Landscape-scale controls of litter decomposition in streams

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Summary

Decomposition of leaf litter is a key process in stream ecosystems and one that has been the focus of a considerable body of research. Much of this research has found that decomposition is sensitive to many common human activities and recently ecologists have suggested that decomposition rates could prove useful as a process-based means of assessing the condition of stream ecosystems. In order to be effective in detecting anthropogenic impacts, knowledge of the spatial variability of this process is needed so that natural variability can be distinguished from human impacts on decomposition rate. This dissertation, presented in 5 chapters, describes spatial patterns of variability in leaf decomposition rates in streams, and implicates some of its causes.

Despite a large number of studies that quantify litter decomposition rates in streams, very few are conducted at scales other than the scale of stream riffle, and assessing large scale patterns in decomposition rates is hampered by inconsistencies among individual studies. Chapter 1 identifies large scale patterns in decomposition across three different spatial scales spanning 5 orders of magnitude: 4th order watersheds, 3rd order streams nested within those watersheds, and riffles nested within those streams. Results show that variability in decomposition rates depend on the scale at which they are measured, tending to increase with decreasing spatial scale. A comparison of leaf decomposition in coarse and fine mesh leaf bags indicates that the observed spatial patterns were driven largely by invertebrates, rather than microbes, the influence of which was highly consistent across the three spatial scales examined.
The flowing water habitats of riverine floodplains often constitute a relatively small percentage of total floodplain area. Very often habitats such as off-channel ponds, bare gravel and vegetated island are much more abundant on a per area basis. Despite this, very little research has assessed litter decomposition in riverine floodplain habitats other than flowing waters. Chapter 2 presents a comparison of decomposition rates across common habitats found on the floodplain in the braided reach of an alpine river. Decomposition rates were fastest in flowing water habitats, slowest in terrestrial sites, and intermediate in still water habitats. Differences in the decay rates between coarse- and fine-mesh litter bags was consistently small across all habitats, suggesting that, unlike the results of Chapter 2 which were driven largely by invertebrates, patterns were largely driven by microbial activity.

Investigations of litter decomposition rates are usually conducted within individual stream riffles and high variability in decomposition rates are often observed. Chapter 3 seeks to identify one possible cause of this variability by contrasting decomposition rates among patches of upwelling groundwater vs. downwelling surface flow across 3 seasons. Downwelling at riffle heads and upwelling at the riffle tail is a common feature of riffles. In the summer upwelling patches had slower decomposition rates relative to other areas of the channel, but no differences between upwelling patches and other areas of the channel were observed during the autumn or winter. Temperature is the likely driving factor in the observed differences. When using leaf decomposition as a means of bioassessment, within riffle variability, as a source of statistical noise, can be minimized by 1) placing leaf bags only in upwelling or downwelling areas, or 2) conducting the assessment only
during the autumn when differences in decay rates between upwelling and downwelling sites are not large or 3) using temperature corrected decomposition rates.

Numerous studies have observed rapid leaf decomposition in situations of limited leaf resources (e.g., pasture streams, grassland streams), suggesting that the quantity of leaves present in stream channels can influence decomposition rates. Chapter 4 presents a manipulative field experiment in which the quantity of leaf litter in stream channels is altered and the response of leaf decomposition rates measured. In instances where leaf litter was removed from stream channels, there was a tendency that an important litter consuming invertebrate, *Gammarus*, aggregated in experimental leaf packs and accelerated decomposition rates relative to controls reaches, and to reaches where litter quantity was experimentally enhanced. Overall, however, and despite large differences in the quantities of leaf litter among treatments, the differences on decomposition rates observed were not large, suggesting that the amount of litter present in the stream channel is not a source of large variability in decomposition rates.

Unlike the first four chapters which attempt to identify spatial patterns of litter decomposition in the landscape, the 5th and final chapter details the use of cotton strips as a surrogate for leaves in decomposition experiments, and tests the appropriateness of the method. Cotton consists of nearly 100% cellulose, a key structural component of most leaf litter. In this regard cotton is similar to natural leaves, but unlike natural leaves, the chemical make-up of which is highly variable both within and among species, cotton can be manufactured in a highly standardized fashion. The suitability of cotton as a surrogate for leaves was assessed by comparing
their relative decay rates when both materials were exposed to differing environmental conditions. Cotton strip decay, measured as loss of tensile strength, broadly tracked patterns of leaf decay (measured as leaf mass loss) across the contrasting riverine habitats examined in Chapter 2, suggesting that, under some circumstances, cotton strips may be a useful substitute for leaf material in decomposition experiments conducted in streams. Differences in decomposition rates between coarse- and fine-mesh bags were minor, suggesting that decomposition performed by invertebrates was minimal and that the patterns observed were caused by microbial activity.

Overall results suggest that natural variability in decomposition rates need not be great and therefore it should not jeopardize the use of decomposition rates for stream assessment. This is especially true of microbial decomposition rates which appear to be highly consistent across reference conditions (Chapter 1), and yet, can be very sensitive to environmental variability, such as that observed in Chapters 2 and 3. Given that invertebrates were not important in the decay of cotton strips (Chapter 5), cotton may prove useful as a standardized means of assessing microbial decomposition, and potentially human impacts to decomposition.
Zusammenfassung


Trotz zahlreicher Untersuchungen, die Streuabbauraten in Fliessgewässern quantifiziert haben, sind die meisten in kurzen, schnellfließenden Bachabschnitten (riffles) durchgeführt worden. Nur in wenige Untersuchungen wurden andere räumliche Massstabebenen betrachtet. Darüber hinaus ist die Beurteilung grossmassstäblicher Muster dadurch erschwert, dass verschiedene Arbeiten unterschiedliche Methoden verwendet haben.

Das erste Kapitel der vorliegenden Arbeit zeigt räumliche Muster von Abbauraten auf drei Massstabebenen, die fünf räumliche Grössenordnungen umfassen: Einzugsgebiete von Fliessgewässern vieter


In verschiedenen Untersuchungen wurde festgestellt, dass der Laubabbau bei geringer Verfügbarkeit von Streu in Fliesgewässern beschleunigt abläuft (z.B. in Gewässern, die durch Weide- oder Grünland fliessen).

(gemessen als Verlust der Reissfestigkeit) in den verschiedenen Auhabitaten, die in Kapitel 2 vorgestellt wurden. spiegelten die gleichen groben räumlichen Muster wider wie die gleichzeitig bestimmten Abbauraten natürlicher Laubstreu (gemessen als Verlust von Blattmasse). Dies deutet darauf hin, dass Baumwollgewebe in Abbaueperimenten in Fliessgewässern in einigen Fällen ein nützliches Ersatzsubstrat für Laubstreu darstellt. Unterschiede zwischen den in grobmaschigen und feinmaschigen Netzeuteln gemessenen Abbauraten waren minimal, was für einen geringen Einfluss wirbeloser Tiere auf den Abbau spricht. Die beobachteten räumlichen Muster in den Abbauraten waren deshalb vermutlich primär auf mikrobielle Aktivität zurückzuführen.

Insgesamt weisen die Ergebnisse der vorliegenden Arbeit darauf hin, dass unter klar definierten Bedingungen die natürliche Variabilität der Streuzersetzungsrate eng begrenzt ist. Natürliche Variabilität sollte deswegen für die Verwendung von Streuabbauuntersuchungen in Fliessgewässerbewertungen kein Hindernis darstellen. Das gilt vor allem für die Bestimmung mikrobieller Abbauraten, die sich in einer Reihe von Referenz-Untersuchungsstellen als sehr gut reproduzierbar erwiesen (Kapitel 1). Gleichzeitig können Abbauraten sehr empfindlich auf veränderte Umweltbedingungen reagieren, wie in Kapitel 2 und 3 dargelegt wurde. Da wirbellose Tiere in der in Kapitel 5 dargestellten Untersuchung für die Zersetzung von Baumwollgewebe weitgehend unbedeutend waren (Kapitel 5), kann Baumwollgewebe in solchen Situationen ein nützliches standardisiertes Material darstellen, um mikrobielle Abbauraten zu bestimmen und möglicherweise auch, um menschliche Einflüsse auf Abbauprozesse festzustellen.
Introduction

Freshwater ecosystems have been increasingly modified from their historic condition by human activities and these changes often have unintended and undesirable consequences such as reduced biodiversity, altered ecosystem functioning, and losses of ecosystem services (Tockner and Stanford 2002; Covich et al. 2004; Dudgeon et al. 2006). Unprecedented levels of resources have recently been allocated to reverse this trend through the implementation of measures such as ecological restoration (Bernhardt et al 2005; Palmer and Allan 2006). An important initial step towards successful restoration is identification of impacted systems and standardized approaches have been developed to assess the condition of freshwater ecosystems (Bonada et al. 2006). Among these approaches is bioassessment which makes use of organisms and their activities to evaluate ecological condition (e.g., EPA Rapid Bioassessment Protocols in the USA). Bioassessment offers numerous advantages over measuring the physical and chemical aquatic environment directly, for example it integrates human impacts through time, across trophic levels, and thus is often less expensive than chemical or physical analysis of the environment.

Bioassessment can be broadly classified into two categories: structural assessment typically evaluates the taxonomic composition of communities (e.g., species richness, diversity), while functional assessment evaluates ecosystem level processes (e.g., respiration, production). Unlike lakes, in which functional bioassessment strategies are routinely used to determine ecological status (e.g., algal community
composition and primary production), bioassessment in streams is based almost exclusively on structural attributes of the stream ecosystem (e.g., macroinvertebrate community indices). This focus on structural attributes and the relative neglect of process-based assessment has been explained by separate traditions among lotic and lentic ecologists (Gessner and Chauvet 2002). Reliance on structural attributes could provide a skewed perspective of stream condition and while there have been calls for using process-based bioassessment (e.g., EU Water Framework Directive), such tools are just now being developed (Young 2006).

Among the qualities that an ecosystem process should have in order to qualify as a candidate for assessing the ecological condition of streams is sensitivity to human impacts. Litter decomposition – a key ecosystem-level process in streams – meets this key criterion in many situations. Litter decomposition responds to mine runoff (Schlief and Mutz 2006, Niyogi et al. 2001), eutrophication (Young and Huryn 1999), highway runoff (Maltby et al. 1995), invasion of exotic species (Graça et al. 2002), and alterations of land use such as timber harvest (Benfield et al. 2001), and agriculture (Hagen et al. 2006), among other anthropogenic activities (Gessner and Chauvet 2002). A second and less understood prerequisite for using litter decomposition as means of bioassessment is that natural spatial variability in decomposition rates be quite low, so that any differences observed, for example, upstream and downstream of wastewater treatment facilities, can be attributed to the human impact of interest, and not natural variability. Stream ecosystems are generally regarded as being highly variable, and this variability, if not accounted for, could threaten the utility of litter decomposition as an assessment tool.
In response to the need for better understanding of the spatial variability of litter decomposition as a key ecosystem-level process, a series of field investigations was conducted. The aim of the studies in this dissertation, presented in 5 chapters, was to identify spatial patterns of decomposition in the landscape, and identify some of the causes of these patterns. All studies made use of a leaf-bag approach in which a known mass of leaf material is introduced to the field site of interest and later retrieved and re-weighed to determine rates of mass loss.

Most litter decomposition experiments have been conducted at small spatial scales in small streams, and little is known about how decomposition rates vary across the larger spatial scales in which ecologists are often interested and which are often most relevant for ecosystem management. Chapter 1 assesses patterns of leaf decomposition across 3 different spatial scales spanning approximately 5 orders of magnitude: 3 fourth-order watersheds, 3 third-order streams nested within each of those watersheds, and 4 riffles within those streams.

Streams and rivers often constitute a small percentage of the floodplain through which they flow. Riparian forests, areas of bare gravel, and lentic water bodies are often more abundant on a per area basis, and yet very little research has examined the decomposition rates in these habitats. Chapter 2 presents a comparison of the decomposition rates across the diverse habitats of the floodplain of a large, near-natural river with the aim of identifying hot and cold spots of decomposition.

Vertical hydrologic exchange in streams, that is, exchange between surface flow and groundwater, is a common feature of stream ecosystems. The water quality of surface flow and groundwater often differs in ways
that may influence decomposition rates. Chapter 3 presents a test of the hypothesis that during the summer, patches of upwelling groundwater, being lower in temperature relative to surface flow, would support relatively slower decomposition rates. By contrast, in the autumn, a season with minimal thermal differences between upwelling and downwelling water, decomposition rates would not differ.

The quantity of resources available to an ecosystem is a key factor that controls distribution of organisms which can in turn influence ecosystem processes. Chapter 4 is a presentation of an experiment in which the quantity of leaf resources available to the stream ecosystem was manipulated and the response of the local abundance of stream macroinvertebrates, and the influence of macroinvertebrates on litter decomposition rates was assessed. In stream reaches where litter was excluded, invertebrates were expected to aggregate in experimental leaf packs and accelerate decomposition relative to controls. The converse situation was anticipated in stream reaches where litter quantities were elevated relative to controls: invertebrates would be dispersed within the reach and decomposition in experimental leaf packs would be slowed relative to controls.

The fifth and final chapter of this dissertation is an evaluation of cotton strips as a substitute for natural leaves in decomposition experiments. Because variability in the decomposition rates within and among leaf species is often large, and because few studies use the same batch of leaf material in their experiments, a standardized, decomposable substrate is needed for broader synthesis. An important consideration for using cotton strips as surrogate for leaves is that they behave similarly to leaves when exposed to different environmental conditions, and an experiment
was designed to evaluate this prerequisite. This evaluation consisted of placing cotton strips together with leaves in the same habitats as in the experiment described above in Chapter 2 and assessing to what extent patterns in cotton-strip decay tracked those of leaf decay.

Collectively results of this dissertation suggest that when controlling for a few large-scale variables, such as vertical hydrologic exchange, levels of natural variability in litter decomposition rates are not necessarily high, and this variability should not jeopardize the use of litter decomposition as a means of assessing the ecological condition of streams. Lastly, cotton strips hold promise as a standardized, comparative method of evaluating the ecological condition of stream ecosystems which, unlike natural leaf material, can be readily be applied to large-scale, long-term studies.

Literature Cited


Chapter 1

Spatial Patterns of Leaf Decomposition in Streams

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Abstract

The physical, chemical and thermal environments of stream ecosystems are highly variable across space at a wide range of scales. The food webs of streams rely heavily on allochthonous plant litter. Much research has been devoted to litter decomposition, largely restricted to field experiments conducted in single streams and short stream reaches, whereas spatial variability of decomposition rates has been given little attention. Despite this lack of attention, spatial variability has potentially important ramifications for the structure and functioning of stream ecosystems, as well as experimental and applied research. In response, we used a leaf-bag approach to conduct two experiments exploring the spatial variability of leaf decomposition rates. In the first a hierarchical experimental design was used to investigate decomposition across three spatial scales spanning five orders of magnitude. In each of 4 replicate 4th-order watersheds in the Black Forest of Germany we selected three 3rd-order streams. Each of the 12 streams contained four replicate riffles in which we installed four coarse- and fine-mesh bags (384 bags in total), which respectively allow and prevent access to the leaves of Populus nigra by macroinvertebrates. In the second experiment we examined whether decomposition rates vary along a stream size gradient ranging from 1st to 4th order streams in 16 streams. In the first experiment, mean decomposition rates were highly consistent among all four watersheds (an overall range of less than 3%) for both mesh types. Significant differences in decomposition rates were observed among streams and riffles in coarse-mesh bags, although the differences were not large. Decomposition rates in fine-mesh bags did not vary at any spatial scale, despite low within-group variability. This discrepancy between mesh types suggests that patchy distribution of macroinvertebrate feeding
accounts for observed differences in decomposition, whereas the more homogeneous distribution of microbial decomposition highly predictable. Results show that 1) variability of leaf decomposition depends on the scale at which it is measured, 2) microbial decomposition responds differently to a change in scale than that by invertebrates and 3) across the range we examined, stream size is not an important source of variability. These results bear relevance for experimental research in that they help define the domain of statistical inference from previous research, and in identifying the spatial scales at which decomposition rates are most variable, inform future researchers about the amount of variability that will likely be encountered. Lastly, results suggest that natural variability need not be a hindrance in using leaf decomposition as a means of functional bioassessment.

Keywords: Spatial Variability; Heterogeneity; Stream; Litter Breakdown; Hierarchy; Scale
Introduction

Current understanding of stream ecosystems is rooted in the notion that streams are highly heterogeneous environments (Pringle et al. 1988, Townsend et al. 2003, Frissell et al. 1986; Cooper et al. 1998, 1997; Ward et al. 2002; Thorp et al. 2006; Tockner et al. 2003; Malard et al. 2006). Spatial heterogeneity of the physical, chemical and thermal environment contributes to both structural diversity (e.g., spatial variability in species composition, diversity, food web structure) and functional diversity, defined here as variability within and among ecosystem processes. While spatial heterogeneity is generally considered to be an intrinsic feature of natural streams, it raises fundamental questions for the analysis of ecosystems. For example, how much variability exists within and among streams and at which spatial scale is variability most pronounced? Or, since different processes operate at different spatial scales (Allen & Star 1982; Wiens 1989; Cooper et al. 1998) and given that most field studies are conducted at small spatial scales (Wiens 1989) with how much confidence can results from small-scale studies be used to characterize the processes and patterns that exist at the larger spatial scales in which ecologists and resource managers are often most interested?

In addition to spatial heterogeneity, the key role of allochthonous plant litter in biogeochemical processes and stream food webs is a second prominent theme in stream ecology. Litter functions as habitat and/or food or substrate for invertebrates (Rowe and Richardson 2001; Reice 1991; Chauvet et al. 1993) and microorganisms (Suberkopp 1998). It also is a source of dissolved nutrients and of both dissolved and fine-particulate carbon (Meyer & O'Hop 1983; Gessner 1991), that may be utilized by downstream communities. The quantitative importance of
allochthonous plant litter is illustrated by an estimate suggesting that litter can constitute most of the energy available to stream food webs (Fisher & Likens 1973). As a result, decomposition of terrestrial plant litter, particularly autumn-shed leaves from woody riparian vegetation, constitutes a central component of energy flow in forested streams.

Decomposition of terrestrial leaf litter in streams is largely caused by detritivorous macroinvertebrates referred to as shredders (Petersen & Cummins 1974, Cuffney et al. 1990, Hieber & Gessner 2002), and the activity of heterotrophic microorganisms, particularly a group of fungi known as aquatic hyphomycetes (Suberkropp 1998, Gessner & Chauvet 1994). The individual processes contributing to litter decomposition and the factors regulating decomposition rates are also broadly understood (Webster & Benfield 1986, Gessner et al. 1999). Very little is known, however, about the spatial variability of decomposition (Royer & Minshall 2003, Langhans et al. submitted), despite the ramifications spatial variation may have for the functioning of stream ecosystems and experimental and applied research. The ecological literature is rife with examples of how results of field observations depend on the scale at which they are measured (e.g. Senft et al. 1988; Downes et al. 1993; Crowl et al. 1997; Li et al. 2001; Sherry and Holmes 1988). Research on litter decomposition in streams is typically conducted at a single spatial scale, such as the habitat unit (sensu Bisson & Montgomery 1996), while other spatial scales have been given little attention or no attention. The lack of diversity in the experimental designs of decomposition studies in streams may contribute to a narrow perspective of how decomposition processes vary in nature.
Quantification of spatial variability is needed for at least four reasons. First, knowledge of variability at a given spatial scale provides insight about the domain of statistical inference from field experiments. When variability is low, generalization to other systems from the same statistical population can be performed with greater confidence than when variability is high. A second reason, related to the first, is that quantifying variability across different spatial scales provides information about the degree to which results from small-scale observations can be applied to larger spatial scales (Turner et al 1989). Third, understanding the spatial scales at which structures or processes vary informs researchers how much statistical noise is to be expected at a particular scale and thus how much replication is required to detect a given treatment effect in experiments. Lastly, spatial overlap between dependent and independent variables (i.e., spatial correlation) suggests the potential causality.

Along with these statistical and methodological implications, the spatial variability of litter decomposition rates is highly relevant for stream ecosystem structure and function. Biogeochemical “hot spots” (sensu McClain et al. 2003) have been identified as important features of ecosystems. In the same vein, hot spots of litter decomposition, that is, areas of relatively high decomposition rates, may serve vital ecosystem functions such as providing areas of high nutrient uptake, rapid conditioning of litter to enhance palatability for stream invertebrates shortly after litter enters a stream, and generation of large amounts of fungal spores that serve as inoculum downstream. Conversely, areas characterized by slow decomposition rates, or “cold spots”, may function in protracting resource availability through times of the year when organic matter in streams is limited but still required by the heterotrophic
stream community, such as the late spring in temperate zones. Since litter functions as both food and habitat (or substrate) for macroinvertebrates and other organisms, the degree to which it is decomposed or conditioned constitutes a measure of resource quality and spatial heterogeneity in the degree to which litter is important in maintaining high levels of biodiversity in streams.

Despite the potential importance of spatial variability for ecosystem structure and function, and despite a large body of literature about litter decomposition in streams, the question of how decomposition rates vary within and across streams and watersheds has not been assessed in a systematic manner. In response, we conducted two field experiments. The first assessed decomposition across 3 spatial scales spanning five orders of magnitude: stream riffles, 3rd-order streams, and 4th-order watersheds. The second addressed decomposition along a stream-size gradient that ranged from 1st to 4th order. Contemporary ecological theory predicts a decrease in heterotrophy with increasing stream size with a concomitant change in the macroinvertebrate community that should influence decomposition rates (e.g., Vannote et al. 1980). Results show that variability in decomposition rates was greatest at the smaller spatial scales examined, that overall variability can be modest within a region, and that the component of variability attributable to microbes can be surprisingly minor. No differences in decomposition rates, whether from microbes or invertebrates, were observed among stream sizes. In informing researchers about the amount of variability that can be expected when conducting research at a particular spatial scale, these results suggest that variability need not inhibit the use of litter decomposition as a means to assess functional stream integrity.
Methods

Site Characterization

Two experiments were conducted in streams located in the southern Black Forest in Germany (47° 50' N, 8° 48'E) to determine the spatial variability in litter decomposition. All streams were circumneutral softwater streams and drained catchments of deciduous vegetation. A range of morphological and physico-chemical site characteristics was determined in autumn 2004 to relate patterns of litter decomposition rates to environmental conditions (Table 1). Most variables were measured at each site, but when variables were thought not to vary appreciably at a particular spatial scale (e.g., temperature within a riffle), replicate measurements were not taken at that scale.

Litter-Bag Preparation, Installation and Sample Processing

A litter-bag approach was used to determine leaf decomposition rates. Freshly fallen poplar (Populus nigra) leaves were gathered from the ground in the autumn, transported to the laboratory, and rinsed with lake water to remove adhering debris. The long and easily broken petioles of the P. nigra leaves were removed with scissors. Leaf material was air-dried, weighed into 4.0 ± 0.1 g portions, remoistened with a spray bottle to make the leaves pliant, and enclosed in litter bags. Litter bags were constructed of two mesh types, coarse and fine (10-mm and 0.5-mm mesh size) to allow or prevent access by macroinvertebrates to leaves and thus facilitate estimation of microbial and macroinvertebrate contribution to leaf-mass loss. Five batches of leaves were chosen at random, oven dried.
(105 °C) to constant mass, and weighed while hot to determine their initial moisture content.

Pairs of coarse-mesh and fine-mesh bags were placed in streams and fixed to the stream bed by tying them with string to an iron rod that was hammered into the substrate. Bags were installed in early November of 2004 to coincide with autumnal leaf fall and removed after 47 days when approximately 50% of the initial leaf mass had been lost. Bags were removed by cutting the string and placing each pair of mesh bags into a separate plastic bag. Mesh bags were returned to the laboratory and frozen. The contents of each leaf bag were later placed into a shallow white tray that contained several centimeters of tap water. Both sides of each thawed leaf were gently cleaned with a soft-bristled paint brush to remove adhering debris. After cleaning, leaves were placed in an aluminum tray, dried at 105 °C for 24 hours, and weighed hot to determine percent of the original leaf mass remaining in each litter bag.

Experimental Design

In Experiment 1, a hierarchical experimental design was used to assess the variability of litter decomposition in streams across three spatial scales: 4th-order watersheds, 3rd-order streams within those watersheds, and riffles within those streams (Fig. 1a). These scales approximate the hierarchical river sub-systems described by Frissell et al. (1986). Fourth-order watersheds that appeared to lack strong anthropogenic impact (i.e., intensive agriculture, urbanization, dams upstream, etc.) were identified using 1:50,000 topographic maps. The unimpacted character of all sites was later verified by field reconnaissance and the four most suitable watersheds selected for the experiment. Within each watershed 3
Table 1. Summary of methods used for riffle, stream and watershed characterization.

<table>
<thead>
<tr>
<th>Variable (units)</th>
<th>Scale at Which Replicated</th>
<th>Variable description/methodology</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stream order</td>
<td>Stream</td>
<td>after Strahler (1957); Topographic map (1:50,000)</td>
</tr>
<tr>
<td>Links</td>
<td>Stream</td>
<td>Number of 1st order streams draining to</td>
</tr>
<tr>
<td>Drainage area</td>
<td>Stream</td>
<td>Topographic map (1:50,000)</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>Stream</td>
<td>Topographic map (1:50,000)</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>Stream</td>
<td>Topographic map (1:50,000)</td>
</tr>
<tr>
<td>Perimeter / Area</td>
<td>Stream</td>
<td>Watershed perimeter/drainage area – (1:50,000)</td>
</tr>
<tr>
<td>Riffle length (m)</td>
<td>Riffle</td>
<td>Water velocity</td>
</tr>
<tr>
<td>Temp (°C)</td>
<td>Riffle</td>
<td>Temperature logger, hourly readings</td>
</tr>
<tr>
<td>Channel width</td>
<td>Within</td>
<td>Field measurement, 4 widths /riffle</td>
</tr>
<tr>
<td>Channel depth</td>
<td>Within</td>
<td>Field measurement</td>
</tr>
<tr>
<td>Flow velocity</td>
<td>Within</td>
<td>Velocity meter. 1 reading just above each leaf pack</td>
</tr>
<tr>
<td>NH$_4$-N (μg/l)</td>
<td>Riffle</td>
<td>Indophenol-blue method (Berthelot reaction)</td>
</tr>
<tr>
<td>NO$_2$-N + NO$_3$-N</td>
<td>Riffle</td>
<td>P/N-autoanalyzer</td>
</tr>
<tr>
<td>PN(mg/l)</td>
<td>Riffle</td>
<td>Standard chemical analysis</td>
</tr>
<tr>
<td>PO$_4$-P(μg/l)</td>
<td>Riffle</td>
<td>Molybdenum-blue method</td>
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<td>PP(μg/l)</td>
<td>Riffle</td>
<td>Standard chemical analysis</td>
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<td>pH</td>
<td>Riffle</td>
<td>pH meter</td>
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<td>Conductivity</td>
<td>Riffle</td>
<td>Conductivity meter</td>
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<td>Riffle</td>
<td>Standard chemical analysis</td>
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<td>Ca$^{2+}$ (mg/l)</td>
<td>Riffle</td>
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<tr>
<td>Alkalinity</td>
<td>Riffle</td>
<td>Standard chemical analysis</td>
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</table>
replicate 3rd-order streams were identified and in each stream 4 replicate riffles were nested. The exact position of a first riffle was governed by access to the study stream. Three additional riffles were chosen within the same stream section. These riffles were separated by a distance of between 60 and 80 channel widths from one another with the number of channel widths chosen at random. Four coarse-mesh and 4 fine-mesh litter bags were placed within each riffle. Thus the design consisted of 4 watersheds, 3 streams per watershed, 4 riffles per stream, and 8 litter bags per riffle, corresponding to a total of 384 litter bags.

In Experiment 2, variability of decomposition rates was tested along a stream-size gradient. A single 1st, 2nd, 3rd and 4th order stream (sensu Strahler 1952) was selected in each of the four 4th-order watersheds described above. In each of the four watersheds from Experiment 1, a single 3rd order stream was also used in Experiment 2. Effort was made to ensure spatial independence among streams of different orders by minimizing situations in which an upstream lower-order stream flowed into a larger stream downstream (Fig 1). This was accomplished with two exceptions (Fig. 1): in one watershed, Kleine Wiese, the 3rd-order stream drained into the 4th-order stream, and the 2nd-order stream flowed into the 4th-order stream. Four riffles were identified within each of the selected streams as described above, and in each riffle a single coarse-mesh and fine-mesh bag was placed. Thus there was a total of 16 streams, 4 riffles per stream, 2 bags per riffle, and 128 litter bags.
Fig. 1: Spatial arrangement of the selected study sites across four watersheds. For each pair of numbers, the first indicates stream order, the second the stream name. * indicates the 3rd-order streams that were included in Experiment 2.
**Statistical Analysis**

Data from both experiments were examined for normality (frequency distributions of percent mass remaining) and equal variances (comparison of standard deviations) and deemed suitable for applying parametric statistical tests. To assess the variability in decomposition rates across spatial scales in Experiment 1, nested analysis of variance (ANOVA) was performed on the percentage of initial leaf mass remaining in litter bags. Riffles were nested within streams, and streams within watersheds. Two-way ANOVA was used to test for differences in decomposition rates among the 4 stream orders in Experiment 2. Mesh type was used as a fixed factor in both analyses. ANOVA was also used to test for differences in the ratio of percent leaf mass remaining in coarse- to fine-mesh bags among the 4 stream sizes. Principal components analysis (PCA) was performed on the physical and chemical data gathered from each riffle, stream and watershed. Subsequently correlations were calculated to examine potential relationship between leaf-mass loss and the factor scores of the principle components with Eigenvalues greater than 1. Nested ANOVA was performed in Statistica (StatSoft, Tulsa, OK, USA), other ANOVAs and PCA were performed in SYSTAT 10 (Systat Software, Point Richmond, CA, USA).

**Results**

In Experiment 1, mean percent leaf mass remaining among all 378 leaf bags retrieved was 49.7%, and a standard deviation of 7.2%, corresponding to exponential decay coefficients of $0.015 \pm 0.056$ day$^{-1}$. 
Percent mass remaining across all bags ranged from 15-66% leaf mass remaining, corresponding to exponential decay coefficients of 0.041-0.009 day^{-1}.

Decomposition rates were highly consistent among watersheds and represented less than 1% of the total variability in the nested ANOVA model (Table 2). As a result, ANOVA revealed no difference in decomposition rates among the 4 watersheds (F=0.22, p=0.88, despite very low within-watershed variability (Figs 2 and 3). The difference between the watershed with the fastest and the slowest decomposition rates was less than 3% of the leaf mass remaining for coarse-mesh bags (Fig. 2) and less than 1% for fine mesh bags (Fig. 3). Mesh size was a highly significant factor (F=105, p=<0.001), while the interaction between watershed and mesh size was not significant (F=0.80, p=0.52).

Table 2. Results of ANOVA to test for effects of mesh size of litter bags, watershed, streams nested in watershed, and stream riffles nested in streams on litter decomposition rate.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Sum of Squares</th>
<th>% Total Variability</th>
<th>Degrees of Freedom</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesh</td>
<td>1282.5</td>
<td>19%</td>
<td>1</td>
<td>1282.5</td>
<td>104.8</td>
<td>0.000</td>
</tr>
<tr>
<td>Watershed</td>
<td>30.8</td>
<td>0%</td>
<td>3</td>
<td>10.3</td>
<td>0.22</td>
<td>0.883</td>
</tr>
<tr>
<td>Stream(Watershed)</td>
<td>381.3</td>
<td>6%</td>
<td>8</td>
<td>47.7</td>
<td>2.5</td>
<td>0.028</td>
</tr>
<tr>
<td>Riffle(Stream(Watershed))</td>
<td>682.0</td>
<td>10%</td>
<td>36</td>
<td>18.9</td>
<td>1.5</td>
<td>0.028</td>
</tr>
<tr>
<td>Watershed*Mesh</td>
<td>63.9</td>
<td>1%</td>
<td>3</td>
<td>21.3</td>
<td>0.8</td>
<td>0.521</td>
</tr>
<tr>
<td>Stream(Watershed)*Mesh</td>
<td>209.0</td>
<td>3%</td>
<td>8</td>
<td>26.1</td>
<td>1.5</td>
<td>0.186</td>
</tr>
<tr>
<td>Riffle(Stream(Watershed))*Mesh</td>
<td>620.3</td>
<td>9%</td>
<td>36</td>
<td>17.2</td>
<td>1.4</td>
<td>0.068</td>
</tr>
<tr>
<td>Error</td>
<td>3450.1</td>
<td>51%</td>
<td>282</td>
<td>12.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Decomposition rates among streams were also similar, although less so than among watersheds (Figs 2 and 3), resulting in a statistically significant difference among streams (F=2.53, p=0.03) (Table 2). Across all 4 watersheds, difference between the two streams with the fastest and slowest decomposition was 9.7% of leaf mass remaining in coarse-mesh bags and 5.6% in fine-mesh bags. The interaction between stream nested in watershed and mesh size was not significant (F=1.52, p=0.19). Within each watershed, variability among streams was lower than that among streams across all watersheds, with a mean range of percent leaf mass remaining of 5.6% and 3.4% for coarse- and fine-mesh bags, respectively. When the mass-loss data from coarse-mesh and fine-mesh bags were analyzed separately in the nested ANOVA model, no difference was observed among streams in leaf-mass remaining in fine-mesh bags (F=1.63, p=0.30), whereas differences in decay rates among streams were observed for leaves placed in coarse-mesh bags approached statistical significance (F=2.25, p=0.08).

Decomposition among all riffles was more variable than among all streams or watersheds (Figs 2 and 3), and statistically significant (F=1.55, p=0.03) (Table 2). The mean difference between riffles with the fastest and slowest decomposition rates was 19.2% for coarse-mesh bags and 13.9% for fine-mesh bags. A nearly significant interaction was observed between riffles and mesh size (F=1.4, p=0.068. Within each stream, variability among riffles was less than that of riffles across all streams, with the mean within-stream range of percent mass remaining being 8.6% and 6.4% for coarse- and fine-mesh bags respectively. Variability among individual leaf bags within individual riffles (i.e., the error term) was the largest source of variability in the ANOVA model, representing 51% of the total variance.
Fig. 2. Mean ± SE percent leaf mass remaining in fine-mesh bags across the three spatial scales examined: riffles, streams and watersheds. No statistically significantly difference were observed among Watersheds, Streams or Riffles (p>0.30 in all cases).

In Experiment 2 decomposition rates of leaves placed in 1st-order to 4th-order streams were highly consistent and ranged from 43-46% of the initial leaf mass remaining in coarse-mesh bags, and from 50-54% in fine mesh bags. No significant difference was observed among streams (F=1.04, p=0.38) (Fig. 4). Mesh size was a highly significant factor affecting leaf mass loss (F=43.8, p=<0.001), whereas the interaction between mesh size and stream order was not significant (F=1.27, p=0.29). No difference among stream orders was observed in the ratio of coarse-mesh to fine-mesh bags (F=0.59, p=0.62).
Fig. 3. Mean ± SE percent leaf mass remaining in coarse-mesh bags across the three spatial scales. No statistically significantly differences were observed among Watersheds. (*) indicates p=0.08 among Streams within Watersheds, ** indicates p=0.02 among riffles within streams.

PCA revealed 5 principal components with Eigenvalues greater than 1. Together these explained 85% of the total variance among the morphological and physico-chemical variables measured to characterize streams. Correlations performed between the factor scores of each of the 5 principal components (PC) and percent leaf mass remaining for each mesh type revealed two statistically significant relationships (p=0.001). Correlation coefficients between the factor scores of PC 1 and 3 and leaf mass remaining were \( r = -0.23 \) and \( r = -0.24 \), respectively. The most important variables defining PC 1 were related to stream size and water
hardness. These were, in order of importance, stream links (i.e., the number of 1st order streams upstream of the sampling point), conductivity, calcium concentration, and drainage area. The most important variables defining PC 3 related to temperature and particulate nutrient concentrations: Mean daily temperature, total particulate phosphorus concentration, elevation, and total particulate nitrogen concentration, in order of importance.

![Bar chart showing the fraction of mass remaining in leaf bags placed in 1st to 4th-order streams.](chart.png)

Fig. 4. Mean ± SE fraction of mass remaining in leaf bags placed in 1st to 4th-order streams. No statistically significant differences were observed among stream sizes.

**Discussion**

Stream environments are widely considered to be variable across time and space (e.g., Vannote et al. 1980; Junk et al. 1989; Frissell et al. 1986; Ward et al. 2002; Thorp et al. 2006; Malard et al. 2006) and this heterogeneity, in turn, is thought to maintain high levels of species
richness (Simberloff and Wilson 1969; Levins 1979; Tiegs et al. 2005) and functional diversity (Langhans et al. in press; Tiegs et al. in press). The results of the present study provide information about the spatial variability of litter decomposition rates and add a new perspective about how decomposition varies both among sites at a given spatial scale, and across scales. Here we observed that the degree of heterogeneity in decomposition rates expressed as % mass loss depended on the scale at which it was measured, and that variability within a particular scale decreased with increasing spatial scale. As the extent of a study increases, the degree of spatial heterogeneity encountered within a sampling must also increase (Wiens 1989; Cooper et al 1998). However, as observed here in our hierarchy experiment, variability among large scale patches, e.g., 4th-order watersheds or 3rd-order streams, need not be great. All watersheds supported highly consistent decomposition rates: streams were more variable, as were riffles, while within-riffle variability was more than half the variability observed in the overall model. This pattern was observed in both coarse- and fine-mesh bags, although across the three spatial scales we examined, variability was much greater for coarse-mesh relative to fine-mesh bags. This suggests that leaf consumption by macroinvertebrates was more spatially heterogeneous than that litter degradation by microbes, especially at smaller spatial scales.

Patchy levels of invertebrate feeding activity, whether they stem from differences in per capita feeding rates or invertebrate abundances, is a plausible mechanism behind the variability we observed in coarse-mesh bags among streams and riffles. In an assessment of invertebrate communities across spatial scales similar to those examined here, Li et al. (2001) observed little variability in invertebrate abundance among
ecoregions; however, significant differences were observed among streams and within streams. Similarly, Downes (1993) observed significant differences in invertebrate abundance among streams and both between and within riffles. Abos et al. (2006), using experimental leaf packs similar to those used here, observed that within a riffle, aggregation by shredder species among leaf packs was greater than could be explained by chance. If shredder species vary significantly in their capacity to decompose leaf material, as has been demonstrated (Dangles and Guérold 2001), aggregation by a species in some leaf packs and a different species in other leaf packs will likely translate to variability in decomposition rates among leaf packs at small spatial scales, such as riffles, and is a possible explanation for the large within-riffle variability relative to among stream and watershed variability observed here. Within-riffle variability has two sources: 1) variability in the decomposition rates among individual leaf packs within each riffle caused by varying environmental conditions and 2) experimental error (e.g., different handling losses between one leaf bag and another within a riffle, or differences in leaf quality among leaf bags). In addition to this aggregation effect of species resulting from invertebrate behavior, stream-flow hydraulics may sort invertebrates and result in patchy invertebrate distributions which also might lead to patchy invertebrate distribution and decomposition rates.

Contrary to expectations from stream ecosystem theory (Vannote et al. 1980) and results from field studies (e.g., Jonsson et al. 2001), we observed no trend in decomposition rates along a stream-size gradient ranging from stream orders 1 to 4. Given the shift predicted by the river continuum concept from dominance of an allochthonous to autochthonous resource base, shredders should become less abundant.
with increasing stream size. This pattern has been variously observed in field studies (Greathouse and Pringle 2006, Minshall et al. 1983; Jonsson et al 2001). It is important to note, however, that 4th-order streams in the region where this research was conducted are still well shaded and receive large inputs of terrestrially derived leaf material. Consequently, a large shift from allochthonous to autochtonous resources for stream communities might not be expected.

While not explicitly addressed in most theoretical models, the activity and effectiveness of aquatic hyphomycetes in decomposition of leaf material might be expected to increase with increasing stream order because of increased temperatures and nutrient concentrations. However, no differences in decomposition rates were observed for either coarse-mesh or fine-mesh bags along the gradient examined here, suggesting that influence of shredders and aquatic hyphomycetes need not necessarily vary among 1st- to 4th-order streams, and that stream size across this range is not a major cause of heterogeneity.

Most decomposition studies are conducted at small scales, such as individual riffles or short stream reaches (sensu Bisson and Montgomery 1996). Our results show that variation between and within riffles accounted for greater than 60% of the overall variance observed. If the variance within riffles is due to variability in local conditions (such as patchy shredding activity), and not experimental error, this suggests that most studies are conducted at a scale that, although small, encompasses the range of variability in decomposition rates encountered at the regional scale (i.e. across 4th order-watersheds). The fairly consistent decomposition rates we observed among streams within each watershed suggests that the decomposition rates of a particular stream are accurately characterized through sampling of multiple riffles, and results can be
confidently generalized to other streams in the watershed. Given that among-stream variability was generally quite low, this in turn suggests that results can be upcaled with a fair degree of confidence to the scale of watershed. This is especially true of microbial decomposition, which was consistently less variable than that resulted from macroinvertebrate feeding. Given this lack of variability, reference values for litter decomposition rates in a given region may be established without extensive studies such as those conducted here.

Decomposition rates have been advocated as a means of assessing the functional ecological integrity of streams. Deviation from reference values has been suggested as a way to detect human impacts (Gessner and Chauvet 2002). In the absence of methodological error and spatial and temporal variability, any differences observed between riffles, streams, etc. could be attributed to human impacts. However, natural variability, as a source of statistical noise, poses a threat to the effectiveness of such assessment approaches if human impacts are to be sensitively detected (Gessner & Chauvet 2002). Despite the statistically significant variability we observed both between and within riffles, differences in mean decomposition rates across all spatial scales were not great relative to the pronounced impact that anthropogenic impacts can have on decomposition rates (e.g., Maltby and Booth 1991; Maltby et al 1995; Niyogi et al 2001,2003; Schlief 2004). Sampling efforts, whether they be for field experiments or using decomposition as an assessment tool, can be optimized by increasing the number of experimental units (e.g., leaf bags) within riffles, and sampling multiple riffles, while among stream and among watershed variability is less of a concern.
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Literature Cited


Chauvet, E., N. Giani, and M. O. Gessner. 1993. Breakdown and invertebrate colonization of leaf-litter in 2 contrasting streams -
significance of oligochaetes in a large river. Canadian Journal of Fisheries and Aquatic Sciences 50:488-495.


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Chapter 2

Leaf Decomposition Across Aquatic and Terrestrial Habitat Types in a Riverine Floodplain Mosaic

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* Authors contributed equally to this research
Abstract

Riverine floodplains consist of a mosaic of aquatic, semi-aquatic and terrestrial habitats which, depending on river flow, are periodically connected and disconnected. Flow and flood pulses also arrange habitats and redistribute organic matter from the river channel to the floodplain, and vice versa, which results in remarkable spatial heterogeneity and temporal dynamics of habitats. Although environmental heterogeneity has been intensively studied, very little is known about how habitat heterogeneity influences ecosystem processes, such as leaf decomposition. The aim of this study was therefore to determine patterns of leaf decomposition across diverse habitat types within a complex floodplain reach and to assess the role that detritivorous invertebrates and fungi play in this system. Black poplar, *Populus nigra* L., leaves were placed in litter bags (coarse and fine mesh) and exposed in seven contrasting habitat types (total of 28 sites), ranging from the river channel to the riparian forest, on the floodplain of the Tagliamento River (NE-Italy). Three distinct classes of decomposition rates emerged: channels (fast), ponds (medium), and terrestrial sites (slow). In channels and ponds, leaf decomposition appeared to be driven by both microbial and detritivore activity, whereas in terrestrial habitats microbial activity was likely the main driver. Our results demonstrate that braided floodplain rivers provide a wide range of habitats with different decomposition potentials, resulting in a large spatial heterogeneity in the decomposition of organic matter. Alterations to the natural flow regime (e.g. water abstraction, or retention by dams) and morphological changes (e.g. channelization) of braided rivers strongly decrease habitat diversity and can be expected to
homogenize decomposition rates within river floodplains, with consequences for ecosystem functioning.

Key words: habitat complexity, ecosystem process, braided river, breakdown, Tagliamento
Introduction

Riverine floodplains are ecosystems of global importance (Tockner and Stanford 2002). Defined as "... areas of low lying land that are subject to inundation by lateral overflow water from rivers with which they are associated ...” (Junk and Welcomme 1990), floodplains consist of a complex mosaic of aquatic, semi-aquatic, and terrestrial habitats (Ward et al. 2002, Naiman et al. 2005). Interaction between physical and biotic 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. 2002, Lorang et al. 2005, Stanford et al. 2005). Periodic flooding, repeated 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, Stanford et al. 2005, Tiegs and Pohl 2005). 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). The juxtaposition of multiple landscape elements creates highly heterogenous floodplain structure and function (Tockner et al. in press) and increases the spatial variation in organic matter input, storage, and decomposition (Xiong and Nilsson 1997, Rossi and Constantini 2000, Hutchens and Wallace 2002).

Riparian zones and aquatic-terrestrial interfaces (e.g., shorelines) function as transition zones and control the transport of nutrients and energy between adjacent habitats (Malanson 1995, Risser 1995, Naiman and
Décamps 1997, Ward et al. 1999). Floodplain forests are often highly productive relative to their adjacent uplands (Naiman and Décamps 1997), which results in large inputs of leaf litter to the riparian forest floor and adjacent floodplain habitats. Exchange of organic material among floodplain habitats, for example, from the riparian forest to the river channel and vice versa, can be extensive and is driven by flow and flood pulses (Tockner et al. 2000, Neatrour et al. 2004, Valett et al. 2005). However, during periods between high-flow events, organic material resulting from lateral movement or direct litter fall accumulates on floodplain soils where it is temporarily stored. Here it is colonized by microbes, and partly degraded before it enters aquatic habitats (Merritt and Lawson 1992). The storage of organic material on floodplains is seen as an important mechanism to increase the efficiency of organic-matter recycling along river corridors (Mayack et al. 1989).

Decomposition of plant litter is an important ecosystem process (Aerts 1997, Webster and Benfield 1986, Gessner et al. 1999) and a driving force in nutrient cycling (Cleveland et al. 2004) across a wide range of aquatic and terrestrial environments. It determines the availability of nutrients for organisms (Aber and Melillo 1991), and is a vital component of ecosystem functioning. Leaf decomposition 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).

Leaf decomposition has been widely studied in both aquatic and terrestrial environments (Webster and Benfield 1986, Aerts 1997).
However, no studies have examined leaf decomposition across the numerous and diverse habitats that are commonly encountered on riverine floodplains (Chauvet 1988, Chergui and Pattee 1988a). Although it is generally acknowledged that natural ecosystems are spatially and temporally complex, heterogeneity tends to be averaged over time and space in ecosystem analyses (Strayer et al. 2003). In view of the complexity of floodplains, however, studies that quantify natural heterogeneity of decomposition are necessary, if ecosystem functioning is to be understood at the landscape scale (Cardinale et al. 2002, Giller et al. 2004). Here, we examine leaf decomposition, and the roles of macroinvertebrates and fungi as decomposers, across a range of aquatic and terrestrial floodplain habitats characteristic of braided river sections. Specifically, we ask (1) how variable are decomposition rates across floodplain habitats, and (2) what factors (e.g., invertebrates, fungi, temperature) may drive this variability among habitats?

**Material and Methods**

*Site description*

The study was conducted in the island-braided reach of the Tagliamento River, a 7th order gravel-bed river located in NE-Italy (46° N, 12°30' E; Ward et al. 1999, Tockner et al. 2003). The Tagliamento has a total catchment area of 2580 km². The active area (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 flashy flow regime driven by intense rainfall events in autumn and snowmelt runoff in spring (Arscott et al. 2002). Long-term average discharge in the study reach is 90 m$^3$s$^{-1}$, with floods returning on average at 2, 5, and 10 years, estimated at 1100, 1500, and 2150 m$^3$s$^{-1}$, respectively (Gurnell et al. 2001). During high flow, large amounts of organic matter are transported downstream and deposited on the floodplain surface (Van der Nat 2003).

During baseflow, the 1-km$^2$ study reach consists of 42% exposed gravel, 35% riparian forest, 15% channels, 7% islands and each 0.5% ponds and large wood (Fig. 1). The relative proportion of these habitats changes in response to the water level, and peaks in the hydrograph rearrange them regularly (Van der Nat et al. 2003b). Average standing stocks of deposited coarse particulate organic matter (CPOM; mainly leaves and large wood) across the floodplain range from <1 g m$^{-2}$ ash free dry mass (AFDM) on exposed gravel to 1000 g m$^{-2}$ AFDM on vegetated islands and in the riparian forest. In aquatic habitats, average annual CPOM standing stock ranges from 5 g m$^{-2}$ AFDM in ponds to 50 g m$^{-2}$ AFDM in 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 water parameters, air temperature, and relative humidity, measured during the experiment, are summarized in Table 1. Temperature was continuously recorded using Vemco Minilog data loggers (MINILOG12-TR-40/+50-064K). Relative humidity at the terrestrial sites was measured with HOBO Pro RH/Temp data loggers.
Field methods

A litter-bag method (Boulton and Boon 1991) was used to study decomposition dynamics across seven floodplain habitats: lotic channels, parafluvial ponds, orthofluvial ponds, exposed gravel, large wood accumulations, vegetated islands, and riparian forest (Tiegs et al. in press, Fig. 1). Fine- and coarse-mesh bags were used to investigate leaf decomposition, an approach which respectively allows and deters access by macroinvertebrates and affords partitioning of the separate influence of microbes and invertebrates/physical abrasion (e.g. Boulton and Boon 1991). A factorial experiment was designed with habitat (seven levels) and mesh size (two levels) as the main factors and decomposition rate (expressed as half-life, T_{50}) as the dependent variable. Four replicate sites of each habitat 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. To minimize the risk of losing litterbags due to floods, the experiment was designed to run for 3.5 months (Arscott et al. 2002) and conducted during baseflow conditions (Fig. 2). Senescent leaves of black poplar (Populus nigra L.) were collected from trees near the study site in the autumn of 2002. Leaves were air-dried to constant weight and then stored in dry conditions. Portions of 5.00 ± 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 litterbags were randomly placed in each site on 16 January 2003. In aquatic habitats, cords tied to
iron bars were weighted down to fix litterbags on the bottom of channels and ponds. Litterbags in terrestrial sites were placed on the respective surface, such as pebbles in the exposed gravel habitat, and litter in the riparian forest and on islands. In the large wood habitat, litterbags were fixed in the upper area of the accumulation on miscellaneous material including sand, gravel, litter, small twigs and roots. One litterbag pair was randomly retrieved from each replicated habitat after 18, 32, 50 (channels only), 62, 80, and 102 days (excluding channels). Litter bags were carefully placed into polyethylene bags, transported to a field research station near the site, and immediately processed.

Fig. 1 Map of the main study area during base flow, descriptions of the different habitat types (1 to 7), and locations of the 4 sites per habitat type (e.g., 1-1 to 1-4).
Laboratory procedures

Leaves were removed from bags, individually rinsed with water, and carefully cleaned with a brush to remove macroinvertebrates and adhering debris. The resulting slurry was passed over a 100-μm mesh screen and captured invertebrates were preserved in 80% ethanol. Individuals were identified under a microscope, counted, and sorted into functional feeding groups according to Tachet et al. (2000), Freude et al. (2004), and Kerney et al. (1983). At one occasion (80 days after leaf exposure) 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 bag, using a cork borer. One set of 5 discs each were placed in a small polyethylene bag and frozen at -20 °C for ergosterol analyses 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 was placed in a separate aluminum pan, and dried to constant mass at 60 °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 the same way to establish an air-dry to oven-dry mass relationship.
Fig. 2. Changes in rainfall and water level over the study period in 2002/2003. Dates of bag retrieval are indicated with arrows. The black bars represent total daily rainfall, and the line shows the water level at Villuzza located 500m downstream of the studied floodplain.

Data analysis

Leaf-decomposition rates (k) were calculated using a negative exponential model (e.g. Webster and Benfield 1986) setting an initial value of 100% at day 0 (i.e. intercept = 100%). To standardize leaf decomposition by temperature, decomposition rates (k') were also calculated on a degree-day (dd) basis (Boulton and Boon 1991) by substituting degree days for time in the negative exponential decay model. Degree days equaled the sum of mean daily temperature during the study period. Half-lives (T_{50} in days and T_{50} in degree-days) were calculated
from decomposition rates as \( \frac{\ln(2)}{k} \) and \( \frac{\ln(2)}{k'} \), respectively. To examine differences in decomposition \( (T_{50}) \) among habitats and mesh type, a two-way ANOVA was performed with habitat and mesh size as Fixed factors. If mesh size showed a significant effect, the data set was analyzed separately for coarse- and fine-mesh bags. Subsequently, Tukey’s post-hoc tests (Janssen and Laatz 2003) were performed to analyze differences between habitats. The same ANOVA model was used to test for differences in temperature-corrected decomposition rates \( (T_{50}') \) and fungal biomass (mg g leaf dry mass\(^{-1}\)) among habitats and between mesh types. When Tukey’s tests did not show differences between habitats, weighted paired contrasts (Lindman 1974) were performed to test for differences among three broader habitat categories: channels, ponds, and terrestrial habitats. Weighting was based on the number of habitats within each habitat category. Repeated measures ANOVA with the between-subjects factors mesh size and habitat types followed by Tukey’s tests were carried out to detect differences in the abundance of total macroinvertebrates and leaf-shredding detritivores. Abundance 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

Physical and chemical characteristics

Mean daily water temperature and nitrate \( (\text{NO}_3^-) \) concentration differed slightly among channels, parafluvial-, and orthofluvial ponds (Table 1a). All other physical and chemical characteristics were similar among
aquatic habitats. In terrestrial habitats, mean air temperature was slightly higher on vegetated islands and relative humidity was lower on exposed gravel than in the other terrestrial habitats (Table 1b).

**Leaf mass loss**

Mean poplar leaf decay in coarse- and fine-mesh bags was fastest in channels and slowest in the riparian forest (Fig. 3). Decomposition rates ranged from \(-0.0245\) d\(^{-1}\) in channels (coarse-mesh bags) to \(-0.0029\) d\(^{-1}\) on large wood (fine-mesh bags: Table 2), corresponding to half-lives of 36 and 239 days (Fig. 4a). Habitat \((F_{6,56} = 163.2, P < 0.001)\), mesh size \((F_{1,56} = 35.8, P < 0.001)\), and the interaction between both \((F_{6,56} = 5.3, P < 0.001)\) significantly influenced leaf decomposition, suggesting that the effect of invertebrates depended on habitat. In all habitats, leaves decomposed faster in coarse-mesh than in fine-mesh bags, although the difference was only marginal in ponds (Fig. 4a). For both mesh sizes, post-hoc tests revealed three distinct categories of decomposition rates: channels (fast: coarse-mesh \(k = -0.0192\) d\(^{-1}\), fine-mesh \(k = -0.0120\) d\(^{-1}\)), ponds (medium: coarse-mesh \(k = -0.0079\) d\(^{-1}\), fine-mesh \(k = -0.0078\) d\(^{-1}\)) and terrestrial habitats (slow: coarse-mesh \(k = -0.0053\) d\(^{-1}\), fine-mesh \(k = -0.0049\) d\(^{-1}\)). In fine-mesh bags, leaf decomposition in terrestrial habitats split into two additional groups with significantly slower decomposition rates on large wood than in all other habitats (Fig. 4a).

Mean daily temperature during the study period was higher in channels than in ponds, and higher in aquatic than in all terrestrial habitats (Table 1). When decomposition rates were calculated using degree days to account for among-habitat temperature differences, neither habitat \((F_{6,52} = 2.0, P = 0.099)\) nor mesh size \((F_{1,52} = 3.0, P = 0.094)\) showed a significant
effect on leaf decomposition (Fig. 4b). However, linear contrasts among habitat categories revealed significant differences between channels and ponds ($F_{1,38} = 5.3, P = 0.027$), and between channels and terrestrial habitats ($F_{1,38} = 7.3, P = 0.010$). The same significant differences were found for contrasts calculated with data from coarse-mesh bags only (channels versus ponds: $F_{1,19} = 8.4, P = 0.009$; channels versus terrestrial habitats: $F_{1,38} = 8.5, P = 0.009$), but not with data from fine-mesh bags.

Density and composition of macroinvertebrates

Total macroinvertebrate abundance was significantly lower in fine-mesh than in coarse-mesh bags ($F_{1,42} = 5.7, P = 0.022$) and significantly differed among habitats ($F_{6,42} = 22.1, P < 0.001$). Channels showed significantly higher numbers of macroinvertebrates than all other habitats, followed by orthofluvial ponds, which had significantly different densities compared to the least colonized habitats, which were large wood and exposed gravel (Fig. 5). Most macroinvertebrates colonizing fine-mesh bags in aquatic habitats were early instars of chironomids.
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 ± 1 SD, n = 20). * continuous records, † a single data logger per habitat type.

a) Aquatic habitats

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Channel Orthofluvial</th>
<th>Parafuvial pond</th>
<th>Parafuvial pond</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Water temperature (°C)</strong></td>
<td>9.3 ± 1.1</td>
<td>8.0 ± 1.8</td>
<td>7.4 ± 1.8</td>
</tr>
<tr>
<td><strong>Current velocity (m s⁻¹)</strong></td>
<td>0.24 ± 0.29</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Water depth (m)</strong></td>
<td>0.20 ±0.19</td>
<td>0.53 ± 0.35</td>
<td>0.54 ± 0.20</td>
</tr>
<tr>
<td><strong>Conductivity (μS cm⁻¹; at 20 °C)</strong></td>
<td>445 ± 127</td>
<td>451 ± 131</td>
<td>465 ± 158</td>
</tr>
<tr>
<td><strong>pH</strong></td>
<td>8.2 ± 0.3</td>
<td>8.1 ± 0.3</td>
<td>7.8 ± 0.1</td>
</tr>
<tr>
<td><strong>O₂ (mg L⁻¹)</strong></td>
<td>12.4 ± 2.3</td>
<td>12.5 ± 4.8</td>
<td>11.5 ± 4.3</td>
</tr>
<tr>
<td><strong>NH₄-N (mg L⁻¹)</strong></td>
<td>&lt; 0.01</td>
<td>&lt; 0.01</td>
<td>0.01</td>
</tr>
<tr>
<td><strong>NO₃-N (μg L⁻¹)</strong></td>
<td>656 ± 77</td>
<td>395 ± 118</td>
<td>580± 325</td>
</tr>
<tr>
<td><strong>Soluble reactive phosphorus (μg L⁻¹)</strong></td>
<td>&lt; 5</td>
<td>&lt; 5</td>
<td>&lt; 5</td>
</tr>
</tbody>
</table>

b) Terrestrial habitats

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Exposed Riparian forest</th>
<th>Large gravel</th>
<th>Island wood</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Air temperature (°C)</strong></td>
<td>3.5 ± 7.7</td>
<td>3.7 ± 7.0</td>
<td>4.1 ± 6.1</td>
</tr>
<tr>
<td><strong>Relative humidity, RH (%)</strong></td>
<td>72 ± 28</td>
<td>95 ± 10</td>
<td>97 ± 9</td>
</tr>
</tbody>
</table>

Total number of macroinvertebrates in coarse-mesh bags increased significantly over time (Wilks’ Lambda: F₃,19 = 5.0, P = 0.010) and varied among habitats (F₆,21 = 24.7, P < 0.001) (Fig. 5). Litter bags from...
channels had significantly more macroinvertebrates than bags in all other habitats, mainly because of large numbers of chironomids. Weighted contrasts revealed significant differences in macroinvertebrate numbers among the three habitat categories with the highest abundance in channels, medium in ponds, and lowest in terrestrial habitats (channels versus ponds: $F_{1,21} = 82.3$, $P < 0.001$; channels versus terrestrial: $F_{1,21} = 141.0$, $P < 0.001$; ponds versus terrestrial: $F_{1,21} = 6.22$, $P = 0.02$). Total numbers of macroinvertebrates peaked on day 62 in para- and orthofluvial ponds, but continued to rise in channels (Fig. 5).

Table 2. Summary of decomposition rates ($k$, mean $\pm$ 1 SE, $n = 4$) of black poplar leaves decomposing in seven different floodplain habitat types and two different mesh types as estimated by nonlinear regression analysis.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Coarse-mesh bags</th>
<th>Fine-mesh bags</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$k$ (d$^{-1}$) $\pm$ SE</td>
<td>$r^2$</td>
</tr>
<tr>
<td>Channel</td>
<td>-0.0245 $\pm$ 0.0134</td>
<td>0.88</td>
</tr>
<tr>
<td>Parafluvial pond</td>
<td>-0.0071 $\pm$ 0.0002</td>
<td>0.61</td>
</tr>
<tr>
<td>Orthofluvial pond</td>
<td>-0.0073 $\pm$ 0.0004</td>
<td>0.56</td>
</tr>
<tr>
<td>Exposed gravel</td>
<td>-0.0036 $\pm$ 0.0001</td>
<td>0.01</td>
</tr>
<tr>
<td>Large wood</td>
<td>-0.0044 $\pm$ 0.0005</td>
<td>0.44</td>
</tr>
<tr>
<td>Island</td>
<td>-0.0039 $\pm$ 0.0001</td>
<td>-0.01</td>
</tr>
<tr>
<td>Riparian forest</td>
<td>-0.0035 $\pm$ 0.0001</td>
<td>-0.01</td>
</tr>
</tbody>
</table>

Habitat type significantly affected total detritivore abundance ($F_{6,21} = 6.16$, $P = 0.001$), with greatest abundances in channels, which were significantly different from exposed gravel, large wood and vegetated islands. Weighted contrasts revealed significantly higher detritivore
abundance in channels than in ponds ($F_{1,21} = 10.3$, $P = 0.004$), and in channels than terrestrial habitats ($F_{1,21} = 26.6$, $P < 0.001$), and slightly greater numbers in ponds than in terrestrial habitats ($F_{1,21} = 4.47$, $P = 0.05$). Total number of detritivores did not significantly change over time (Wilks’ Lambda: $F_{3,19} = 1.99$, $P = 0.15$).

The aquatic macroinvertebrate community in litter bags exposed in channels was dominated by chironomids and *Baetis spp.* Stonefly larvae, such as *Leuctra spp.*, and caddisfly larvae (mainly Limnephilidae) were the main shredders present in these bags. In ortho- and parafluvial ponds, the macroinvertebrate community was more diverse than in channels, consisting of snails (*Bythinia spp.* and *Gyraulus spp.*), dragonfly larvae (*Boyerina irene*), chironomids, amphipods (*Gammarus spp.* and *Echinogammarus spp.*), and caddisfly larvae (mainly Limnephilidae). In terrestrial habitats, springtails, spiders, beetles (mostly Carabidae and Staphylinidae) and snails were dominant.

Habitat significantly affected fungal biomass after 80 days of leaf exposure ($F_{6,55} = 4.82$, $P = 0.001$). In some habitats, fungal biomass was higher in coarse-mesh compared to fine-mesh bags (Fig. 6), leading to an overall tendency for higher biomass in coarse-mesh bags. This difference between mesh sizes was not significant, however ($F_{1,55} = 3.4$, $P = 0.07$), nor was the interaction between habitat and mesh size strong enough to result in a significant effect ($F_{6,55} = 2.0$, $P = 0.095$). Specifically, fungal biomass was significantly higher in channels than on exposed gravel and in channels than in orthofluvial ponds, and orthofluvial ponds showed lowest fungal biomass which was significantly different from that on large wood (Fig. 6). Weighted contrasts revealed higher fungal biomass in channels than in ponds ($F_{1,41} = 12.3$, $P = 0.001$) and in terrestrial
habitats ($F_{1,41} = 20.7, P < 0.001$). Separate analyses for fungal biomass data from bags with different mesh sizes revealed that fine-mesh bags contributed mostly to these significant contrasts (channels versus ponds: $F_{1,21} = 24.0, P < 0.001$; channels versus terrestrial habitats: $F_{1,21} = 13.4, P = 0.001$; ponds versus terrestrial habitats: $F_{1,21} = 4.9, P = 0.04$), with none of these contrasts being significant for coarse-mesh bags ($P = 0.062$ to 0.473).

Fig. 3. Dry mass remaining of poplar leaves decomposing a) in coarse-mesh and b) in fine-mesh bags in seven different habitat types on the Tagliamento flood-plain (mean ± 1 SE, $n = 4$ sites per habitat type).
Fig. 4 Half-lives ($T_{50}$) of poplar leaves decomposing in seven different habitat types on the Tagliamento floodplain (mean ± 1 SE, n = 4 sites per habitat type); a) $T_{50}$ values calculated on a daily basis (d) and b) $T_{50}$' on a degree-day (dd) basis (i.e. temperature corrected).
Fig. 5 Number of detritivorous and other macroinvertebrates associated with coarse-mesh bags in seven different habitat types on the Tagliamento floodplain (mean ± 1 SE, n = 4 sites per habitat type).

Fig. 6 Fungal biomass (mg g leaf dry mass⁻¹) after 80 days of poplar leaf decomposition in coarse- and fine-mesh bags in seven different habitat types on the Tagliamento floodplain (mean ± 1 SE, n = 4 sites per habitat type).
Discussion

Patterns of leaf decomposition across floodplain habitats

Leaf-decomposition rates varied widely across the seven floodplain habitats we examined. Leaves decomposed fastest in channels, at intermediate rates in ponds, and slowest in terrestrial habitats, a result consistent with previous studies that compared channels and adjacent terrestrial habitats (Gurtz and Tate 1988), and ponds and terrestrial floodplain sites (McArthur et al. 1994). However, these studies were conducted in lower-order streams, which are spatially much less complex and not representative for large floodplain systems (Melillo et al. 1983) such as the braided reach of the Tagliamento River. Studies conducted in the alluvial corridor of the Garonne River, a 7th order river in southwestern France, showed no significant differences in leaf-decomposition rates between some aquatic and terrestrial sites (Chauvet 1988) nor between the mainstem and a parafluvial pond on the 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). Especially in flowing waters, leaching (Petersen and Cummins 1974) and fragmentation (Heard et al. 1999, but see Ferreira et al. 2006) may interact to promote leaf decomposition more than in other environments. Furthermore, organisms can benefit from higher temperatures in aquatic than in terrestrial sites during the winter (Hutchens and Wallace 2002). Factors related to chemical properties of water, such as the constant supply of nutrients, can enhance leaf
decomposition further (e.g. Elwood et al. 1981, Robinson and Gessner 2000, Gulis and Suberkropp 2003). We found that leaves in para- and orthofluvial ponds decomposed more slowly than in channels, but at similar rates to each other, suggesting similar environmental drivers for leaf decomposition in the two different pond types.

In terrestrial environments, the effect of local climate on leaf decomposition has often been summarized by a composite variable, actual evapotranspiration, which predicts faster decomposition in warmer, wetter conditions (Meentemeyer 1978a, Aerts 1997). In our study, decomposition rates across terrestrial habitats were similar and exhibited extremely small within-habitat variability. This suggests that among-habitat differences in environmental conditions were insufficient to measurably influence the decomposition process over the 3.5-month study period.

Strong temperature dependence of leaf decomposition has been widely reported (e.g., Robinson and Jolidon 2005). In our study, differences in temperature explained some of the observed variability among habitats, but also revealed new perspectives. Differences in leaf decomposition per day between channels, ponds, and terrestrial habitats did not appear in temperature-corrected analyses when using a degree-day model. The only observed differences were in coarse-mesh bags between channels and ponds and between channels and terrestrial habitats. This overall similarity in temperature-corrected rates suggests that temperature may have played a notable role in determining leaf decomposition across both aquatic and terrestrial habitats. In particular, leaf decomposition in aquatic habitats was apparently promoted by higher temperatures (cf. Webster and Benfield 1986), whereas lower temperatures in terrestrial
habitats (Table 1b) appeared to slow decomposition (cf. Meentemeyer 1978b, Hobbie 1996).

*Leaf decomposition and invertebrates*

Differences in total macroinvertebrate and detritivore abundance in litter bags may partly account for the observed differences in leaf decomposition among habitats. Although after temperature correction no overall significant difference in decomposition rate was found between coarse-mesh and fine-mesh bags, rates were clearly faster in channel habitats in coarse-mesh bags (in both temperature-corrected and uncorrected analyses; Fig. 4). This indicates that leaf consumption by macroinvertebrates was greater in channels than in other habitats. Overall, numbers of detritivores in litter bags were low (Fig. 5) compared to values reported in the literature (Chergui and Pattee 1988b, Chauvet et al. 1993), but total macroinvertebrate and detritivore abundance were significantly higher in channels than ponds and higher in channels than terrestrial habitats. Given the typically fast decomposition in flowing waters, the major period for leaf decomposition by stream invertebrates is normally in fall and winter (cf. Merritt and Lawson 1992). In terrestrial habitats, the relationship between soil biota and leaf decomposition depends on site-specific characteristics such as soil type and leaf-litter quality (Swift et al. 1979, Heneghan et al. 1998, Heneghan et al. 1999). Additionally, soil biota is strongly constrained by seasonal climatic patterns (Heneghan et al. 1999) whereby increasing soil moisture is associated with higher microarthropod numbers (Crossley and Hoglund 1962). However, leaf decomposition in terrestrial habitats of floodplain ecosystems is complex as it is time-constrained by spring floods during which large amounts of leaves are washed out of their original habitats.
Leaf decomposition and fungi

Fungi play an eminent role in leaf decomposition in flowing waters (Bärlocher and Kendrick 1974, Gessner and Chauvet 1994, Suberkropp 1998), even in larger rivers where direct input of leaf litter is limited (Baldy et al. 1995, 2002). Accordingly, we observed highest fungal biomass in channels, 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 a channel of the Garonne river system. Chergui and Pattee (1988b), who studied the spatial distribution of aquatic fungi associated with decomposing black poplar leaves on floodplain habitats of the Rhone River, France, found faster leaf-decomposition rates in channels with present and active aquatic fungi, compared to still-water habitats where practically no aquatic fungi were found. The current in channels supplies organic material with a continuous source of fungal propagules for inoculation, which in ponds is much more restricted. However, 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), and in terrestrial environments (Bärlocher 1992). Consistent with the higher fungal biomass in channels compared to both ponds and terrestrial habitats, decomposition rates were also greatest in channels, suggesting that part of the faster decomposition in flowing water may be attributable to fungal activity, in addition to detritivore feeding.
Interestingly, we found some variation in fungal biomass between coarse- and fine-mesh bags among terrestrial habitats, although environmental conditions, such as mean temperature and relative humidity were not notably different. Microclimatic conditions within litter bags may have been responsible for those differences. In contrast to litter bags in open habitats (such as exposed gravel and large wood), where mean temperature in litter bags can be higher and mean relative humidity lower, leaves in bags exposed in wooded habitats (i.e. vegetated islands and riparian forest) can experience lower mean temperature but higher mean relative humidity. Mean relative humidity in wooded habitats can be higher in fine- than in coarse-mesh bags and vice versa in open habitats (S. D. Langhans - unpublished data). This together with fungal biomass data suggests that fungal growth in terrestrial habitats may have been mainly governed by moisture availability, as suggested by Hutchens and Wallace (2002). Additionally, fungal growth in fine-mesh bags in open habitats could have been curbed by high temperatures (Pietikäinen et al. 2005). Thus, the most rapid leaf decomposition among the four terrestrial habitats in fine-mesh bags deployed in large-wood accumulations could be related to more benign (warm, moist) conditions for microbial decomposers, which is in agreement with the highest fungal biomass observed in fine-mesh bags in this terrestrial floodplain habitat.

Conclusions

Our results demonstrate that natural floodplain habitats provide a wide range of decomposition potentials. Leaf decomposition in channels and ponds appeared to be driven by both microbes and invertebrates, whereas in terrestrial habitats microorganisms were more important than
invertebrates. Channels were clearly identified as “hot spots” of leaf decomposition. Although the seven habitat types we investigated are spatially distinct during baseflow conditions, they become physically connected during periods of high flow. The dynamic flow regime is not only a main determinant of leaf decomposition in floodplains (Langhans and Tockner 2006), but also exacerbates spatial heterogeneity in leaf decomposition in such systems. Morphologically intact floodplains, together with a natural river flow regime, distribute organic matter on a large scale, thus ensuring physical connectivity within river corridors and markedly affecting overall ecosystem functioning (i.e. processes such as organic matter decomposition, primary production, and nutrient transformations; Valett et al. 2005). Accordingly, leaf decomposition is controlled at the floodplain scale by tree species composition in specific habitats, the spatio-temporal arrangement of individual habitats, and a dynamic river flow regime which rearranges habitats, distributes organic matter, and sustains physical heterogeneity. Modification of flow regimes decreases habitat heterogeneity in floodplain systems and homogenizes spatially-complex variation in decomposition rates even when riparian species composition is unchanged and litter quality thus remains similar. Due to the lack of storage areas for organic matter in such modified systems (Allan and Flecker 1993), the major input of leaf litter in late autumn is quickly decomposed or exported. As a result, nutrients from litterfall are either unavailable or released in a single pulse, which is likely to have repercussions for organisms by affecting their life histories and for ecosystem processes other than litter decomposition (e.g., primary production, sediment/soil carbon mineralization).
Acknowledgements

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Literature Cited


Chergui H, Pattee E (1988b) The dynamics of hyphomycetes on decaying leaves in the network of the River Rhone (France). Arch Hydrobiol 114:3-20


Gurtz ME, Tate CM (1988) Hydrologic influences on leaf decomposition in a channel and adjacent bank of a gallery forest stream. Am Midl Nat 120:11-21


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Chapter 3

Vertical Hydrologic Exchange Affects Leaf Decomposition in a Stream

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Abstract

We conducted a litter-bag experiment in a stream that has spatially heterogeneous exchange between surface flow and ground water, resulting in thermally distinct patches of the stream bed. We hypothesized that decomposition rates are attenuated in patches where cool groundwater upwells in summer and predicted the converse pattern in winter when temperature of upwelling groundwater exceeds that of surface flow. We expected no differences in decomposition rates during autumn when thermal differences between patches are minimal. To test these hypotheses we repeated a litter-bag experiment across 3 seasons in 5 upwelling and 5 downwelling patches of a 4th-order stream. We used 2 leaf species, alder (Alnus glutinosa) and poplar (Populus nigra), enclosed in both coarse-mesh and fine-mesh bags to allow and exclude macroinvertebrates, respectively. Results were largely consistent with hypothesized patterns. Decomposition in summer was significantly attenuated in upwelling patches, where average temperature was 4 °C lower than in downwelling zones, across both leaf species and types of litter bags. Dissolved nutrient concentrations were slightly higher in upwelling zones and temperature-corrected decomposition rates did not differ between patches regardless of leaf species and type of mesh bag, suggesting that temperature was a major factor accounting for the observed differences. During the autumn and winter, regardless of bag type or leaf species and in spite of low variability among replicate samples, no differences in decomposition were observed between patches, consistent with only slight differences in temperatures during these seasons. Flow of upwelling groundwater and/or heat loss from surface water was not strong enough during the winter experiment to produce the opposite temperature pattern to the summer situation, partly because of
increased stream discharge. Together these results show that distinct vertical hydrologic exchange patterns within streams can generate small-scale heterogeneity in environmental conditions that lead to seasonally varying heterogeneity in ecosystem functioning. Ecosystem processes other than decomposition (e.g., denitrification rates, primary production) could be affected to a similar extent.

Introduction

Environmental heterogeneity has a demonstrated importance for many aspects of communities and populations including species diversity (Simberloff and Wilson 1969), dispersal (Huffaker 1958), and distributions (Salminen and Sulkava 1996). The relevance of environmental heterogeneity for important ecosystem processes, however, such as decomposition, remains poorly understood (Sulkava and Huhta 1998). The persistence of most ecosystems requires the recycling of organic matter and decomposition is a fundamental aspect of these biogeochemical transformations. Among the most important governors of decomposition rates is temperature which controls the activity of bacteria (Pietikainen et al. 2005), fungi (Chauvet and Suberkropp 1998) and detritivorous invertebrates (Allan 1995). As temperature often varies spatially within ecosystems so too might decomposition rates. Scant research, however, has been carried out to investigate whether spatially variable temperatures translate to spatially variable rates of organic matter decomposition.

Stream ecosystems are well suited to investigate the significance of thermal heterogeneity on organic-matter decomposition. First, large
quantities of terrestrially derived leaves annually enter stream channels as litter which often constitutes the dominant basal resource of stream food webs (Kaushik and Hynes 1968; Reice 1974; Wallace et al. 1997). Decomposition is the transformational process by which this organic matter is physically and chemically rendered available to higher trophic levels and higher stream orders (Gessner et al. 1999), and the degree to which organic matter is decomposed is a measure of resource quality (Boulton and Boon 1991; Graça et al. 2001).

Second, thermal heterogeneity is a common feature of streams, and upwelling groundwater (i.e., where groundwater enters the stream channel) and downwelling stream flow (i.e., where stream water infiltrates into the subsurface) are ubiquitous and important hydrologic features of many flowing waters (Brunke and Gonser 1997; Boulton et al. 1998; Malard et al. 2002; Boulton and Hancock 2006) that contribute to this variability. For example, in streams with coarse sediments, downwelling is often observed at the head of riffles, and upwelling at riffle tails (Valett et al. 1994). Larger-scale exchange is also common and is driven by changes in geologic conditions (Arscott et al. 2001; Malard et al. 2002). Temperature of surface flow is strongly influenced by air temperature, which in temperate zones often fluctuates on a seasonal and daily basis (Caissie 2006). Groundwater temperatures are much more stable, and typically conform to the mean annual temperature of the region (Brunke and Gonser 1997). These conditions and exchange patterns, coupled with the high specific heat of water, often create distinct thermal patches in streams that are likely to be more persistent and pronounced than the ephemeral thermal patches in terrestrial ecosystems (e.g., an area of soil shaded by a tree). As such, flowing water environments lend themselves to investigating thermal heterogeneity and
its relevance to ecosystem processes, especially when the processes require a long time relative to the life span of the thermal patches.

To investigate the potential role of thermal heterogeneity on leaf decomposition, the research presented here was conducted in a stream that has distinct patches of exchange between surface water and groundwater. We anticipated that thermal heterogeneity stemming from vertical hydrologic exchange translates to functional heterogeneity, that is having decomposition occurring at different rates. Given that annual temperature amplitudes in groundwater are greatly attenuated compared to surface flow, we hypothesized that the effect of vertical hydrologic exchange on decomposition varies with season. Thus, we examined specifically whether 1) decomposition in summer is slower in upwelling patches where temperatures are lower relative to downwelling surface flow, 2) decomposition rates do not differ in autumn when temperatures of upwelling and downwelling patches are level, and 3) decomposition in winter is higher in upwelling patches where water is warmer than in patches where surface flow downwells.

Materials and Methods

Site Description

Experiments were conducted in the River Töss, a 4th-order, pre-alpine stream (elevation 460 m) that flows through a forested watershed near the town of Winterthur, Switzerland (47° 27’ N; 8° 44’ E). Landuse activities consist of scattered agriculture, limited urbanization, and selective forestry. Hydro-engineering projects conducted over the past 150 years
converted the historically braided River Töss to a single channel. Rip-rap and other bank structures stabilize the channel laterally and small but frequently-spaced channel-spanning weirs prevent channel incision. These engineering measures have resulted in a spatially fixed stream channel.

The position of the study reach (approximately 70 m in length) coincides with an area where the flow of shallow groundwater intersects the stream channel at right angle (Brunke and Gonser 1999). This results in a hydrologic situation where distinct patches of upwelling groundwater characterize the margins of the left bank, whereas downwelling dominates along the right bank of the channel (Brunke and Gonser 1999). Temperature measurements prior to initiation of the present experiment confirmed the position of upwelling and downwelling patches identified earlier with pieziometric measurements (Brunke and Gonser 1999). Average width and depth at base flow measure 20 and 0.2 m, respectively, in the study reach. Very coarse pebbles and small cobbles dominate the substrate (after Wentworth 1922). Additional information on reach characteristics is provided by Brunke and Gonser (1999).

Methods

Ten patches were selected in the study reach, five on the left side of the channel with upwelling ground water and five on the right with downwelling ground water. Water depth, distance from shore, substrate size, water velocity and degree of turbulence were assessed visually at each site and deemed to be similar. Ten data loggers (Ibuttons, Dallas Semiconductor, Dallas Texas, USA), one at each of the 10 patches, were deployed to record water temperature at hourly intervals. Water samples
were also collected from all patches to determine nutrient concentrations on 3 separate sampling dates in each of the three seasons when experiments were conducted (see below). Based on previous measurements in the study reach (e.g., Brunke and Gonser 1999) and occasional point measurements during the study, dissolved oxygen concentrations were similar among patches with concentrations always at saturation level or above.

To test our hypotheses that the upwelling groundwater sites supported slower decomposition in the summer, faster decomposition in the winter, and no differences would be observed among patch types in the autumn, we repeated a litter-bag experiment in these three seasons. Litter bags (15cm x 20cm) were constructed of two mesh types, coarse (10-mm mesh size) and fine (0.5-mm mesh size), which respectively allow and prevent access by detritivorous macroinvertebrates to leaves and enable estimation to which degree decomposition is driven by microbes or macroinvertebrates.

Litter bags were filled with leaf material from either of two native riparian tree species common throughout much of Europe: Black Alder (*Alnus glutinosa*) and Black Poplar (*Populus nigra*). In August of 2003, alder leaves were picked fresh from several trees, pooled and mixed in a large plastic garbage bag, air-dried and stored for later use in all experiments in the 3 seasons. Thus alder leaf material did not vary in quality among individual experiments, enabling strict comparison of decomposition rates in response to differing environmental conditions among seasons. Batches of 5.00 ± 0.25 g dry mass (mean ± range) of alder leaves were placed in each litter bag.
In addition to a batch of standard alder leaves, three different qualities of poplar leaves were used in summer, autumn and winter in an attempt to simulate the quality of leaf material naturally delivered to the stream in each of the three seasons. For poplar leaves, within-season patterns between upwelling and downwelling patches mirrored those that naturally occur in the stream. Poplar leaf quality consisted of: green leaves delivered to the stream during summer rainstorms; naturally senesced and abscised leaves in autumn; and floodplain-conditioned autumn-shed leaves as they may be delivered to a stream during a winter flow-pulse. In all seasons a fresh mass of poplar leaves was used that was anticipated to correspond to 5 g of dry material per leaf bag. For the summer experiment initiated in August 2003 fresh poplar leaves were picked from 5 individual trees. The long and easily broken petioles were removed with scissors, the leaf blades mixed in a plastic garbage bag, and 15.00 ± 0.25 g (mean ± range) placed in litter bags. For the autumn experiment initiated in October 2003, recently fallen poplar leaves from the same 5 trees as the summer experiment were gathered from the ground, the petioles removed, the leaves mixed, and 12.00 ± 0.25 g placed in litter bags. Extra leaves were collected in autumn for use in the winter experiment. These leaves with their petioles removed were air-dried and stored at room temperature in cardboard boxes. In the late autumn of 2003, the leaves were placed in a large coarse-mesh litter bag (approximate dimensions, 1m x 1m) which was placed on the forest floor of a local floodplain where it remained for 6 weeks. Leaves were then retrieved, rinsed briefly with water to remove adhering debris, air-dried, weighed in batches of 5.00 ± 0.25 g, re-moistened to render them soft and pliable, and then placed into litter bags. In all seasons litter bags were stored at 4°C before introducing them into the stream within 24 hours.
In each of 5 upwelling and 5 downwelling patches in the study reach a steel rod was hammered into the stream bed to which litter bags were affixed. The rod remained in place during the entire study, thus assuring that bags were in the exact same place in each season. Bags were attached to the rods with nylon cord in clusters of four representing all possible mesh-species combinations: fine-mesh alder; coarse-mesh alder; fine-mesh poplar; coarse-mesh poplar. Order of the bags on each rope was random. In each season a total of 40 bags were installed, corresponding to 2 vertical hydrologic exchange situations (upwelling and downwelling), 5 patches per treatment, and 4 different kinds of bags per patch. Thus across the entire study encompassing 3 seasons there was a total of 120 litter bags.

Litter bags were removed from the stream when approximately 50% of leaf mass remained. This estimate of 50% mass remaining was informed by visual examinations of bags in situ, and by retrieving and weighing the material from some additional litter bags installed in the stream for this purpose. Retrieved litter bags were placed in a plastic bag and transported to the laboratory for processing within 24 hours. Each side of each leaf was cleaned by hand with a soft-bristled paint brush to remove invertebrates and accumulated debris. Leaves were dried for 48 hours at 105 °C and weighed while hot.

Statistical Analysis

Data were examined for normality and homoskedasticity and deemed appropriate for parametric statistical testing. Analysis of variance (ANOVA) was used to compare decomposition rates of either alder or poplar leaves across 3 seasons (Season), 2 mesh types (Mesh), and the
two hydrologic patch types (Hydrology). The response variable was the exponential decay rate coefficient (k). Decay coefficients were calculated for each individual litter bag using a simple exponential decay model, 

\[ X_t = X_0 e^{-kt} \]

where \( X_t \) is the leaf mass upon removal of the litter bags from the field, \( X_0 \) is the initial value, and \( t \) is the elapsed time in days. As a means of assessing the influence of temperature on decomposition rates, temperature-corrected k-values were calculated by substituting degree days for time in the exponential decay model. Additional ANOVAs were performed separately for each season with mesh size (Mesh), leaf species (Species) and hydrological situation (Hydrology) as fixed factors on k-values and temperature-corrected k-values. Lastly, finer-resolution analysis was performed using t-tests to compare decay rates between hydrologic patch types for each of the four possible leaf species/mesh type combinations in each season. Similar analyses were performed on mean temperature and concentrations of dissolved nutrients. All analyses were performed in SYSTAT 10.0 (Systat Software, Richmond, CA, USA).

**Results**

Pronounced differences, consistent between leaf species and mesh sizes, were observed in decomposition rates between upwelling and downwelling patches during the summer, but not during the autumn or winter (Fig. 1). This pattern gave rise to a significant interaction between Hydrology and Season, observed across both alder and poplar leaves (Table 1). Since a standard quality of alder leaves was used in all seasons, this interaction indicates that differences among seasons were due to seasonally variable environmental conditions, at least in part. Other interactions were not significant in this analysis.
Figure 1. Mean temperature-corrected decomposition rates (n=5; ± 95% confidence intervals) across seasons, mesh types, and hydrologic patch types. Temperature correction was achieved by substituting degree days for time in the negative exponential decay model used to calculate decomposition rates. * indicates p<0.05 and >0.01.
Table 1. ANOVA comparing decomposition rates (k values) for alder (A) and poplar (B) with Season, Mesh and Hydrology treated as fixed factors.

A) Summer k Values

<table>
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<tr>
<th>Source of Variation</th>
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<th>Mean-Square</th>
<th>F-ratio</th>
<th>P</th>
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B) Autumn k Values

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C) Winter k Values

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</table>
Separate analyses by season confirmed that decomposition rates in summer were clearly lower in upwelling patches relative to downwelling patches, across both leaf species and mesh types (Fig. 1, Table 2A). Patch type (i.e. hydrological condition) accounted for the largest part of the total variance (41%) in the analysis of the summer data set. The significant interaction observed between Species and Hydrology in the summer (Table 2A) was due to the larger differences between patch types for poplar relative to alder leaves, but the direction of the effects was the same for both species (Fig. 1). Unlike the summer situation, no differences were observed in decomposition rates between upwelling and downwelling patches during either autumn or winter (Fig. 1), regardless of leaf species or mesh type, and despite fairly low within-group variability. In fact, patch type accounted for only 1.5 and 1.8% of the total variance in the autumn and winter data sets, respectively. Only mesh size affected decomposition rates in these seasons (F=41.3, p < 0.001; and F = 4.95, p< 0.001). Species had a significant effect in autumn (F = 12.2, p = 0.001) but not in winter (F = 1.11, p= 0.30)(Table 2).

ANOVA performed on mean daily temperature measured at each patch of upwelling and downwelling water revealed highly significant differences among seasons (F= 824, p<0.001) and between hydrological patch types (F=9.38, p=0.005) (Fig. 2). A highly significant interaction between these two factors was also observed (F=76.3, p<0.001), due to the 4 °C higher temperature in downwelling patches in summer and the slightly lower temperature in autumn (average difference of 1.3 °C) and winter (0.7 °C) (Fig. 2). On hot summer days differences in water temperature between upwelling and downwelling sites were particularly pronounced, sometimes approaching 8 °C.
The differences in leaf decomposition rates observed between upwelling and downwelling patches were greatly reduced when decay rates were temperature-corrected with a degree-day model (Fig. 3). ANOVA performed on these temperature-corrected k-values showed that Hydrology had no longer a significant influence on poplar leaf decomposition (F=2.8, p=0.10) and produced only a weak effect for alder (F=4.1, p=0.049). Moreover, the interaction effect between Hydrology and Season, which was highly significant for decomposition rates not corrected for temperature, disappeared for alder leaves (F=0.39, p=0.68). For poplar leaves, whose quality differed among seasons, the Hydrology × Season interaction was greatly weakened and remained barely significant (p=0.050).

Concentrations of total dissolved nitrogen (Fig. 4a), which occurred mostly as nitrate, were significantly different between upwelling and downwelling patches (F=26.8, p<0.001) and seasons (F=910, p<0.0001). However, interaction between these two factors was also significant (F=5.64, p=0.005), caused by lower concentrations in downwelling patches in both summer (F=10.0, p=0.003) and winter (F=54.2, p<0.001) but not in autumn (F =0.39, P= 0.85). However, the difference in mean concentration between the two hydrologic patch types was relatively small (upwelling= 2.0 mg/l; downwelling; 2.1 mg/l), while the differences among seasons were more pronounced (Fig. 4a). Tukey’s post-hoc tests revealed that concentrations in all seasons were different from each other (p<0.0001). Summer concentrations were the lowest (1.5 mg/l), winter the greatest (2.5 mg/l), and autumn values were intermediate (1.9 mg/l).
Table 2. ANOVA comparing decomposition rates of A) Alder and B) Populus with Season, Mesh and Hydrology as fixed factors.

A) Alder K Values

<table>
<thead>
<tr>
<th>Source of Variation</th>
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<th>df</th>
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B) Poplar K Values

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<th>Mean-</th>
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</table>
Table 3. ANOVA comparing temperature-corrected decomposition rates for alder (A) and poplar (B) with Season, Mesh and Hydrology treated as fixed factors.

A)

### Alder Temperature-corrected K Values

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<tr>
<th>Source of Variation</th>
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<th>Mean-Square</th>
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B)

### Poplar Temperature-corrected K Values

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Figure 2. Mean daily temperature (n=5; ±95% confidence intervals), across hydrologic patch types and season. * indicates p<0.05 and >0.01; ***p<0.001.

Figure 3. Mean temperature-corrected decomposition rates (n=5; ±95% confidence intervals) across seasons, mesh types, and hydrologic patch types. Temperature correction was achieved by substituting degree days for time in the negative exponential decay model used to calculate decomposition rates. * indicates p<0.05 and >0.01.
Soluble reactive phosphorus concentrations were invariably low in all seasons and patch types, with average values ranging from 3 to 6 µg/l (Fig. 4b). Concentrations did not differ between upwelling and downwelling patches (F=0.05, p=0.82), but differences were significant among seasons (F=9.06, p=0.001). Tukey’s post-hoc tests revealed that concentrations did not differ between summer and autumn (p=0.79), while both concentrations were lower than in winter (p<0.007). A significant interaction between season and hydrologic patch type (F= 3.61, p=0.03) was caused by higher concentrations at upwelling sites in summer (F=6.56, p=0.02), whereas no differences between upwelling and downwelling patches were observed during the other two seasons (autumn F = 1.05, p=0.31; winter F=0.45, p=0.52).
Figure 4b. Dissolved phosphorus concentrations in stream water across hydrologic patch types and season. (n=3; ±95% confidence intervals). * indicates p<0.05 and >0.01.

Discussion

While environmental heterogeneity is often measured, its ecological relevance, such as the influence on ecosystem functioning, is rarely assessed (Kolasa and Rollo 1991; Levin 1992; Palmer, 1997). The results presented here demonstrate that environmental heterogeneity in the form of patterns of vertical hydrologic exchange in streams can be highly relevant for litter decomposition as one measure of ecosystem functioning, and suggest that spatial variation in temperature regimes of hydrological patch types is a driver of spatial and temporal variation in decomposition rates.
Our general hypothesis that the effect of vertical hydrologic exchange on litter decomposition varies with season was clearly supported by our experiments. Results from the summer and autumn experiments, in particular, were consistent with our predictions for these seasons that decomposition is attenuated in patches where cool groundwater is upwelling in summer. No differences in decomposition rates are apparent in the fall when temperature differences between upwelling and downwelling patches are small. Two lines of evidence suggest that temperature was indeed the main factor accounting for the differences in summer. First, temperature correction of decomposition rates with a degree-day model consistently offset differences between hydrologic patch types in summer but did not change patterns observed in autumn. Secondly, differences between patch types in dissolved nutrient concentrations, which are important in controlling decomposition rates of litter in streams (Elwood et al. 1981; Suberkropp and Chauvet 1995; Gessner & Robinson 2000; Gulis and Suberkropp 2003; Ardon et al. 2006), failed to explain the observed difference in decomposition during the summer. Concentrations of both total dissolved nitrogen and soluble reactive phosphorus were slightly higher in upwelling zones, where decomposition rates were attenuated compared to the downwelling patches, suggesting that stimulation by enhanced nutrient supply can be ruled out as a cause for faster decomposition in patches where surface water is downwelling.

Our hypothesis that decomposition in winter with cold surface water is stimulated in warmer upwelling groundwater patches could not be tested, because differences in temperature between patch types were less pronounced than anticipated. Mixing of upwelling groundwater with
surface water and/or heat loss from surface water were not strong enough to produce the opposite temperature pattern to the summer situation. This appeared to be partly due to a period of increased discharge that occurred during the winter experiment, whereas the summer and autumn experiments were conducted when discharge was largely at or near baseflow. Nevertheless, given similar temperature conditions, lack of differences in decomposition rates between upwelling and downwelling patches during winter underscores our conclusion that in absence of thermal differences, differences in decomposition between hydrologic patch types do not emerge.

The degree to which upwelling groundwater influences decomposition likely hinges on two factors: the magnitude of difference in water quality between groundwater and surface flow, and the volume of upwelling groundwater relative to stream discharge. When strong differences exist between groundwater and surface flow with regards to important parameters such as temperature and nutrients, differences in decomposition rates are more likely to emerge. It is possible, however, that different aspects of water quality have opposite effects. For example, groundwater may be colder than surface flow, but have higher nutrient concentrations (Hendricks and White 1995), as found often in the present study. The degree of groundwater influence on decomposition also hinges on the volume of upwelling groundwater, which depends on hydraulic head and hydraulic conductivity of the sediments. Elevated discharge during the winter relative to the other two seasons likely lessened the influence of warm upwelling groundwater in two ways. First, greater mixing caused by higher flow may have brought the leaf bags at the sediment surface in closer contact with surface water as opposed to upwelling groundwater. Secondly, the hydrostatic force of the surface
flow may have suppressed upwelling. Either mechanism would have weakened the thermal signal of upwelling groundwater during winter, and under such circumstances differences in decomposition rates would not be expected between upwelling and downwelling patches.

The results of our experiments are consistent with other field investigations on the role of temperature in influencing decomposition rates in streams. Rowe et al. (1996) compared decomposition rates in three streams during two periods of the year to evaluate the role of temperature. They observed differences in mean temperature of 2 °C between the two sampling periods, which apparently were not sufficient to induce measurable differences in decomposition rate. However, a range of environmental factors other than temperature as well as seasonal differences in microbial decomposer and detritivore communities may have masked temperature effects in that study. MacArthur et al. (1988) observed differing decomposition rates at various sites along stream continua below points where springs contributed markedly to discharge. These differences in decomposition were attributed to thermal differences between sites, which were on the order of 4 °C, as between upwelling and downwelling patches during our summer experiment.

An influence of vertical hydrologic exchange on decomposition has been previously observed among upwelling and downwelling patches in streams, but differences in decomposition rates were limited to hyporheic sediments where groundwater influence is conceivably greater than at the stream bottom (Boulton and Quinn 2000; Tilman et al. 2003). The results presented here are consistent with those of Tillman et al. (2003) in that decomposition of leaves buried in upwelling patches was slower than in downwelling zones. However, temperature, not being appreciably
different among these upwelling and downwelling sites was not implicated as cause of the differences in decomposition rates that were observed. In the same study, differences in decomposition were not observed between upwelling and downwelling areas in leaves placed in surface flow. In a similar study, Boulton and Quinn (2000) compared cellulose decomposition in hyporheic sediments among upwelling and downwelling sites in a New Zealand stream and found reduced decomposition in upwelling zones, which in this case was attributed to greater sedimentation.

Several environmental parameters influence litter decomposition, with temperature (Rowe et al. 1996) and concentrations of dissolved nutrients (e.g. Elwood et al. 1981; Suberkropp and Chauvet 1995; Robinson and Gessner 2000; Gulis et al. 2003) being particularly important. In addition to the pronounced thermal differences between upwelling and downwelling patches observed in our study, nutrient concentrations also differed. In streams that are not strongly enriched with nutrients, higher concentrations generally translate to more rapid decomposition rates (Ardon et al. 2006; Robinson and Gessner 2000). However, the differences in concentrations detected here were unlikely to have a notable influence on the observed patterns of decomposition between hydrologic patch types. First, the differences in mean nutrient concentrations were not large, although significant in summer. Second, in the summer, despite slightly greater concentrations of dissolved nitrogen and phosphorus species in upwelling patches, decomposition was slower than in downwelling zones. Lastly, decomposition rates were fastest in the summer, followed by autumn, and then winter, whereas the opposite pattern among seasons was observed in dissolved nutrient concentrations.
Inadequacy of the degree-day model may explain some of the persisting differences between upwelling and downwelling zones when temperature-corrected decomposition rates were compared. Any differences in decomposition rates observed after addition of degree-days to the exponential decay model are often assumed to be due to factors other than temperature (e.g., McArthur et al. 1988). However, use of degree-days for temperature correction assumes a linear relationship between temperature and decomposition rate. This assumption is not always a good approximation to describe temperature effects, because biological activity can respond in an exponential manner (as in Q10 and Arrhenius models; Davidson and Janssens 2006) or more complex ways (e.g. Pietikainen et al. 2005) to increases in temperature. Given the diverse taxa involved in decomposition, a simple degree-day model may therefore not entirely capture temperature effects on decomposition in natural settings.

Here we demonstrated that patchy hydrologic exchange translates to patchy leaf decomposition, an extension of the notion proposed by Boulton (1993) who suggested that vertical hydrologic exchange could influence decomposition in streams. Upwelling groundwater can attenuate decomposition, and possibly other processes, during a time of the year when in-stream decomposition rates are at their highest (Maloney and Lamberti 1995), and food for litter-consuming detritivores (shredders) and resources for microbial litter decomposers are potentially most limited (Richardson 1991; Gonzalez and Pozo 1996). Given that shredders have a strong preference for conditioned leaf material (Arsuffi and Suberkropp 1985; Graça et al. 2001)(i.e., for material well colonized by microbes) and the ability to discern among leaf packs of differing
quality in streams (Palmer et al. 2000), having patches of leaf material in various stages of decay within the same stream reach may have ramifications for invertebrate communities. The low degree of shredding that was observed in this study was low relative to others in the same ecoregion (e.g., Hieber and Gessner 2002) and suggests that differences in breakdown between upwelling and downwelling patches were largely microbially driven.

Temperature is a key environmental variable and several field studies have aimed at determining its role in governing decomposition rates in streams. A challenge faced by comparative studies is that differences in temperatures are concomitant with differences in other variables that are temporally (Rowe et al. 1996) and spatially (e.g., Irons et al. 1994; MacArthur et al. 1988) variable and can influence decomposition. This includes for example the structure of macroinvertebrate (Li et al. 2001) and fungal communities (Suberkropp 1984, Chauvet 1991, Gessner et al. 1993), shredder biomass (Hieber and Gessner 2002), fungal spore densities in flowing water to inoculate leaves (Laitung et al. 2002), and nutrient concentrations (Suberkropp and Chauvet 1995). In our study, conducted in a single stream reach, the relatively long persistence of spatially fixed thermal patches allowed us to control such confounding factors to a greater degree than in most other field studies and thus better isolate the influence of temperature in situ, and we observed that relatively modest temperature differences are sufficient to induce fairly large differences in decomposition rates. Previous studies have emphasized the need to identify and understand “hot spots” (McClain et al. 2003; Kobayashi and Kagaya 2005), areas of disproportionately high rates of biogeochemical processes. Similarly, “cold spots”, areas of relatively low rates of material transformations, such as our summer
upwelling patches, may harbor leaves of a different food and habitat quality and thus contribute to the functional heterogeneity of stream ecosystems.

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Literature Cited


Chapter 4

Leaf Decomposition Response to Manipulated Litter Quantity in Streams

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Abstract

The quantity of resources available to communities is a key variable that determines their structure and function. Many streams ecosystems are base on allochthonous leaf litter and we manipulated the quantity of benthic litter in streams and assessed the response of leaf decomposition and colonization by invertebrates. Specifically, we tested whether 1) greater quantities of benthic litter increase rates of microbial decomposition (since larger amounts of litter could potentially increase inoculum potential), and 2) reduced quantities of litter increase decomposition by invertebrates in experimental leaf packs (because of possible aggregation by shredders). To this end, in each of three streams, we identified three morphologically similar reaches to which we randomly assigned a treatment consisting of 1) augmented quantities of litter, 2) manually depleted litter quantities or 3) a control that was not manipulated. We quantified decomposition with a litter-bag approach that used coarse- and fine-mesh bags intended to allow or prevent access by macroinvertebrates. Benthic litter quantities responded significantly to the treatments, but the response varied among streams, especially in the control reach of one stream which received unusually high inputs of litter. Contrary to our hypothesis, leaf decomposition rates in fine-mesh bags were highly consistent across all reaches and streams. That decomposition was significantly faster in coarse-mesh than in fine-mesh bags suggested that leaf mass loss was partially mediated by invertebrates. In the two streams where benthic litter manipulations were successful, decomposition in coarse-mesh bags was faster in reaches where benthic litter was scarcer, consistent with our second hypothesis. Abundances of total shredders and macroinvertebrates in litter bags did not differ among
reaches. However, the leaf-shredding amphipod *Gammarus* was significantly more abundant in bags placed in reaches where benthic litter was depleted, suggesting that *Gammarus* was instrumental in causing the observed pattern in decomposition across litter-manipulated reaches. Deviating patterns of most response variables observed in one stream with similar basic characteristics than the other two emphasize the importance of replication of treatments in ecosystem experiments.

Keywords: retention; stream; leaf breakdown; leaf litter; invertebrate aggregation, benthic organic matter

**Introduction**

The quantity of resources available to organisms is a key factor that determines their spatial distribution in ecosystems, which in turn may govern important ecosystem-level processes. A crucial resource in streams is terrestrially derived leaf litter (Petersen and Cummins 1974, Richardson and Neill 1991, Wallace et al. 1997). During the growing season in temperate zones the leaves of stream-side vegetation cast shade that exerts strong limitation of in-stream primary production (Sabater et al. 2000). In autumn, these same leaves enter stream channels as litter where they function as food and habitat to benthic primary consumers such as macroinvertebrates, and as substrate and habitat for microbes such as aquatic fungi (Rowe and Richardson 2001, Hieber and Gessner 2002). As a result, these terrestrially derived leaves often constitute the major basal resource of stream food webs (Wallace et al. 1997) and thus the quantity of leaves present in stream channels can be expected to be a key variable that governs the structure and functioning of stream ecosystems.
Benthic litter in stream channels is highly variable across time and space and amounts hinge on three processes: 1) litter input, 2) retention by in-stream channel structures and 3) decomposition. Rates of litter input in temperate zones vary strongly with season (Richardson 1991), density and composition of vegetation adjacent to streams (Benfield 1997, Jones 1997), and hillslope processes (i.e., lateral input) that deliver litter to the stream after it lands on the forest floor (Wallace et al. 1999). Litter retention is mainly determined by interactions between hydrologic variables (e.g., discharge, flow velocity, turbulence) and geomorphic features of streams such as depth of the channel, streambed structures protruding above the water surface (Jones 1997, Hoover et al. 2006), and presence of large wood accumulations. As a result of spatial and temporal variation of these factors, litter retention is highly variable both within and among streams (Minshall et al. 2000) and can be as important as litter input in determining quantities of benthic litter. For example, in a multiple regression analysis with data from 19 streams located throughout the United States, variables related to channel retentiveness explained more variability in benthic litter quantities across streams than variables related to input (Jones 1997).

Two groups of organisms are particularly important in litter decomposition in streams: a functional feeding group of macroinvertebrates referred to as shredders (Cuffney et al. 1990, Graça 2001, Hieber & Gessner 2002) and a group of fungi known as aquatic hyphomycetes (Bärlocher & Kendrick 1974, Suberkropp 1991, Gessner & Chauvet 1994). Bacteria may also play a significant role (Suberkropp and Klug 1976; Baldy et al. 1995; Baldy and Gessner 1997). Rates of litter decomposition are controlled by several variables, which include
temperature (McArthur et al. 1988; Vought et al. 1998), dissolved nutrient concentrations of stream water (Suberkropp & Chauvet 1995; Tank and Webster 1998; Robinson and Gessner 2000, Gulis & Suberkropp 2003, Ardon et al. 2006), litter quality (Petersen & Cummins 1974, Webster & Benfield 1986, Gessner & Chauvet 1994, Maharning & Bärlocher 1996), and shredder abundance and community structure (Cuffney et al. 1990, Dangles et al. 2004). In addition to these factors, all subject to intense study, the quantity of litter in stream channels can influence decomposition rates (Benfield 1991); however, the mechanisms behind this response remain unclear.

Understanding of how litter depletion influences stream ecosystems has been largely founded on long-term, unreplicated, whole-system reductions of litter input to small stream channels. A long-term litter-exclusion experiment on a whole stream produced very convincing evidence that stream food webs can, to a large extent, be based on leaves (e.g., Wallace et al. 1997, 1999; Eggert and Wallace 2003). Such large-scale, whole-system manipulations are among the best means to assess ecosystem processes and properties (Carpenter et al. 1989, 1995) but a key drawback is that practical constraints tend to preclude replication of treatments (sensu Hurlbert 1984). While a range of approaches has been proposed to accommodate non-replicated designs in ecosystem experiments (e.g., Carpenter et al. 1989, 1995, Wallace et al. 1999) epistemological problems remain (Murtaugh 2002) and the domain of statistical inference from such studies is nonetheless limited.

Although not always practical, it is often possible to use replicated designs in ecosystem experiments (e.g. Maron et al. 2006), and headwater streams, because of their relatively small size, are prime candidates for
such manipulations. Here we experimentally manipulate quantities of benthic litter in three streams at the scale of stream reach (\textit{sensu} Bisson and Montogomery 1996) to test two hypotheses relating to the response of leaf decomposition. First, we predicted that experimentally augmented quantities of benthic litter would promote microbial decomposition relative to controls because greater quantities of decomposing litter increase fungal spore inoculum, which in a microcosm study has been shown to markedly advance decomposition (Treton et al. 2004). Second, we anticipated increased decomposition rates by shredding invertebrates in stream reaches where quantities of benthic litter were depleted. Our rationale was that shredders, when faced with depleted food resources, would aggregate in experimental leaf packs (Abos et al. 2006), quickly take advantage of these “resource islands”, and thus accelerate decomposition.

\textbf{Methods}

\textit{Study Sites}

Three streams were selected in the southern Black Forest in Germany: Andelsbach, Fohrenbach and Mühlebach. Streams had similar characteristics with regards to geology of their watersheds (granitic) and land-use (selective forestry), and drained watersheds of mixed deciduous vegetation. All streams were 3\textsuperscript{rd} order, consisted of pool and riffle sequences, had substrates dominated by coarse gravel and small cobble (\textit{sensu} Wentworth 1922) and had similar volumes of large wood as judged by visual inspection along the study sections. Riparian vegetation consisted of a mixed, closed canopy, including alder, maple, ash, and
beech. Table 1 summarizes major chemical and physical attributes of the streams.

Table 1. Physical and chemical characteristics of the three streams investigated. n/a means data not available

<table>
<thead>
<tr>
<th>Stream</th>
<th>Temp. °C (mean daily ±1 SD)</th>
<th>Elevation (m a.s.l.)</th>
<th>Width (m ±1 SD)</th>
<th>Discharge (l/s)</th>
<th>Conductivity (µS/cm)</th>
<th>NH₄-N (µg/l)</th>
<th>SRP (µg/l)</th>
<th>Turbidity (NTU)</th>
<th>-PO₄ (µg/l)</th>
<th>NO₃-N (µg/l)</th>
<th>Alkalinity (mEq/l)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andelsbach</td>
<td>5.5 (1.5)</td>
<td>530</td>
<td>2.3 (0.53)</td>
<td>30</td>
<td>108</td>
<td>5.0</td>
<td>6.6</td>
<td>2.3</td>
<td>3.46</td>
<td>n/a</td>
<td>981</td>
</tr>
<tr>
<td>Fohrenbach</td>
<td>5.3 (1.6)</td>
<td>740</td>
<td>3.0 (0.71)</td>
<td>65</td>
<td>115</td>
<td>4.3</td>
<td>87.0</td>
<td>n/a</td>
<td>81.1</td>
<td>649</td>
<td>0.47</td>
</tr>
<tr>
<td>Mühlbach</td>
<td>6.9 (1.2)</td>
<td>420</td>
<td>2.9 (0.65)</td>
<td>33</td>
<td>151</td>
<td>3.0</td>
<td>1.7</td>
<td>1.3</td>
<td>5.28</td>
<td>2500</td>
<td>1.08</td>
</tr>
</tbody>
</table>

Experimental Design

Three similar experimental reaches were delineated in each stream (Fig. 1), each reach 40m in length and homogeneous in terms of morphological characteristics and riparian vegetation. One of three possible treatments was assigned to each reach: augmented litter quantities above background levels, litter depletion, and unmanipulated control. To deal with possibly confounding upstream-downstream effects, random assignment of treatments to reaches was constrained by the criterion that each of the treatments had to be positioned in an upstream, middle and downstream reach in one of the three streams. In addition, reaches were separated by a minimum distance of 100m to minimize influences of upstream treatments on the experimental reaches downstream. Thus, the result was a constrained complete block design with stream as the blocking factor.

Litter augmentation was achieved by means of litter traps (Dobson and Hildrew 1992; Dobson 2005). The traps consisted of plastic mesh (20 x 20 cm, 1-cm mesh size) supported by two rebars hammered into the stream bed and oriented perpendicular to stream flow. Just prior to peak
leaf fall, 105-140 traps were placed in each of the augmented reaches to yield an average trap density of 1 per m$^2$ (Dobson 2005).

Litter depletion was accomplished by removing leaf material by hand at weekly intervals. Each handful of leaf material was gently rinsed in the stream in an attempt to minimize removal of resident invertebrates. The first depletion occurred the same day the litter traps were installed. Litter volume removed during each depletion campaign was quantified by placing the collected leaf material into a rigid plastic garbage container (volume: 0.20 m$^3$) and measuring the height of leaf material in the bin. Numerous holes (2 cm diameter) drilled into the bin allowed free water drainage. Mass of subsamples was multiplied by the volume of leaf material in the bin to estimate the total mass of leaf material removed from the channel on each removal campaign. The content of the bin was well mixed by hand and three subsamples (1.6 L each) of the leaf material were taken to the laboratory where they were oven-dried (105°C, 5 d) and weighed.

Effectiveness of the litter enhancement and depletion treatments in influencing the quantity of benthic litter was determined with a cylindrical sampler (area 0.071 m$^2$) 58 days after initiation of the experiment. The sampler was placed at 20 locations that were randomly selected within an imaginary grid along each stream reach, the enclosed litter on the stream bed gathered, placed in plastic bags, transported to the laboratory, oven-dried (105°C, 5d), and weighed.
Figure 1. Schematic of the constrained randomized block design used to test for the effect of benthic litter quantities on leaf decomposition and colonization by macroinvertebrates. Reach treatments included litter-depleted, litter-augmented and unmanipulated control reaches in each of the three study streams. Random assignment of treatments to reaches was constrained to ensure each treatment was located once upstream, downstream and in the middle section of one of the streams. Streamflow direction is from the top of the figure downward. Distance between reaches was approximately 100m.
A litter-bag approach was used to determine leaf-decomposition rates. Bags were constructed of either coarse mesh (10 mm mesh size) or fine mesh (0.5 mm mesh size) to respectively allow or prevent macroinvertebrate access to enclosed leaves. This approach enables estimation of the respective contributions to decomposition by macroinvertebrates and microbes. Recently senesced leaves of *Alnus glutinosa* (L.) Gaertn., a common riparian species throughout much of Europe, were collected, air-dried and weighed into batches of 5.00 ± 0.25g (mean ± range). After weighing, each sample was remoistened to render the leaves pliant, and placed into either a coarse- or fine-mesh bag. Five randomly selected litter bags were used to estimate initial leaf moisture content by drying (105 °C, 24 h) and re-weighing the material while still hot.

Litter bags were brought to the field and 6 coarse-mesh and 6 fine-mesh bags were placed in the middle of each of the 9 study reaches. Bags were fixed in place by hammering rebars into the stream bed and attaching the bags with nylon cord. Flat cobbles were placed on the cord immediately upstream of each bag to prevent bags from moving in the current and to ensure contact with the sediment. After 41 days of exposure in the streams, all leaf bags were retrieved and placed individually into plastic bags. Care was taken to capture invertebrates that had colonized litter within the coarse-mesh bags. Bags were returned to the laboratory in a cool-box and frozen for later processing.
In the laboratory, the contents of each plastic bag were emptied into a shallow tray along with a small amount of water and allowed to thaw. Each leaf was individually cleaned by hand with a soft-bristled paint brush to remove adhering debris and invertebrates, placed in aluminum trays, oven-dried (105°C, 48 h), and weighed while hot to the nearest 0.01g. Invertebrates were collected on a 500-μm mesh screen, preserved in 70% ethanol, identified to the lowest practicable taxonomic unit, enumerated, and assigned to functional feeding groups (Merritt & Cummins 1996, Gessner & Dobson 1993).

**Statistical Analysis**

Analysis of variance (ANOVA) was used to test for differences in percent leaf dry-mass remaining among litter manipulations (Reach), mesh types (Mesh), and streams (Stream). In the absence of a consistent response among blocks (i.e., streams), interactions with the block factor were tested following the rational of Newman (1997) and Quinn & Keough (2002). Two-way ANOVA was used to test for differences in litter invertebrate abundance in leaf bags among litter manipulations. Invertebrate data were log(x+1) transformed to meet assumptions of normality and equal variances. ANOVA, with stream as a blocking factor, was also used to test for differences in amounts of benthic litter. These data were also log(x+1)-transformed. As above, when the treatment effect of litter treatments was inconsistent across streams, interaction between Stream and Reach was included in the ANOVA model. When significant differences were observed (i.e., p<0.05) among litter treatments, Tukey’s post-hoc tests were performed.
Results

Quantities of Benthic Litter

ANOVA on log(x+1)-transformed data with stream as a blocking factor revealed highly significant differences in the quantities of benthic litter among streams (p < 0.001) and reaches (p < 0.001). Depleted reaches had consistently less benthic litter than either control or litter augmented reaches (Fig. 2). However, when the Reach x Stream interaction was included in the ANOVA (Model 1 of Newman et al. 1997), it was also significant (p = 0.011) (Table 2), indicating an inconsistent effect of litter treatment among streams. This effect was due to large quantities of benthic litter in the control reach of Mühlebach (Fig. 2). Accordingly, neither the interaction (p = 0.34) nor Stream (p = 0.13) remained significant when that stream was excluded from analysis, whereas Reach still had a virtually significant effect (p = 0.051). Tukey’s posthoc comparisons with this restricted data set showed that standing stocks in the litter augmented reaches were higher than in both the control and depleted reaches (p <0.001), and litter reduction in the depleted reaches approached significance (p = 0.08).

Table 2. Results of ANOVA performed on the standing stock of benthic litter dry mass.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stream</td>
<td>12.70</td>
<td>2</td>
<td>6.35</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Reach</td>
<td>22.32</td>
<td>2</td>
<td>11.16</td>
<td>5.44</td>
<td>0.07</td>
</tr>
<tr>
<td>Reach x Stream</td>
<td>8.21</td>
<td>4</td>
<td>2.05</td>
<td>3.35</td>
<td>0.011</td>
</tr>
<tr>
<td>Error</td>
<td>104.77</td>
<td>171</td>
<td>0.61</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Decomposition

Mesh and Stream were highly significant factors affecting leaf decomposition (Table 3). Reach, in contrast, had no significant influence nor was the interaction between Reach and Mesh significant. Decomposition in coarse-mesh bags was more variable across streams and reaches than in fine-mesh bags (Fig. 3A). As with benthic litter quantities, two of the streams (Andelsbach and Fohrenbach) showed similar patterns across reaches, whereas the pattern in Mühlebach differed (Fig. 3A). When ANOVA was performed separately on data from the two former streams, Reach approached statistical significance (p=0.08) and the interaction between Reach and Mesh became significant (p = 0.045). This was due to the consistent tendency of leaves in coarse-mesh bags to decompose faster in reaches of Andelsbach and Fohrenbach when amounts of benthic litter were lower (Fig. 3A). Decomposition in fine-mesh bags was highly consistent, with the mean differences in decomposition between the most rapid and slowest reach being less than 4% across all streams and reaches (Fig. 3B).
Table 3. ANOVA performed on percent leaf mass remaining among Reaches (depleted, control, enriched); Streams (Andelsbach, Fohrenbach, Mühlebach); and Mesh types (coarse, fine).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sum of squares</th>
<th>df</th>
<th>Mean square</th>
<th>F-ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stream</td>
<td>0.0481</td>
<td>2</td>
<td>0.0241</td>
<td>8.13</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Reach</td>
<td>0.0115</td>
<td>2</td>
<td>0.0057</td>
<td>1.94</td>
<td>0.15</td>
</tr>
<tr>
<td>Mesh</td>
<td>0.0929</td>
<td>1</td>
<td>0.0929</td>
<td>31.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mesh × Reach</td>
<td>0.0044</td>
<td>2</td>
<td>0.0022</td>
<td>0.74</td>
<td>0.48</td>
</tr>
<tr>
<td>Error</td>
<td>0.2961</td>
<td>100</td>
<td>0.0030</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Macroinvertebrates

Thirty-two taxa of macroinvertebrates were identified in coarse-mesh bags. Shredders accounted for 46% of all macroinvertebrates and consisted of stoneflies (*Amphinemura, Leuctra, Nemoura, Protonemura, Taeniopteryx*), limnephilid caddisflies, and the amphipod *Gammarus*. The genus *Nemoura* accounted for 60% of all shredders, and all stonefly shredders together for 77%. A considerable number of small nemourids was also found in fine-mesh bags (449 out of a total 1732), suggesting that roughly one third of the specimens in the coarse-mesh bags were very early instars, small enough to pass through 0.5 mm mesh. In contrast, only two individuals of *Gammarus* (<0.5% of the total number) were observed in fine-mesh bags, indicating that these shredders were typically larger. Most of the remaining individuals (39% of all macroinvertebrates) were chironomids. The numbers of other collector-gatherers, collector-filterers, scrapers, and non-chironomid predators were
consistently small across streams and reaches. Differences in invertebrate abundance between litter treatments were not detected for any functional feeding group.

![Bar graph showing benthic litter across reaches and streams](image)

Figure 2. Mean quantities of benthic litter across Reaches and Streams. Error bars denote ±1 SE, n=20 for each reach.

Total numbers of invertebrates differed among streams, but not among reaches within streams (Fig. 4A). Likewise, abundance of macroinvertebrates assigned to the shredder functional feeding group did not significantly differ among reaches and showed a pattern across streams and reaches similar to total invertebrates (Fig. 4B). Like patterns were also apparent for nemourid stoneflies, although here differences in numbers among reaches were significant (p=0.03) (Fig 4C). This difference in nemourid abundance is explained by the pattern observed in Mühlebach, where nemourids were less abundant in the litter depleted reach relative to the control and augmented reach. When Mühlebach was excluded from analysis, there were also significant differences among
streams (p < 0.001) and reaches (p < 0.05) in the number of *Gammarus* colonizing coarse-mesh bags (Fig. 4D). Andelsbach and Fohrenbach both showed a decreasing tendency in *Gammarus* abundance with increasing benthic litter quantities, while all reaches in Mühlebach had extremely low abundances of *Gammarus*. Tukey’s post-hoc comparisons among reaches in Andelsbach and Fohrenbach indicated that litter augmented reaches had significantly fewer *Gammarus* than depleted reaches, while control reaches did not differ from either depleted or augmented reaches.

Figure 3. Mean leaf mass remaining in (A) coarse-mesh bags and (B) fine-mesh bags after 41 days of decomposition in litter-depleted, litter-augmented and control reaches of three streams. Error bars denote ±1 SE, n = 6 for each reach and mesh type.

*Benthic Litter Removed from Depletion Reaches*

Amounts of litter removed from the depleted reaches varied among streams. A total of 7.2 kg dry mass was collected in Andelsbach, 7.7 kg in
Fohrenbach, and 21.8 kg in Mühlebach, corresponding to a depletion of 72, 51 and 189 g/m² of stream channel. The mass of benthic litter removed from depletion reaches declined over the first month after litter traps were installed and subsequently remained at a low level (Fig. 5). An exception to this pattern is the marked increase in benthic litter removed from Mühlebach in late November, a time that coincided with increased stream flow in this watershed but not the two others.

Figure 4. Mean number of (A) total macroinvertebrates, (B) total shredders, (C) nemourid stoneflies and (D) *Gammarus* in coarse-mesh bags after 41 days of leaf decomposition in litter-depleted, litter-augmented and control reaches of three streams. Error bars denote ±1 SE, n = 6 for each reach.
Figure 5. Dry mass of benthic litter removed from each of the litter-depleted reaches through time. The abrupt increase observed in the Mühlebach on 25 November coincided with a rainfall event in this watershed and not the others.

Discussion

Previous studies on the effects of litter depletions on decomposition in streams have yielded equivocal responses, but most have reported an acceleration of decomposition when benthic litter was scarce (e.g., Webster and Waide 1982, Benfield 1991, Tank and Webster 1998, Benfield et al. 2001). Results from coarse-mesh bags in two of our three study streams are consistent with this pattern in that leaf decomposition tended to be fastest in litter-depleted and slowest in litter-augmented reaches. We hypothesized that the mechanism behind such an acceleration or slowdown of decomposition is shredder aggregation in experimental leaf bags in an otherwise resource-depleted environment, whereas shredders would be distributed across a large number of resource islands in control and especially litter augmented stream reaches. Testing of these hypotheses requires demonstration 1) that shredders caused significant litter mass loss and 2) that they aggregated in experimental leaf bags in reaches where benthic litter was scarce, and vice versa.
The first requirement was met in our study streams, as evidenced by significantly faster decomposition in coarse-mesh compared to fine-mesh bags. Aggregation by shredders was less evident, because total numbers of macroinvertebrates, shredders or nemourid stoneflies did not follow the expected pattern. However, distribution across stream reaches of a leaf-shredding amphipod, *Gammarus*, supports the idea that this shredder converged on the resource islands provided by our experimental litter bags, as hypothesized. Specifically, *Gammarus* was more abundant in bags placed in litter-depleted reaches and rarer in litter augmented reaches. This pattern matched both those of benthic litter quantities and leaf decomposition in the two study streams where litter manipulations were successful (i.e. Andelsbach and Fohrenbach). *Gammarus* are very effective leaf shredders (Groom & Hildrew 1989, Baldy & Gessner 1997, Dangles et al. 2004), can show highly selective feeding behavior (Bärlocher & Kendrick 1973, Arsuffi & Suberkropp 1989), and more than other invertebrates in our study, are highly mobile and thus have the ability to actively seek out and make use of resource islands. Furthermore, *Gammarus* were almost never encountered in fine-mesh bags (0.5 mm mesh size). This suggests that specimens were larger and more effective as comminuting leaves than other taxa assigned to the shredder functional feeding group. For example, the numerically abundant nemourid stoneflies were often found in fine-mesh bags, indicating that a large proportion of them were early instars with limited capacity to shred leaves. Collectively this evidence suggests, thus, that *Gammarus* aggregating in experimental litter bags were instrumental in causing the decomposition patterns we observed across stream reaches in response to benthic litter manipulations.
Our second hypothesis, that greater quantities of benthic litter result in faster microbial decomposition relative to control and litter-depleted reaches, was not supported by the results of our experiment. The rationale behind this hypothesis was that larger amounts of decomposing benthic litter increase concentrations of fungal spores in stream water. As a result, increased fungal inoculum could accelerate fungal colonization of fresh litter and thus microbial decomposition, as has been previously observed in a microcosm experiment (Treton et al. 2004). Furthermore, fungal spore concentrations in stream water were increased in stream reaches to which logs or litter traps (identical to those used in the present study) had been added as retention structures (Laitung et al. 2002). It is unknown whether litter manipulation increased fungal spore output also in the present experiment. However, if it did, the effect on decomposition was negligible because mass loss of leaves in fine-mesh bags was highly consistent across treatments in all three of our study streams. This finding is in contrast with the results from a wood decomposition experiment conducted by Tank and Webster (1998) who observed increased decomposition rates of wood veneer and elevated cellulase activity and fungal biomass associated with veneers in a litter-exclusion stream relative to a control stream. However, wood and leaf-litter decomposition in streams differ in many respects, one of them being distinct communities of fungi developing on the two substrates (Shearer 1992, Gessner and van Ryckegem 2003), so that apparent discrepancies between these studies should be interpreted with caution.

A distinction between the experiment presented here and whole-stream litter exclusion experiments is that shredders and fungal spores could drift into experimentally augmented or depleted reaches from unmanipulated stream sections upstream. It is possible, therefore, that we did not
observe stronger effects because movement of invertebrates and fungal spores into and/or out of experimental reaches counteracted local effects of the benthic litter treatments. Additionally, the manual removal of litter from our depleted reaches unavoidably resulted in localized mortality to invertebrates residing in the natural litter accumulations, because not all individuals could be washed from the litter. Further losses of macroinvertebrates may have occurred by downstream drift induced by the physical disturbance associated with the weekly litter depletions. Thus, local abundance of shredders and other macroinvertebrates, and hence potential to colonize experimental leaf packs, was likely reduced in the litter-depleted reaches, thus weakening the effect of shredder aggregation on decomposition of experimental leaf packs.

In contrast to large-scale litter-depletion experiments, investigations involving litter augmentation are typically conducted at smaller spatial scales and mainly looked at responses of macroinvertebrates to altered litter availability rather than at effects on litter decomposition or other processes. Shredders have shown positive responses where benthic litter quantities were experimentally elevated (Dobson et al. 1992, 1995; Reice 1991). For example, in streamside experimental channels where amounts of benthic leaf litter were varied, shredders responded to greater litter availability by both higher density and biomass (Richardson 1991). Similarly, boulders or litter traps installed in stream channels markedly increased abundance of both benthic litter and invertebrates relative to controls (Dobson et al. 1992, Negishi and Richardson 2003). However, in a similar boulder introduction experiment that also yielded increased litter retentiveness, shredder abundance in the benthos was not influenced (Lepori et al. 2005; see also Wallace et. al 1995). Like shredder abundance, leaf-decomposition rates determined in the latter experiment,
were similar between treatment and control reaches (Lepori et al. 2005). This consistency lends indirect support to the hypothesis that shredders are important in accelerating leaf decomposition in resource-limited environments.

One of the streams in the present study, the Mühlebach, showed different response patterns than the two other streams in several respects. The control reach of this stream flowed along the base of a steep, densely vegetated hillslope which delivered large lateral inputs of litter to the channel and resulted in quantities of benthic litter higher than those in the litter augmented reach. As a consequence, relative amounts of benthic litter in the three reaches of this stream differed from those intended by our manipulations. Furthermore, Gammarus were very rare in all three reaches of this stream. If our conclusion above about the critical role of Gammarus in leaf decomposition is correct, then lack of this species in this stream would explain why patterns across reaches in leaf mass remaining in litter bags did not mirror shredder abundances, although patterns in benthic litter quantities mirrored decomposition rates.

Ecosystem ecologists and resource managers are often interested in ecological phenomena occurring at large scales (e.g., effects of landuse change, climate change, or atmospheric nitrogen deposition on ecosystem properties), yet an analysis by Wiens (1989) showed that more than 80% of field experiments are conducted on plots of less than 1m². In light of the fact that results from small-scale investigations often differ from those performed at larger scales (Wiens 1989), there is clear need for large-scale field manipulations as an approach to understand ecosystem dynamics (e.g. Carpenter et al. 1995, 1998) - an approach that can provide key insights (Schindler 1974, Maron et al. 2006). Unfortunately,
practical constraints often limit the replication of experimental treatments which in turn limits the degree to which results from ecosystem experiments can be extrapolated to other systems. The need for treatment replication may be particularly acute in stream and river ecosystems which are generally thought to be highly heterogeneous environments across time and space (Vannote et al. 1980; Frissell et al. 1986; Thorp et al. 2006; Tockner et al. 2003; Malard et al. 2006). The results presented here underscore the notion that appreciable heterogeneity can exist within and among-streams. These results also emphasize that in the absence of replication, extrapolation of results beyond the particular ecosystem on which the experiment was conducted, can be an uncertain venture.

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Literature Cited


stream of southwestern British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 60:247-258.


Chapter 5

Cotton strips as a leaf surrogate to measure decomposition in river floodplain habitats

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Abstract

Leaf-litter assays have advanced our understanding of decomposition processes in both terrestrial and aquatic ecosystems. Some shortcomings inherent in the technique may be overcome through use of a cotton-strip assay. Key assumptions for using cotton strips as proxies for natural leaves are: 1) decomposition rates of the 2 materials are related, and 2) the materials decay in a similar way when exposed to the same environmental conditions. These assumptions were tested by comparing cotton-strip decomposition (loss of tensile strength and mass) and leaf decomposition (mass loss) across different floodplain habitats of the Tagliamento River (northeastern Italy). Patterns of loss of cotton-strip tensile strength and leaf mass were broadly comparable across river channels, ponds, and terrestrial sites. Differences between river channels and ponds were greater for loss of cotton-strip tensile strength than leaf mass, indicating that, in some situations, loss of cotton-strip tensile strength may be more sensitive to differing environmental conditions than loss of leaf mass. Loss of cotton-strip mass was less sensitive than loss of either tensile strength or leaf mass. Although combined data from all floodplain sites and additional sites in Swiss streams yielded a curvilinear relationship between loss of cotton-strip tensile strength and mass, the slope was extremely steep in the range of 20 to 30% mass loss (corresponding to 0 to 95% loss in tensile strength), indicating that inferring one variable from the other is unreliable. Leaf mass loss was significantly correlated with loss of tensile strength in fine- and coarse-mesh bags in ponds and in coarse-mesh bags in terrestrial sites. However, these correlations were relatively weak \((r = 0.50–0.63)\), suggesting that loss of tensile strength did not accurately reflect leaf mass loss. Thus, the cotton-strip assay should not be used uncritically as a surrogate for leaf-
litter assays, but it has potential as a standardized method to measure organic-matter decomposition in fluvial settings and as a functional indicator for stream assessment.

**Key words:** cotton-strip assay, standardization, stream ecology, habitat heterogeneity, Tagliamento River, litter breakdown, bioassessment.

**Introduction**

Leaf decomposition is a vital process in forested stream and floodplain ecosystems (Cummins et al. 1989, Wallace et al. 1997). Current understanding of this process has been advanced mainly through use of the leaf-litter assay (e.g., Petersen and Cummins 1974, Gessner et al. 1999, Webster and Benfield 1986) in which leaf material is incubated in the field and later retrieved to determine leaf mass remaining and other response variables related to decomposition. The leaf-litter assay, adopted by stream ecologists from soil scientists (e.g., Bocock and Gilbert 1957), attempts to mimic decomposition of naturally occurring litter in streams (Cummins et al. 1980, Webster et al. 2001). However, the approach has some important shortcomings (Webster and Benfield 1986, Boulton and Boon 1991).

Limitations of the leaf-litter assay can stem from variability in leaf quality (Wallace et al. 1996, Benfield et al. 2001). Pronounced differences in leaf quality result in a wide continuum of decomposition rates across species (Petersen and Cummins 1974, Webster and Benfield 1986, Gessner and Chauvet 1994). Individual studies can control for this variability by using one or several model species (e.g., Wallace et al.
2005); however, broader synthesis is hampered because different species
are used across studies. Even within a given species, variation in leaf
quality and decomposition rate can be significant; it can result from
variation among genotypes (Leroy et al. 2006), differences in edaphic or
meteorological factors (Austin 2002), or herbivore-induced plant defenses
(Irons et al. 1991). Light gradients in the canopy may lead to variation in
leaf quality even among leaves from individual trees (Sariyildiz and
Anderson 2003). Regardless of its cause, variability among batches of
leaves creates statistical noise in data sets, and it can call the validity of a
study into question when care is not taken to ensure that a homogeneous
batch of leaf material is used across treatments (e.g., at different sites or
in different years). In addition, variability in leaf quality can mask an
ecologically meaningful effect if within-species variability is large and
the level of replication is constrained by practical considerations. This
problem may be particularly acute when leaf decomposition is used in
bioassessment (Maltby and Booth 1991, Wallace et al. 1996, Gessner and
Chauvet 2002, Lepori et al. 2005) where costs tend to limit the number of
experimental units.

Cotton strips, which have been used widely in soil science (Treonis et al.
2002, van Gestel et al. 2003), may offer a solution to the problems of
within- and among-leaf species variability. However, their potential has
not been fully explored in fluvial environments (but see Hildrew et al.
1984, Boulton and Quinn 2000, Claret et al. 2001). Cellulose, a major
constituent of both cotton strips and leaf litter (Roberts and Rowland
1998), is a suitable substrate for leaf-colonizing fungi (Singh 1982) and
bacteria (Rabinovich et al. 2002) and can serve as a food source for some
leaf-shredding stream invertebrates (Sinsabaugh et al. 1985). Decay of
cotton strips can be measured by determining mass loss (Eggliswaw 1972), as is usually done for leaf litter, but more commonly, loss in cotton-strip tensile strength is used as the response variable (Boulton and Boon 1991). The standard quality of cotton strips, in contrast to natural leaves, could be especially useful in studies that compare different sites or detect change through time, including functional bioassessment of stream ecosystems.

Cotton strips also offer other advantages. Loss of cotton-strip tensile strength tends to occur much faster than mass loss of leaf litter from typical riparian trees. As a result, incubation times in the field can be kept short, making cotton strips less susceptible to damage or loss by vandalism or flooding and especially useful in environments where leaves decompose slowly (Newman et al. 2001). Moreover, cotton strips are less prone to fragmentation than leaves (Eggliswaw 1972), are smaller than the leaf packs and leaf bags usually used in decomposition experiments, more transportable, and free of nutrients such as N and P. This lack of nutrients may be particularly useful when the effects of dissolved nutrients on litter decomposition are of interest (e.g., Newman et al. 2001). Thus, cotton strips may be a good surrogate for assessing patterns of organic-matter decomposition in fluvial environments.

An important consideration for using cotton strips as a surrogate for natural leaves is that a strong relationship exists between decay rates of leaves and cotton strips (Howard 1988), but the extent to which cotton-strip assays reflect decomposition of natural litter is not currently known. Therefore, the goal of our study was to ascertain whether patterns of cotton-strip decomposition mimic those of natural leaves. We compared leaf mass loss to losses of cotton-strip tensile strength and mass across a
range of river floodplain habitats to address the questions: 1) Does cotton-strip decomposition match leaf-litter decomposition across differing environmental conditions? 2) Are losses of leaf mass and cotton-strip tensile strength correlated? 3) Can loss of cotton-strip tensile strength be predicted from loss of cotton-strip mass?

**Methods**

The main portion of our study was conducted on the Tagliamento River, a 7th-order gravel-bed river that drains the Julian Alps of northeastern Italy. The experiment was initiated in December 2002 shortly after peak leaffall in the area. The island-braided reach of the river (river km 79.8–80.8, 135 m asl) selected for study has a variety of distinct habitats (Tockner et al. 2003, Langhans et al. 2006, Langhans and Tockner 2006; Fig 1). Sites were chosen in 7 habitat types (4 replicate sites in each habitat type, 28 sites total; described in Tables 1, 2). Habitat types were classified into 3 broader categories: river channels, ponds, and terrestrial habitats.

Coarse- and fine-mesh bags (mesh sizes = 10 mm and 0.5 mm, respectively) were used to allow or exclude macroinvertebrates and to facilitate estimation of decomposition attributable to invertebrates or microbes. Two types of substrate were placed in each leaf bag: 1) air-dried, recently senesced leaves (5.00 ± 0.25 g) from black poplar, *Populus nigra* L., the dominant tree species on the Tagliamento floodplain (Karrenberg et al. 2002), and 2) a single cotton strip. Cotton strips (4 cm × 6 cm) were cut from Shirley Soil Burial Test Fabric (Shirley Institute, Manchester, UK). This standardized fabric consists of 100% unbleached cotton (96% cellulose). Groups of 10 cotton strips
were wrapped in aluminum foil and autoclaved (Howson 1988) for 20 min at 120°C before being placed in the mesh bags.

Pairs of coarse- and fine-mesh bags were randomly assigned to the 28 sites. Five pairs of bags were fixed at each site with rope and an iron rod (280 mesh bags total). After 17, 31, 49, 61, or 80 d of incubation, 1 pair of bags was removed from each site, placed in a plastic bag, and transported to the laboratory. Each bag was emptied into a shallow plastic tray that contained several centimeters of tap water. Each side of the cotton strip and leaves was cleaned with a soft-bristled paint brush to remove adhering debris. Cleaned leaves were oven-dried to constant mass and weighed. Cleaned cotton strips were soaked in 70% ethanol to inhibit microbial decay during storage (Correll et al. 1997), then air dried, and stored individually in small plastic bags until tensile strength and mass were determined at a later time.
Fig. 1. The braided-island reach of the Tagliamento River showing locations of sites. Numbers correspond to habitat types, and the letters (a–d) correspond to replicates within habitat types (n = 28 sites). The small dark features in the active channel indicate patches of large wood and vegetation, whereas those in the riparian forest indicate orthofluvial ponds.

A complementary study was conducted in 20 low-order streams in Switzerland with similar general characteristics. Streams were 2nd or 3rd order, had elevations ranging from 350–700 m asl, and drained calcareous watersheds. Fifteen streams drained fully forested watersheds and 5 flowed through pastures. Cotton strips were deployed in a manner similar to that used in the study on the Tagliamento floodplain. Cotton strips were retrieved from streams after 42–51 d and processed as described above.
Table 1. Mean (±1 SE) physical and chemical characteristics of aquatic habitat types on the Tagliamento River floodplain during the experiment. Temperature was measured continuously at each site.

<table>
<thead>
<tr>
<th>Variable</th>
<th>River channel</th>
<th>Paraluvial ponds</th>
<th>Orthofluvial ponds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water temperature (°C)</td>
<td>9.3 ± 0.5</td>
<td>8.0 ± 0.8</td>
<td>7.4± 0.8</td>
</tr>
<tr>
<td>Conductivity (µS/cm)</td>
<td>445 ± 56</td>
<td>451 ± 58</td>
<td>465 ± 70</td>
</tr>
<tr>
<td>pH</td>
<td>8.2 ± 0.1</td>
<td>8.1 ± 0.1</td>
<td>7.8 ± 0.0</td>
</tr>
<tr>
<td>O₂ (mg/L)</td>
<td>12.4 ± 1.0</td>
<td>12.5 ± 2.1</td>
<td>11.5 ± 1.9</td>
</tr>
<tr>
<td>NH₄-N (mg/L)</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>NO₃-N (µg/L)</td>
<td>656 ± 34</td>
<td>395 ± 52</td>
<td>580 ± 143</td>
</tr>
<tr>
<td>Soluble reactive P (µg/L)</td>
<td>&lt;5</td>
<td>&lt;5</td>
<td>&lt;5</td>
</tr>
</tbody>
</table>

Tensile strength of all cotton strips was measured with an Instron Series IX Tensiometer (Instron Corporation, Canton, Ohio). Measurements were made at 20°C and 65% relative humidity in a climate-controlled room. Five randomly selected cotton strips were used to determine the mean and standard deviation of preincubation tensile strength (631 ± 17 kg) and mass (497.0 ± 4.3 mg). Strips were soaked in ethanol and air dried before measurements were made as a procedural control. Individual cotton strips were not weighed initially because of very low variability among strip masses (coefficient of variation <1%). Some strips were not included in analyses because they were too decomposed to determine tensile strength with confidence.
Table 2. Mean (±1 SE) physical and chemical characteristics of terrestrial habitat types on the Tagliamento River floodplain during the experiment. Temperature was recorded continuously with at each site. Relative humidity was measured once at each site.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Exposed gravel</th>
<th>Large wood</th>
<th>Island</th>
<th>Riparian forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean air temperature (°C)</td>
<td>3.5</td>
<td>3.5</td>
<td>4.1</td>
<td>3.4</td>
</tr>
<tr>
<td>Temperature range (°C)</td>
<td>-6.8–36.3</td>
<td>-6.8–36.3</td>
<td>-5–36.1</td>
<td>-3.7–26.6</td>
</tr>
<tr>
<td>Mean relative humidity (%)</td>
<td>72</td>
<td>95</td>
<td>97</td>
<td>96</td>
</tr>
<tr>
<td>Humidity range (%)</td>
<td>20–100</td>
<td>63–100</td>
<td>35–100</td>
<td>26–100</td>
</tr>
</tbody>
</table>

Exponential decay coefficients \( (k) \) were calculated for leaves (mass loss) and cotton strips (tensile-strength loss) by fitting data to a simple exponential decay model, \( X_t = X_0 e^{-kt} \), where \( X_t \) is the cotton mass, leaf mass, or tensile strength upon removal of the litter bags from the field, \( X_0 \) is the initial value, and \( t \) is the elapsed time in days. Pearson correlation coefficients were calculated between loss of cotton-strip tensile strength and leaf mass loss. Separate 2-way analyses of variance (ANOVA) were used to test for differences in leaf and cotton-strip decay coefficients between the 2 mesh types (fixed factor) and among the floodplain habitat types (fixed factor). When a significant habitat effect was detected, weighted contrasts were used to test for differences between pairs of the 3 broad habitat categories (i.e., river channels vs ponds, ponds vs terrestrial sites, and river channels vs terrestrial sites). Contrasts were weighted by
the number of habitat types in each habitat category. Paired 1-tailed \( t \)-tests were used to test the hypothesis that decay coefficients of cotton strips and leaves in individual habitat categories were greater in coarse-mesh than fine-mesh bags. Data did not perfectly meet test assumptions of homoscedasticity and normality (Kolmogorov–Smirnov test), but in light of the robustness of ANOVA and \( t \)-tests to moderate violations of these assumptions (Box 1954), their use was deemed acceptable. Analyses were done using Systat 10 (Systat Software, Point Richmond, California) except for \( t \)-tests which were run in Microsoft Excel 2003.

Results

Decay rates of cotton strips (tensile strength and mass) and leaves (mass) were faster in river channels than in ponds and terrestrial sites (Fig. 2A, B). Leaf mass loss was the only measure that differed significantly between ponds and terrestrial sites. Significant interactions between mesh size and habitat type were also observed for both types of cotton-strip decay rates, but not for leaf mass loss (\( p = 0.07 \)). Both cotton-strip decay rates were significantly higher in coarse-mesh than fine-mesh bags in river channels, and leaf decay rates tended to be higher in coarse-mesh than in fine-mesh bags (\( p = 0.052 \); Fig 2A, B). None of the decay rates differed between mesh types in ponds (Fig 2A, B). In terrestrial habitats, rates of leaf and cotton-strip mass loss differed between mesh types, but rates of loss of cotton-strip tensile strength did not (Fig 2). Statistical detection of the very minor differences in mean decay rate between coarse- and fine-mesh bags in terrestrial habitats (Fig. 2A, B) were a consequence of extremely low within-habitat variability and large total sample size.
Leaf mass loss and loss of cotton-strip tensile strength were not consistently correlated across habitat categories and mesh types except in pond habitats (Table 3). Even in pond habitats, significant correlation coefficients were low (ranging between 0.50 and 0.63) and strong curvilinear relationships were not detected either. This result indicates that loss of cotton-strip tensile strength captured only a modest amount of variability in leaf mass loss across floodplain habitats.

Combined data from the habitats on the Tagliamento floodplain and the Swiss streams showed that the range of losses of cotton-strip tensile strength (0–99%) corresponded to a much narrower range of losses of cotton-strip mass (most values between 20–60%; Fig. 3). Loss of cotton-strip tensile strength at Swiss sites was rapid, and as a result, most data points clustered in the upper portion of the graph. Overall, a curvilinear relationship emerged that was characterized by an extremely steep increase in tensile-strength loss between ~20% and 30% mass loss and a nearly 100% loss of tensile strength when only ~45% of mass had been lost.
Fig. 2. Mean (±1 SE) exponential decay rates \((k)\) of \(Populus\ nigra\) leaves (mass loss) and cotton strips (loss of tensile strength and mass) in coarse-mesh (A) and fine-mesh (B) bags in 3 habitat categories (4 river sites, 8 ponds, and 20 terrestrial [terr] sites) on the Tagliamento floodplain. Horizontal lines over bars indicate no significant difference between habitat categories. Vertical black lines between bars indicate no significant difference between coarse- and fine-mesh bags within habitats. \((*) = p = 0.052, * = p < 0.05, ** = 0.001 < p < 0.01, *** = p < 0.001.\)

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Fig. 3. Relationship between loss of tensile strength and mass of cotton strips across all sites from the Tagliamento floodplain and 20 low-order streams in Switzerland.

Discussion

Variation in cotton-strip decay broadly matched the variation in leaf decay across different habitat categories on the Tagliamento floodplain. Decomposition in the river channel was significantly faster than decomposition in ponds or terrestrial sites, regardless of whether cotton-strip tensile strength, cotton-strip mass, or leaf mass were used as an indicator variable. This broad match of patterns across habitats is consistent with the findings of Baldy et al. (2002), who observed faster decay of *P. nigra* leaves in the main river channel compared to a floodplain pond (oxbow lake) in southwestern France, and of Gurtz and Tate (1988), who measured faster decay of hackberry leaves in a stream channel relative to a nearby terrestrial site in Kansas, USA. In coarse-mesh bags, the ratio between rates of decay in river channels and ponds was >6× higher for cotton strips (measured as loss of tensile strength)
than for *P. nigra* leaves (measured as mass loss) in our study and 12× higher than for *P. nigra* leaves in the study by Baldy et al. (2002). However, cotton-strip mass loss was less sensitive than leaf mass loss to differences between habitats, with the ratio of decay rates in channels and ponds >4× greater for cotton-strip tensile strength than for leaf mass. Thus, loss of tensile strength, but not mass, of cotton strips can be a more sensitive measure of differences in environmental conditions than leaf mass loss. These results suggest that, in some instances, cotton strips can be an appropriate and sensitive surrogate for natural leaf material in decomposition experiments done in fluvial environments.

A consideration for using cotton strips as a surrogate for natural leaf material in decomposition studies is that decomposition rates of both materials are related. In several instances loss of cotton-strip tensile strength and leaf mass were correlated in the present study. However, loss of cotton-strip tensile strength failed to predict loss of leaf mass precisely, suggesting that cotton strips and leaves capture different aspects of organic-matter decomposition. Cotton strips were typically in a more advanced state of decay than the leaf material when our experiment was terminated. Because leaf species vary widely in their decay rates (Petersen and Cummins 1974, Webster and Benfield 1986, Gessner and Chauvet 1994), strength of the relationship between loss in leaf mass and cotton tensile strength could hinge on the particular leaf species used, and correlations with cotton-strip decay might have been stronger had a faster-decomposing species been used. However, even if stronger relationships exist in other circumstances, loss of cotton-strip tensile strength should not be equated indiscriminately with leaf mass loss, but rather should be used as an indicator of cellulose decomposition in its
own right (Hildrew et al. 1984, Boulton and Quinn 2000).

Leaf-shredding invertebrate taxa were rare or absent in a survey across the aquatic habitats within our study reach (Arscott et al. 2005). This fact, the modest or nonsignificant differences in rates of decay of leaves and cotton strips in coarse- and fine-mesh bags, and the low abundance of macroinvertebrates in litter bags in all habitats except the river channel (SDL, SDT, MOG, and KT, unpublished data) suggest that shredding by invertebrates was not a major cause of decay in most habitats on the Tagliamento floodplain. In other situations, invertebrates can be important agents of litter decomposition (Webster and Benfield 1986). For example, leaf decay rates in fine-mesh bags were \(~1/2\) the rates in coarse-mesh bags in a polluted river (Pascoal et al. 2005), and in a more natural mountain stream, shredders were estimated to contribute to \(>1/2\) of the overall leaf mass loss (Hieber and Gessner 2002). Likewise, Cuffney et al. (1990) observed up to 74% reduction in decomposition rate when shredder abundance was experimentally reduced with insecticide in a small headwater stream.

The palatability of cotton strips and extent to which stream invertebrates feed on them is not well known, but both may depend on the degree to which cotton strips are conditioned by microorganisms, as is the case with leaf litter in streams (Suberkropp 1992, Graça 2002). The short time that cotton strips typically reside in the field may limit accrual of microbial biomass even when microbial activity is pronounced. Thus, cotton strips could prove most useful as an integrator of decomposition through microbial activity rather than through invertebrate shredding. The idea that cotton strips are more appropriate for determining microbial than invertebrate activity is corroborated by a terrestrial study in which loss of cotton-strip tensile strength was not correlated with invertebrate
density (van Gestel et al. 2003).

Cotton strips consist almost entirely of cellulose, whereas leaves contain a complex of structural and other compounds whose full degradation requires a suite of enzymes. As a consequence, different mechanisms are likely to be involved in the decomposition of cotton and leaves. For example, leaf decomposition in streams is mediated to a significant extent by pectinases (Jenkins and Suberkropp 1995), which degrade the middle lamellae of plant tissues and result in leaf disintegration, a process that would not occur with cotton strips. Microbial leaf decomposition in streams is largely caused by leaf-degrading fungi (aquatic hyphomycetes). The degree to which aquatic hyphomycetes colonize and degrade cotton is not currently known, but these fungi are capable of degrading cellulose (Singh 1982), suggesting that they may colonize and degrade cotton strips as well.

One drawback of the cotton-strip assay is that a tensiometer, an instrument required to measure tensile strength, is not readily available to many researchers. Therefore, measuring cotton-strip mass loss instead of loss of tensile strength could be useful, provided that loss of mass is correlated with loss of tensile strength. Our study and others in streams (Egglishaw 1972) and soils (Latter and Howson 1977) indicate that the relationship between loss of cotton-strip mass and tensile strength is curvilinear, although the specific relationship may depend on the particular conditions of the study (e.g., soil, stream, experimental procedures; Latter and Howson 1977). In our study, the fact that the steep slope of the relationship in the narrow range of 20 to 30% mass loss corresponds to 0 to 95% loss in tensile strength is a matter of concern. Thus, sensitivity of the cotton-strip assay may be greatly diminished if it
is based on mass loss rather than loss of tensile strength, as has been observed elsewhere (A. J. Boulton, University of New England, Armisdale, Australia, personal communication).

Last, cotton strips could be useful in comparative studies, especially in stream bioassessment where a need exists to include functional criteria as a complement to traditional structural criteria (Wallace et al. 1996, Boulton 1999, Gessner and Chauvet 2002). The cotton-strip assay has been shown to be sensitive to human activities (Chew et al. 2001, Rapp et al. 2001) and to different environmental conditions (our study). It has been advocated as a means to assess soil health (Trettin et al. 1996, Chew et al. 2001, Rapp et al. 2001), and it was also useful to assess effects of siltation in a New Zealand stream (Boulton and Quinn 2000). Thus, although the cotton-strip assay should not be used uncritically as a surrogate for natural leaf decay, it has potential as a standard method for measuring some aspects of organic-matter decomposition in fluvial environments, and it may prove useful for assessing the health of river floodplain systems.

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**Literature Cited**


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Tiegs, S.D., and M.O. Gessner. (draft). Vertical Hydrologic Exchange Affects Leaf-litter Decomposition and Decomposer Community Structure. for Ecosystems
Tiegs, S.D., P. Akinwole and M.O. Gessner. (draft). *Spatial Variability of Leaf-litter Decomposition Across Multiple Scales.* for *Journal of the North American Benthological Society*


Tiegs, S.D., A. Wagenhoff and M.O. Gessner. (in preparation). *Decomposition of Alien vs. Native Poplar Leaves under Ambient and Elevated Nutrient Conditions.* for *Freshwater Biology*

**Other Publications**


**Conference Presentations**


