{AFDM}	-0.30	ns	0.19	ns	0.66	***
$AFDM_{leach}$	0.07	ns	0.24	ns	0.17	ns
N_{leach}	0.08	ns	0.30	*	0.40	*
C_{leach}	0.04	ns	0.34	ns	0.40	*
P_{leach}	0.09	ns	-0.23	ns	-0.38	*

597 Table 4 Mesh size and site (S1, S2) effects on the litter breakdown rates (k) (mean±1SE, n=3;

598 symbol meanings: $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***, ns-non significant, W_0-initial mass)

Site a.	Species	Mesh mm	Mesh effect	k day^{-1}	SE	W_0	SE
S1	Populus	0.04	ns	0.0105	0.0018	86.49	2.93
		1.00		0.0100	0.0015	91.30	0.53
	Salix	0.04	ns	0.0096	0.0096	90.23	1.29
		1.00		0.0102	0.0015	93.57	1.93
S2	Fraxinus	0.04	*	0.0156	0.0018	87.94	0.38
		1.00		0.0211	0.0043	92.18	2.40
	Ulmus	0.04	**	0.0131	0.0011	91.23	2.04
		1.00		0.0196	0.0017	89.54	1.95
	Quercus	0.04	***	0.0051	0.0002	95.47	1.08
		1.00		0.0068	0.0001	98.90	0.81
b.			Site effect				
S1	Fraxinus	1.00	*	0.0140	0.0010	90.17	2.27
S2		1.00		0.0211	0.0043	92.18	2.40

599
600

601 Table 5 ANOVA results of litter breakdown rates and of % AFDM, N and P remaining (a.
602 species, mesh, time effects; b. site and time effects)

Measure	Effect	DF	F	p	DF	F	p
a.		Site 1			Site 2		
3-way Anova							
% AFDM	Species (Sp.)	1,32	5.33	0.0275	2,48	126.16	0.0000
	Mesh	1,32	6.16	0.0185	1,48	6.52	0.0139
	Time	3,32	333.41	0.0000	3,48	431.68	0.0000
	Sp. x Mesh	1,32	1.14	0.2928	2,48	3.01	0.0587
	Sp. x Time	3,32	1.07	0.3089	6,48	19.11	0.0000
	Mesh x Time	3,33	13.89	0.0000	3,48	7.54	0.0003
	Sp. x Mesh x Time	3,33	0.16	0.9194	6,48	0.60	0.7303
% N remaining	Species	1,32	11.72	0.0017	2,48	119.97	0.0000
	Mesh	1,32	6.45	0.0162	1,48	0.02	0.8861
	Time	3,32	40.23	0.0000	3,48	25.37	0.0000
	Sp. x Mesh	1,32	10.11	0.0033	2,48	7.33	0.0017
	Sp. x Time	3,32	15.18	0.0005	6,48	27.96	0.0000
	Mesh x Time	3,32	14.38	0.0000	3,48	12.20	0.0000
	Sp. x Mesh x Time	3,32	3.08	0.0412	6,48	1.91	0.0985
% P remaining	Species	1,32	10.35	0.0030	2,48	22.46	0.0000
	Mesh	1,32	34.85	0.0000	1,48	10.02	0.0027
	Time	3,32	32.38	0.0000	3,48	6.97	0.0005
	Sp. x Mesh	1,32	1.52	0.2264	2,48	0.24	0.7910
	Sp. x Time	3,32	8.23	0.0073	6,48	5.04	0.0103
	Mesh x Time	3,32	10.75	0.0000	3,48	2.72	0.0550
	Sp. x Mesh x Time	3,32	1.88	0.1520	6,48	1.22	0.3122
2-way ANOVA							
k_{AFDM}	Sp.	1, 8	0.14	0.7164	2,12	60.46	0.0000
	Mesh	1, 8	0.01	0.9453	1,12	21.35	0.0006
	Sp. x Mesh	1, 8	0.35	0.5723	2,12	2.20	0.1530
b.		Comparison of S1, S2					
% AFDM	Site	1,16	1.44	0.2470			
	Time	3,16	128.99	0.0000			
	Site x Time	3,16	5.26	0.0103			
% N remaining	Site	1,16	6.02	0.0260			
	Time	3,16	72.80	0.0000			
	Site x Time	3,16	1.51	0.2501			
% P remaining	Site	1,16	17.94	0.0006			
	Time	3,16	12.69	0.0002			
	Site x Time	3,16	9.18	0.0009			

603

604 Table 6 Pearson's correlation of chironomid densities

Chironomidae	k_{AFDM}	$AFDM_{total\ loss}$	$N_{total\ loss}$	$N:P_{initial}$	$C:N_{initial}$
ind. bag^{-1}	r=0.49	0.48	0.58	0.45	-0.30
	p<0.05	p<0.05	p<0.05	p=0.06	p=0.22
ind. g_{AFDM}^{-1}	r=0.77	0.67	0.75	0.54	-0.44
	p<0.001	p<0.01	p<0.001	p<0.05	p=0.07

605

606 Table 7 Pearson's correlation of microbial activities (symbol meanings: p<0.05 *, p<0.01 **,

607 p<0.001 ***, ns - non significant)

	ETS-activity		Ergosterol	
	2day	62day	2day	62day
k_{AFDM}	0.29	0.29	-0.29	-0.55
	ns	ns	ns	***
$AFDM_{leached}$	-0.36	0.17	0.30	-0.17
	*	ns	ns	ns
$C_{leached}$	-0.49	0.25	0.39	-0.27
	**	ns	*	ns
$AFDM_{total\ loss}$	-0.44	0.12	0.26	-0.58
	**	ns	ns	***
$N_{total\ loss}$	-0.46	0.12	0.21	-0.60
	**	ns	ns	***
$C_{total\ loss}$	-0.36	0.24	0.26	-0.60
	*	ns	ns	***
$C:N_{initial}$	0.24	-0.23	0.33	0.55
	ns	ns	ns	***
$C:P_{initial}$	-0.15	0.08	0.41	0.21
	ns	ns	*	ns
$N:P_{initial}$	-0.62	0.41	0.14	-0.56
	***	*	ns	***

608

609

610 Table 8 Leaching losses observed in this study compared with those observed in other studies

Species	Time	Pre-drying	Leaching loss	Site	Reference
Quercus alba	24 h	air dried	5%	Augusta Creek	Petersen & Cummins (1974)
Populus tremuloides	24 h	air dried	19%	Augusta Creek	Petersen & Cummins (1974)
Fraxinus nigra	24 h	air dried	11%	Augusta Creek	Petersen & Cummins (1974)
Salix lucida	24 h	air dried	23%	Augusta Creek	Petersen & Cummins (1974)
Ulmus americana	72 h	air-dried	19%	laboratory experiment	Bärlocher (1992)
Salix fragilis	24 h	air-dried	25%	laboratory experiment	Gessner & Schwoerbel (1989)
Populus nigra	72 h	oven-dried 40°C	25%	River Rhône side arm	Chergui & Pattee (1990)
Salix sp.	72 h	oven-dried 40°C	26%	River Rhône side arm	Chergui & Pattee (1990)

611

612 Table 9 Litter breakdown rates in this study compared with those observed in other studies
613

Species	Mesh mm	Decomposition period, days	Site	k day^{-1}	References
Salix alba	2	185	River Garonne	0.0050	Chauvet (1987)
Salix alba	2	140	River Garonne	0.0091	Baldy et al. (1995)
Salix triandra	0.5	61	Schelde estuary	0.0059	Lecerf et al (2008)
Salix alba	1	62	side arm of River Danube	0.0102	This study
Salix alba	0.04	62	side arm of River Danube	0.0096	This study
Populus nigra	2	185	River Garonne	0.0054	Chauvet (1987)
Populus nigra	2	140	River Garonne	0.0070	Baldy et al. (1995)
Populus nigra	0.5	80	channel of River Tagliamento	0.0083	Langhans et al. (2008)
Populus nigra	0.5	102	floodplain pond of River Tagliamento	0.0047	Langhans et al. (2008)
Populus nigra	10	80	channel of River Tagliamento	0.0188	Langhans et al. (2008)
Populus nigra	10	102	floodplain pond of River Tagliamento	0.0051	Langhans et al. (2008)
Populus hybrids	1	62	side arm of River Danube	0.0100	This study
Populus hybrids	0.04	62	side arm of River Danube	0.0105	This study

Table legends

Table 1 Water chemistry of the sites S1 and S2 and Anova results

Table 2 Initial quality indices of leaf litter (mean±1SE, n=3; significant differences ($p<0.05$) are indicated by different letters), the C, N, P concentrations are given in mg g^{-1} and the ratios are molar ratios

Table 3 Pearson's correlations of initial litter quality parameters (symbol meanings: $p<0.05$ *, $p<0.001$ ***, ns - non significant, leach - the amount of AFDM or nutrients leached)

Table 4 Mesh size and site (S1, S2) effects on the litter breakdown rates (k) (mean±1SE, n=3; symbol meanings: $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***, ns - non significant, W_0-initial mass)

Table 5 ANOVA results of litter breakdown rates and of % AFDM, N and P remaining (a. species, mesh and time effects, b. site and time effects)

Table 6 Pearson's correlation of chironomid densities

Table 7 Pearson's correlation of microbial activities (symbol meanings: $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***, ns - non significant)

Table 8 Leaching losses observed in this study compared with those observed in other studies

Table 9 Litter breakdown rates in this study compared with those observed in other studies

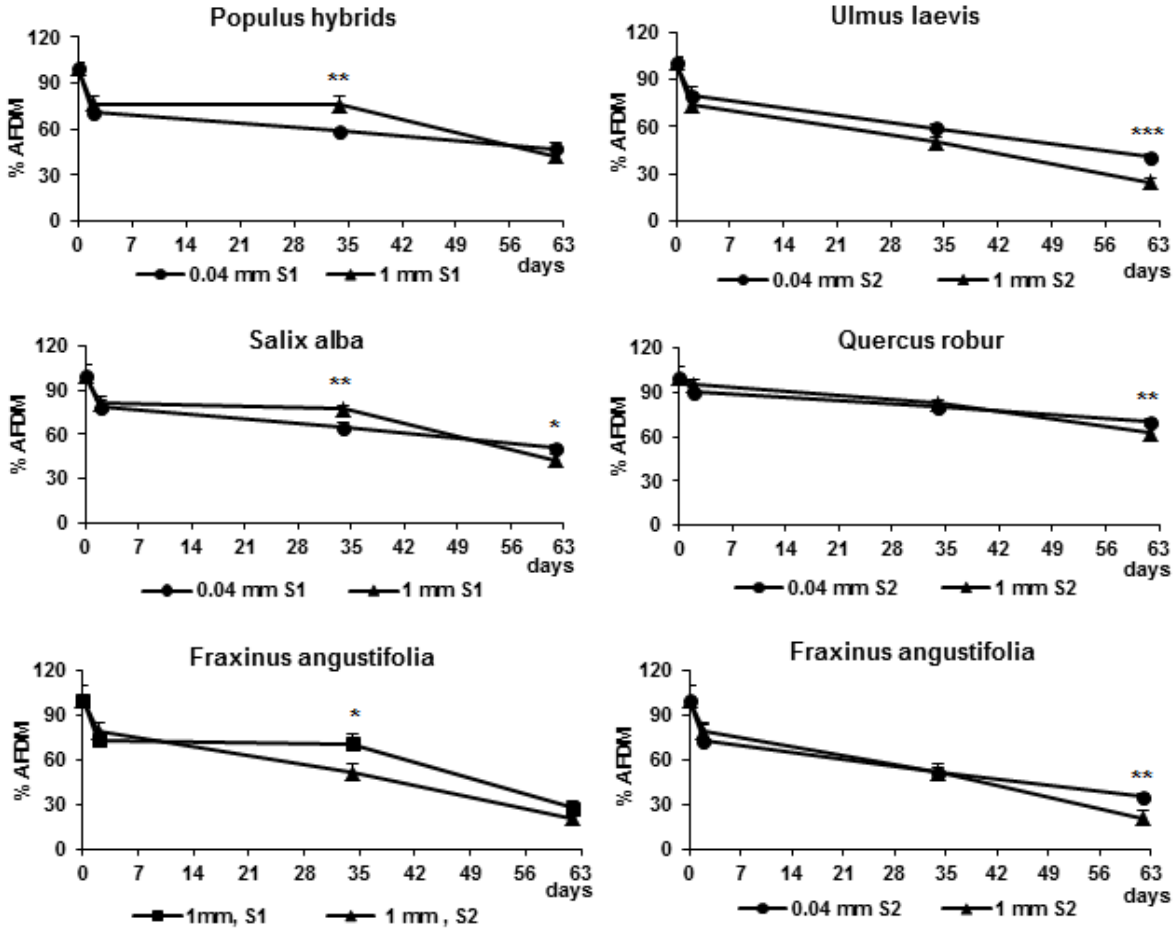
Figure captions

Figure 1 Mesh size and site (S1, S2) effects on the % of remaining ash free dry mass (AFDM) (mean±1SE, n=3; symbol meanings: $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***)

Figure 2 Mesh size and site (S1, S2) effects on the % N and P leached and remaining on 62 day (mean±1SE, n=3; significant differences, $p<0.05$ are indicated by different letters)

Figure 3 Chironomid larval densities in litter bags with 1 mm mesh size (mean±1SE, n=3, significant differences ($p<0.05$) are indicated by different letters)

638 Figure 4 Mesh size and site (S1, S2) effects on respiratory electron transport system (ETS)
639 activity (mean±1SE, n=3; symbol meanings: $p<0.05$ *, $p<0.01$ **)
640 Figure 5 Mesh size and site (S1, S2) effects on fungal biomass (mean±1SE, n=3; symbol
641 meanings: $p<0.05$ *, $p<0.01$ **)
642
643



644

645 Figure 1 Mesh size and site (S1, S2) effects on the % of remaining ash free dry mass (AFDM)

646 (mean±1SE, n=3; symbol meanings: $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***)

647

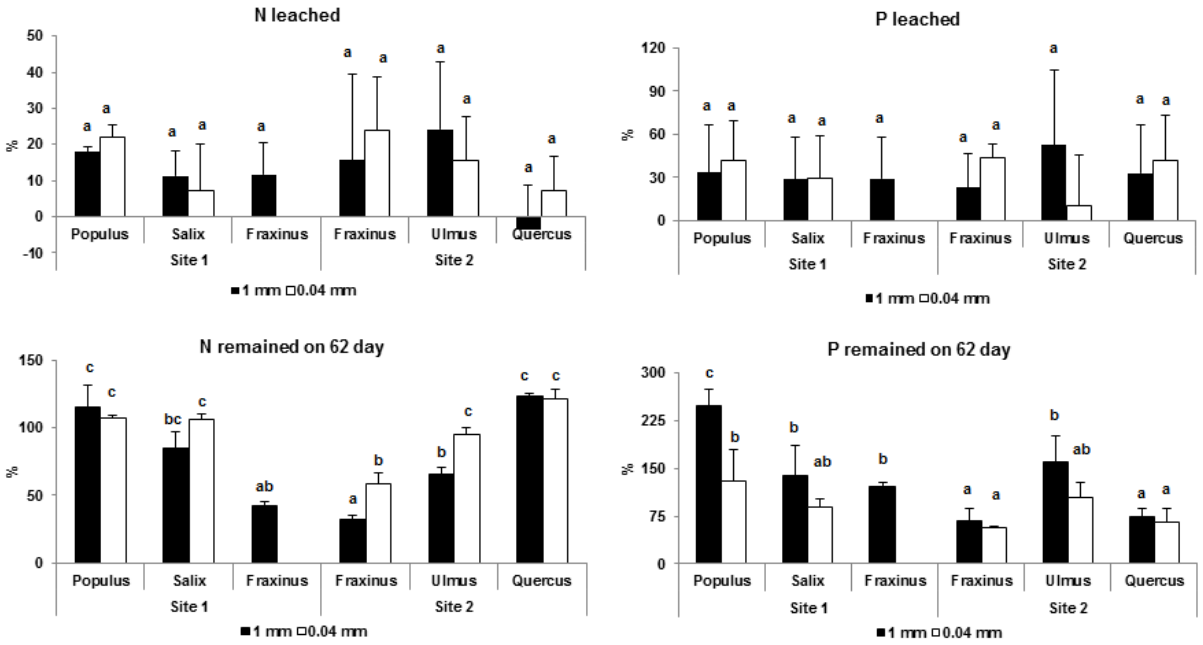
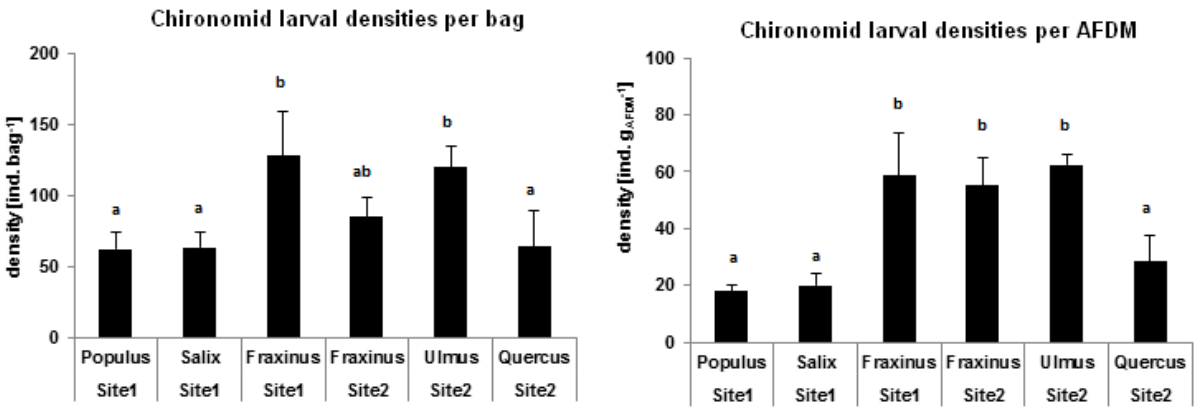


Figure 2 Mesh size and site (S1, S2) effects on the % N and P leached and remaining on 62 day (mean±1SE, n=3; significant differences, $p<0.05$ are indicated by different letters)

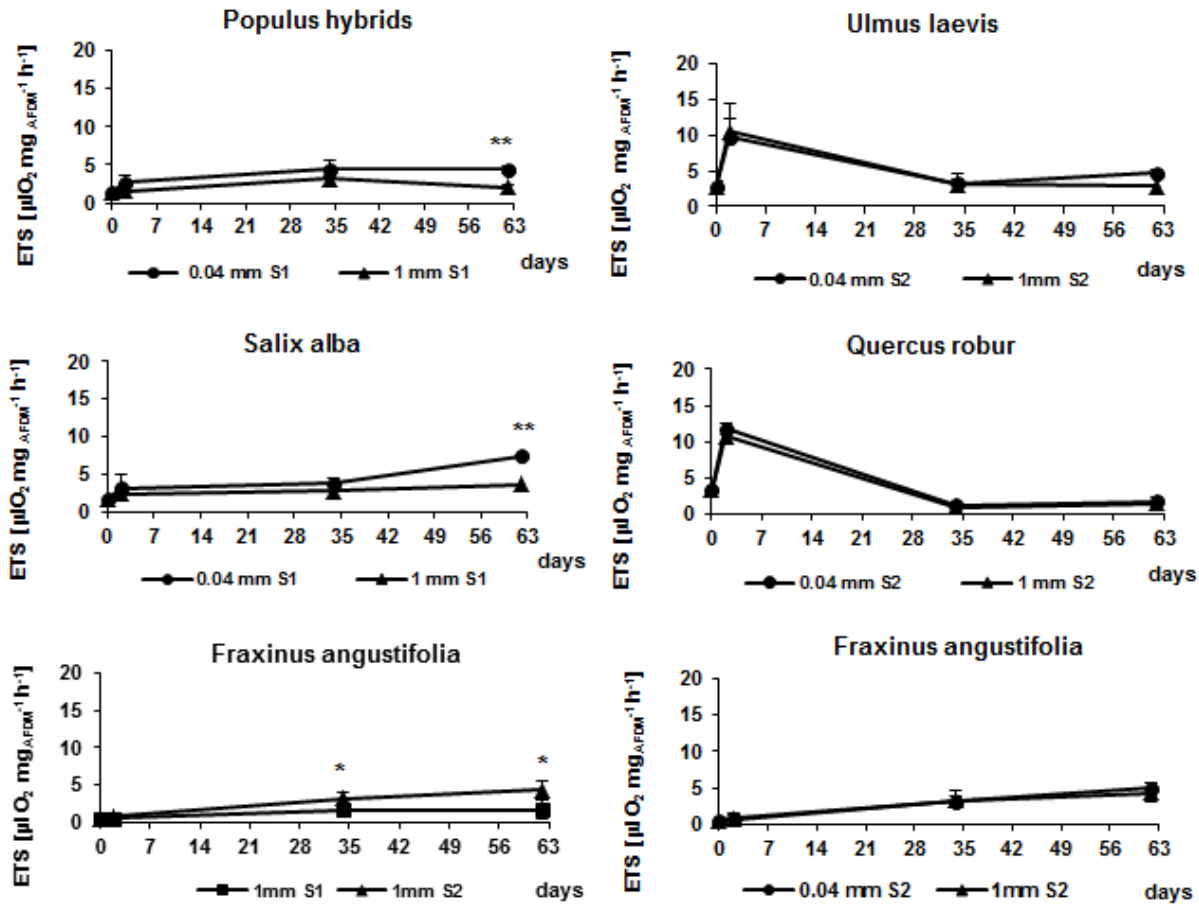


652

653 Figure 3 Chironomid larval densities in litter bags with 1 mm mesh size (mean±1SE, n=3,

654 significant differences ($p<0.05$) are indicated by different letters)

655

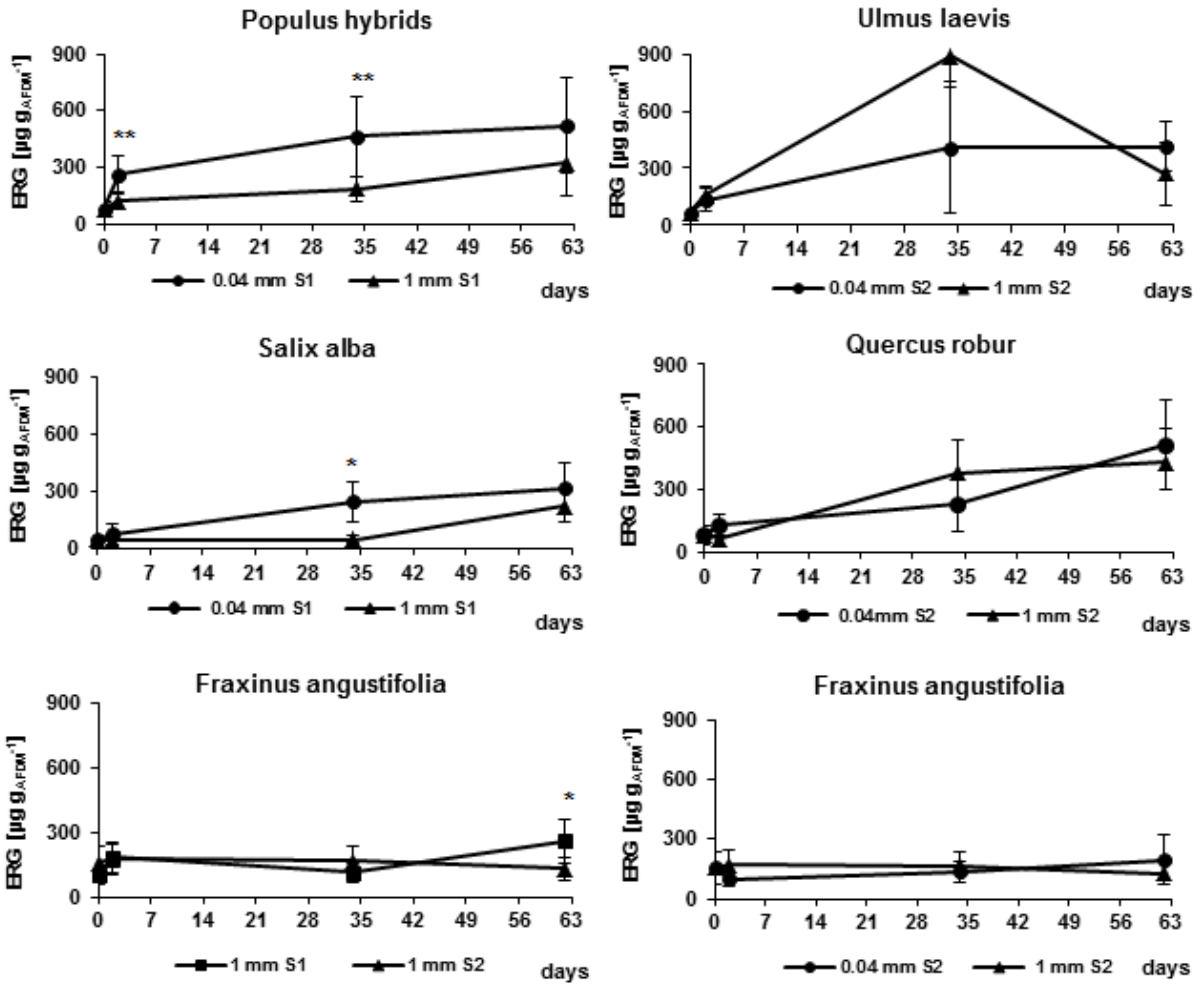


656

657 Figure 4 Mesh size and site (S1, S2) effects on respiratory electron transport system (ETS)

658 activity (mean±1SE, n=3; symbol meanings: $p<0.05$ *, $p<0.01$ **)

659



660

661 Figure 5 Mesh size and site (S1, S2) effects on fungal biomass (mean±1SE, n=3; symbol

662 meanings: $p<0.05$ *, $p<0.01$ **)

663