Arch. Hydrobiol. **163** 2 211–223 Stuttgart, June 2005

Food web properties in aquatic microcosms with litter mixtures are predictable from component species

Martin Schädler[1], **Tanja Rottstock** and **Roland Brandl**

University of Marburg, Faculty of Biology – Dept. Animal Ecology

With 4 figures

Abstract: Many aquatic systems depend on allochthonous organic matter. Quality of litter differs between plant species. Therefore, the composition of the surrounding vegetation may influence litter decomposition and other processes in aquatic food webs. We recorded the abundance of insect larvae, as well as the diversity of cultivable fungi and bacteria, the metabolic diversity of the microflora, and leaf litter decomposition rates in aquatic outdoor microcosms, using litter from four broad-leaved tree species and a mixture of the four litter types. Diversity of fungi, abundance of bacteria and functional diversity of the microflora and decomposition differed between microcosms with litter from each of the four tree species. For microcosms with the mixture of litter, observed values of all measured variables did not differ from the expectations derived from microcosms with litter from only one tree species. We conclude that specific traits of the component litter species (e. g. C/N ratio) outweigh possible non-additive effects in mixtures. Our results contrast with findings in terrestrial systems where decomposition rates of mixtures are not always predictable from the rates measured for the component species.

Key words: allochthonous litter, litter decomposition, microflora, insect larvae, temporary ponds.

Introduction

The importance of litter from terrestrial plants for aquatic systems has long been recognized (for river ecosystems e. g., MINSHALL 1967, EGGLISHAW 1968; lake ecosystems e. g., RICH & WETZEL 1978). Although litter is not the

[1] **Authors' address:** University of Marburg, Faculty of Biology, Dept. Animal Ecology, Karl-von-Frisch-Straße, 35032 Marburg, Germany;
E-mail: schaedle@staff.uni-marburg.de

DOI: 10.1127/0003-9136/2005/0163-0211 0003-9136/05/0163-0211 $ 3.25
© 2005 E. Schweizerbart'sche Verlagsbuchhandlung, D-70176 Stuttgart

only basal resource in temporary ponds, terrestrial litter is the major energy source for aquatic food webs in these systems. Thereby, food web structure may depend on the traits of litter. Due to the differences in the chemical composition (e. g. concentration of nutrients, contents of carbon-based secondary compounds), the available energy for the food web will differ between litter from different plant species. Consequently, not only the structure of the aquatic food web but also ecosystem processes within the aquatic community may depend on the composition of the surrounding vegetation.

Studies on terrestrial ecosystems suggested that the structure of detritivore food webs and associated ecosystem processes depend on the traits of litter from different plant species. Furthermore, ecosystem processes showed unpredictable changes when supplied with mixtures of litter (Wardle 2002, Wardle & van der Putten 2002). Explanations for these non-additive effects in mixtures of litter from different plant species range from physical, chemical to biological processes (reviewed in Gartner & Cardon 2004). For instance, litter mixtures may provide a greater structural diversity and thereby a greater number of microhabitats for decomposers (Hansen & Coleman 1988), or nutrients and secondary compounds may become transferred between litter types, sometimes mediated by the microflora (Gartner & Cardon 2004).

Against the background of the ongoing and lively debate on the importance of species diversity on the stability and the functioning of ecosystems (Loreau et al. 2002), there is a need to explore the processes and mechanisms behind these patterns. The effects of species mixtures of living plants have already attracted a number of investigators. However, the "after life effects" (Findlay et al. 1996) of plant material remain poorly investigated.

The use of artificial aquatic microcosms has increased our understanding of the patterns and processes within aquatic food webs (Kitching 2001). Therefore, these systems may also become model systems for the study of litter composition and litter species richness on food web structure and ecosystem processes in aquatic systems (Petchey et al. 2002). Experiments are, however, still rare. The aim of our study was to evaluate the importance of litter type and litter mixing on certain food web components and litter decomposition rates. We approached the following questions: (1) Does litter from different plant species change diversity and abundance of food web components? (2) Do these changes translate into different decomposition dynamics? (3) Do multi-species assemblages of litter influence decomposers and decomposition rates in a non-additive way? We focussed on the microflora and insect larvae since they represent a large proportion of biomass of the food webs in temporary ponds.

Methods

Experimental set-up

In autumn 2001, freshly fallen leaf litter of four tree species with no sign of decomposition was collected and dried at room temperature (oak *Quercus robur*, ash *Fraxinus excelsior*, beech *Fagus sylvatica*, maple *Acer platanoides*). These species were chosen as they are common in the study area. Contents of carbon and nitrogen of litter species (assessed from three subsamples of leaves using an element analyser; Elementar, Hanau, Germany) were 0.91 % N, 45.1 % C, C/N ratio 49.6 for oak, 1.07 % N, 45.4 % C, C/N ratio 42.4 for beech, 1.67 % N, 41.6 % C, C/N ratio 24.9 for ash and 0.99 % N, 43.6 % C, C/N ratio 44.0 for maple. To establish the microcosms we used plastic containers (21 cm diameter, 18 cm height) filled with 2.5 l of tap water. Each container had an overflow to maintain a constant water level during rain. During dry weather, we added water to the containers to keep the water level constant. The general chemistry of the water was representative for temporary ponds in the area around Marburg, with a pH value of about 6.5 and a calcium concentration of 39 mg/l (unpublished data). Furthermore, tap water was free of chlorine which is known to prevent microbial growth (personal communication, water authorities of Marburg). Containers were covered by a net to avoid litter fall from the surrounding vegetation, while allowing free access of insects (mesh width 12 × 12 mm). The experimental setup allows for colonization of microcosms via air only, which may be considered a general shortcoming of microcosm experiments. However, for the insect larvae as well as for specialised microorganisms this reflects the natural way to colonize temporary ponds. Hence, using water and other possible inocula from a natural system would have introduced organisms not typical for temporary ponds. Nevertheless, the reader should be aware that our experimental setting restricts the diversity of the food webs to species arriving via air.

Litter of all four tree species was used as monocultures. In addition, we set up a mixture with litter from all four tree species. We used 10 g of litter for each microcosm which is an approximation of natural litter fall per unit area in the study region. Thus, all monocultures contained 10 g of litter, whereas the four-species mixture contained 2.5 g of each species. All treatments (monocultures and mixture) had five replicates.

The experiment was set up in a small wooded area dominated by birch (*Betula pendula*). The microcosms were arranged in five randomised blocks in an area of approximately 10 × 10 m. We placed them on the soil surface instead of levelling them with the ground to avoid trapping of animals. The microcosms remained in the field for 10 weeks. After that time, pH-values in the microcosms were measured using a handheld pH-meter in the laboratory.

Decomposition rate and assessment of insect larvae

After 10 weeks, the contents of the microcosms were filtered through a 200 µm gauze. The leaves were removed manually, washed carefully and dried at 80 °C to weight constancy. Decomposition rate was defined as the relative loss of litter dry weight dur-

ing the experiment. All insect larvae found in the samples were stored in 96 % alcohol and counted at the genus level.

Microflora

Species richness and abundance of fungi as well as bacteria were assessed from the culturable part of the microflora. We are aware that this represents only a minor part of the microbe community. Nevertheless, this part is considered as representative for the whole microflora (Hattori et al. 1997). Even if morphotypes are subjectively defined, in most cases they represent homogeneous taxonomic units and provide a rather accurate estimate of microbe diversity (Haldeman & Amy 1993, Westergaard et al. 2001). Furthermore, Griffiths et al. (2001) showed that bacterial morphotypes from soil samples are correlated with diversity estimates derived from DNA. The microflora was examined from water samples after agitation of the contents of each microcosm. For the assessment of fungi, 100 µl of undiluted solution were spread on Czapek-Dox agar plates (Merck). This culture medium contains sucrose as the sole carbon and nitrate as the sole nitrogen source. This agar is selective to fungi and prevents growth of most bacteria. However, we also added Ampicilin (5 mgl^{-1}), Tetracyclin (20 mgl^{-1}) and Streptomycin (20 mgl^{-1}) to inhibit bacterial growth. We used three replicate plates for each microcosm. For the assessment of bacteria we used plates of R2A-agar (Merck). The low concentration of yeast extract, casein hydrolisate, peptone and glucose in this medium allows a wide spectrum of bacteria to grow and minimises the risk that fast-growing bacteria suppress slow-growing species (Eaton et al. 1995). A subsample of 100 µl water from each microcosm was serially diluted with a sterile saline solution (NaCl 0.9 %) and 100 µl of a 10^{-3} dilution was spread on the agar plates. All plates were incubated at 22 °C for five (fungi) and two days (bacteria). Species richness of fungi and bacteria was estimated by counting the number of different colony types, distinguished by colour, shape, texture and growth form (see also Palumbo et al. 1996). Further on, we will call this measure the number of morphotypes. Abundance of fungi and bacteria was assessed by counting all colonies on the plate (further called number of colony forming units = number of CFU). For all analyses we used the mean across the three replicates.

Functional diversity of microflora was evaluated by the utilization of different carbon sources. We used Biolog EcoPlates containing 31 carbon sources and a redox-colourant (tetrazolium violet) in wells. Colour development caused by the reduction of tetrazolium violet in the wells indicates respiratory activity of the microflora and oxidation of carbon. Even if the relevance of these 31 substrates in terrestrial and aquatic ecosystems requires further investigation, carbon source utilization patterns from EcoPlates has the capacity to discriminate among communities of heterotrophic microbes. This method has been used successfully to characterise microbial communities in soil, seawater, freshwater, sediments or activated sludge (Choi & Dobbs 1999). We used undiluted solution from each sample to inoculate EcoPlates with 100 µl per well to create a high initial activity and minimize the risk of contamination during incubation. Plates were incubated at room temperature. Development of colour was noted for every well after 24, 48 and 72 h.

Data analyses

Prior to statistical analyses, the number of insect individuals, number of morphotypes for fungi and bacteria (mean of three replicates), number of CFU for fungi and bacteria (mean of the three replicates) as well as number of used carbon sources were log-transformed to reduce heterogeneity of variances (Bartlett's test) and non-normality (Kolmorgorov-Smirnov test). Decomposition rate of litter was arcsin√-transformed. The effect of the specific litter assemblage (monocultures, litter mixture, hereafter referred to as factor *composition*) on these variables was tested by means of one-way ANOVA. All ANOVAs included the block effect. Interactions with the factor block were pooled into the error term (NEWMAN et al. 1997). In general, blocking of replicates had no effects on all variables investigated. We therefore only refer to the effects of *composition* and do not report statistics for the block effect in detail. Every ANOVA with significant effects was followed by Tukeys HSD *post-hoc* test. For every response variable, values of monocultures were used to calculate expected values in the mixture for each block following the procedure in BLAIR et al. (1990) and WARDLE et al. (1997). Relative deviations of observed from expected values were tested using 95 % confidence intervals.

Effects on the number of used carbon sources was analysed by means of a repeated-measures ANOVA to account for temporal dynamics. Again, means were compared using Tukeys HSD *post-hoc* test. The relationships between litter decomposition rate and microbial variables were tested with Pearson's correlation coefficient.

Results

Insect larvae

We found larvae from only two genera of aquatic insects in the microcosms [a culicid midge, *Culex* sp. (Diptera: Culicidae), and a soldier fly, *Stratiomys* sp. (Diptera Stratiomyidae)]. Some terrestrial species were accidentally trapped in the microcosms (not included in the analyses). Since nearly all microcosms were colonised by these two genera and determination to the species level was not possible, no attempt was made to check for differences in diversity of insect between treatments. Abundance (number of larvae) increased in the order ash < oak < beech < maple (Fig. 1). However, means were associated with high standard errors. Consequently, we found no significant effects of litter composition on the abundance of insect larvae (Fig. 1). For the mixture of the four litter species no significant deviations of observed from expected values of abundance could be found.

Microflora

Fungi

The number of morphotypes was significantly influenced by litter type (Fig. 2). Whilst monocultures with beech litter supported the highest number of mor-

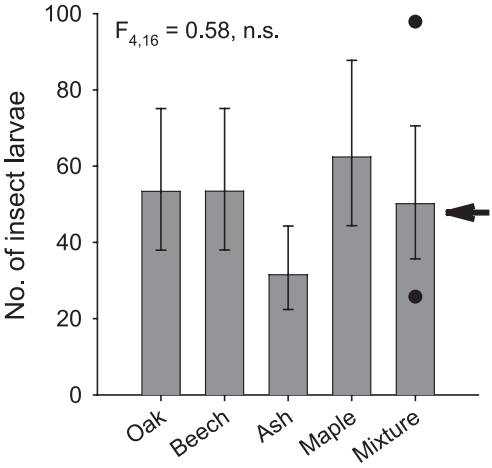

Fig. 1. Effects of litter type and mixture of litter on abundance of insect larvae (means ± standard error, back transformed values). The arrow indicates the expected value for the mixture from the monocultures. Points indicate the lower and upper confidence limit of the observed mean in the mixture.

photypes, we found the lowest numbers in monocultures with ash (difference 40 %). The number of CFU was not affected by litter *composition*. The number of morphotypes as well as CFU in the mixture showed no significant deviations from the values expected from monocultures.

Bacteria

The number of morphotypes was not affected by *composition*. However, numbers of morphotypes were rather low (means between 2 and 3). Mean number of CFU, however, ranged from 120 to 300. The highest values were found in monocultures of ash and maple (Fig. 2; significantly different from the other treatments). Again, number of morphotypes and CFU in the mixture did not differ significantly from the expected values.

Functional diversity

Carbon utilization pattern differed between treatments after 24 h and 48 h of incubation (Fig. 3, repeated-measures ANOVA, effect of treatment: $F_{4,16}$ = 12.44, $P < 0.001$, interaction term treatment × time: $F_{8,32} = 6.87$, $P < 0.01$). This was due to the high number of used carbon sources in the microcosms with litter from ash. This treatment differed significantly from all other treatments (Tukeys HSD test, $P < 0.001$). The remaining treatments did not differ significantly. After 72 hours, nearly all carbon sources were used by the microflora on all plates. The number of used carbon sources showed a positive correlation

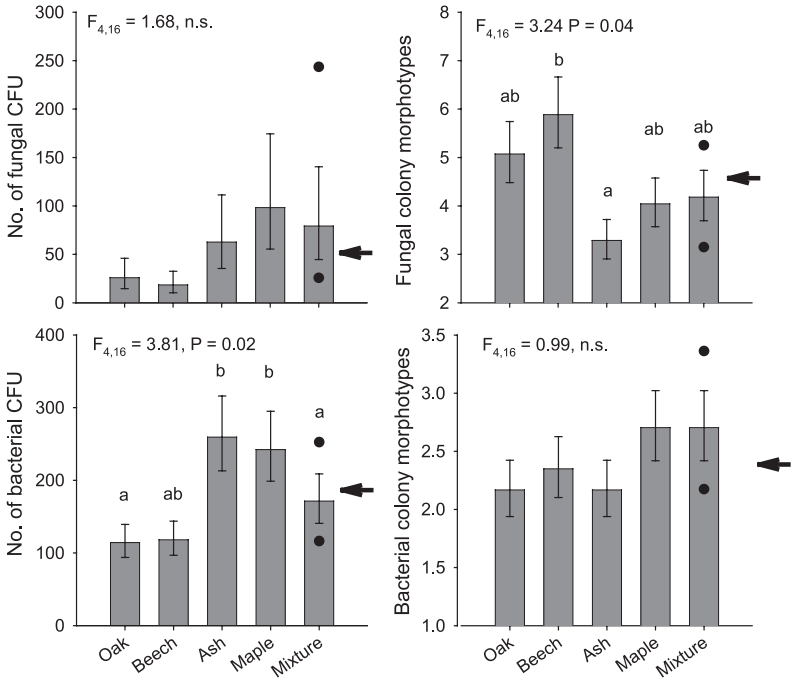

Fig. 2. Effects of litter type and mixture of litter on abundance and diversity of fungi and bacteria in the microcosms (means ± standard error, back transformed values). Different letters indicate statistically different means (Tukeys HSD test, $p < 0.05$). Arrows indicate the expected values for the mixture from the monocultures. Points indicate the lower and upper confidence limit of the observed mean in the mixture.

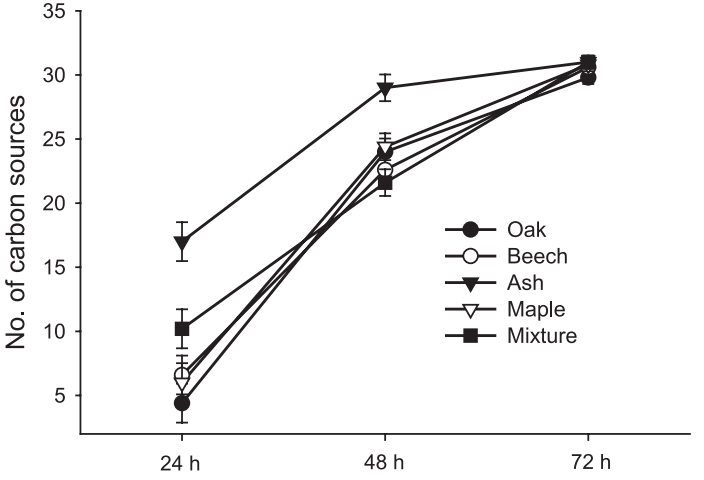

Fig. 3. Carbon sources utilization (EcologPlates) of microflora in aquatic microcosms according to litter treatment during three days of incubation (means ± standard error).

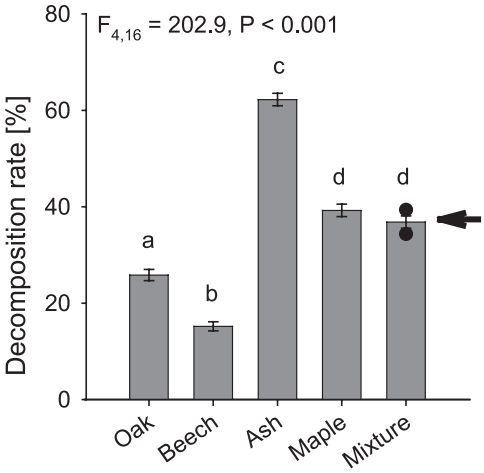

Fig. 4. Effects of litter type and mixture of litter on litter decomposition rate (means ± standard error, back transformed values). Different letters indicate statistically different means (Tukeys HSD test, $p < 0.05$). The arrow indicates the expected value for the mixture from the monocultures. Points indicate the lower and upper confidence limit of the observed mean in the mixture.

with the number of bacterial CFUs after 24 ($r = 0.65$, $P < 0.001$) and 48 h ($r = 0.52$, $P = 0.003$).

Decomposition

Decomposition rates differed considerably between litter types (Fig. 4). Beech litter showed a dry weight loss of only 16 % in the monoculture. In contrast ash litter showed a dry weight loss of about 64 % (Fig. 4). All monocultures showed significant differences (Tukeys HSD test, all $P < 0.05$). Decomposition rates in the mixture did not differ significantly from the expected values. Litter decomposition rate in microcosms was significantly correlated to the number of CFU of bacteria ($r^2 = 0.25$, $P < 0.001$), but not to the number of morphotypes of bacteria, number of morphotypes as well as CFU of fungi and number of used carbon sources.

Discussion

With respect to the questions posed in the introduction, one may summarize our results as follows: (1) Litter from different plant species influence abundance and diversity of certain components of the food web (in our case abundance of bacteria, diversity of fungi, functional diversity of the microflora). (2) Decomposition rates differed for litter from different species and decom-

position rates were correlated to the abundance of bacteria. (3) We found only additive effects when mixing litter from the different plant species. We found no significant differences of the observed values in the litter mixture from the expected values for all the investigated parameters. Furthermore there was also no general trend to higher or lower values (non-additivity).

Before discussing the ecological consequence of our findings, we want to comment on three experimental issues. Firstly and without doubt water chemistry (e. g., pH, dissolved oxygen) influences communities and decomposition processes in ponds (Webster & Benfield 1986, Kitching 2001). However, in our microcosms pH-value ranged from 6 to 7 and did not differ between the treatments. Hence, it is rather unlikely that differences in the decomposition rates between treatments were due to differences in water chemistry. Secondly, as mentioned in material and methods our experiments contained only food web components, which colonised the microcosms via the air. Hence, our experiments mimic the situation in temporary ponds and our results may be not be representative for permanent ponds. Thirdly, the methods used to characterise the microbial communities have been under criticism, as they are selective for a small subset of the total species pool in environmental samples (Amann et al. 1995). This most likely resulted in the low number of morphotypes we observed for bacteria, and consequently, we will not discuss this variable in detail. Nevertheless, several studies (mainly from terrestrial biomes, see Methods) consider colony forming units appropriate proxies for microbial diversity and biomass, although such correlations need to be shown for aquatic systems, and we observed a close relationship between the number of bacterial colony forming units and other variables which characterize the microbial community as well as ecosystem processes (number of used carbon sources, decomposition rate of litter). However, further studies on the reliability of cultivation methods to characterize microbial communities are badly needed.

Quality of litter seems to be one of the major factors influencing decomposition rates. Ash litter, which had the lowest C/N ratio of all investigated litter types, decomposed rather fast, whereas the litter with the highest C/N ratio (beech) decomposed fairly slowly. Further, ash litter supported the highest number of bacterial CFU. Note that the number of bacterial CFU was correlated with decomposition rate. Furthermore, the high abundance of bacteria in the ash litter treatment was also evident in the rapid utilization of a high number of carbon sources. C/N ratio has been shown to be a crucial trigger of litter decomposition in terrestrial (Swift et al. 1979, Berg et al. 1982, Cornelissen & Thompson 1997, Schädler et al. 2003) and aquatic ecosystems (Webster & Benfield 1986, Boulton & Boon 1991). A high content of carbon indicates a high concentration of fibre and secondary plant compounds, which decreases activity of herbivores and decomposers (Grime et al. 1996, Schädler et al. 2003). However, C/N ratio is a rather integrative measure of tissue qual-

ity. It is well known that the contents of certain secondary metabolites such as phenolics are species specific (HEAL et al. 1997), which influences composition and dynamics of the microflora during breakdown of the litter (GESSNER & CHAUVET 1994). Litter from *Fagus* is known for its high phenolic concentrations. Accordingly, *Fagus* decomposition rates were the lowest in our experiment. Since the microflora provides the food source for many invertebrate taxa, diversity and abundance of the latter may be indirectly affected by litter type. WALKER et al. (1997) showed an enhanced growth of mosquito larvae with young, intact litter compared to old, damaged and leached litter. The authors explain this with the higher nutrient content of fresh leaves. However, in our study the abundance of insect larvae was not affected by litter type (see also RICHARDSON et al. 2004).

In terrestrial ecosystems, some studies showed a positive effect of litter mixing on the diversity and abundance of decomposers whereas other studies failed to do so. Other studies demonstrated negative effects (WARDLE & VAN DER PUTTEN 2002). Furthermore, in terrestrial systems non-additive effects on composition, diversity of decomposers as well as ecosystem processes are common during experiments with mixtures of litter. Even if litter mixtures support higher diversities of consumers, this may not necessarily translate into an enhanced rate of litter processing, probably due to functional redundancy of species (MIKOLA et al. 2001, WOLTERS 2001, WARDLE 2002). Accordingly, JONSSON & MALMQVIST (2003) showed that increased species richness within specific functional groups of stream invertebrates did not affect rates of filtration, grazing and predation in a consistent way (see also DUFFY et al. 2001 for marine grazers). However, the decomposition rate in mixtures of litter species may be associated with a changed composition of the food web when compared to monocultures. None of the variables measured during our experiments differed in the mixture of all litter types from values expected from the monocultures, a first hint that the basic structure of the food webs in temporary ponds did not depend on the diversity of litter.

Our experiment suggests that in temporary ponds with allochthonous litter the structure of the food web and ecosystem processes depends on the litter quality of the surrounding vegetation. In contrast to studies in terrestrial systems, mixing of litter had only additive effects. It is, however, far from clear whether aquatic systems differ consistently from terrestrial systems in respect to the importance of non-additive effects in mixtures of litter types. Further experimental studies are needed before such generalisations are possible.

Acknowledgements

We thank H.-W. BOHLE for the help with the identification of insect larvae and two anonymous referees for valuable comments on the manuscript.

References

Amann, R. I., Ludwig, W. & Schleifer, K. H. (1995): Phylogenetic identification and in situ detection of individual microbial cells without cultivation. – Microbiol. Rev. **59:** 143–169.

Berg, B., Hannus, K., Popoff, T. & Theander, O. (1982): Changes in organic chemical components of needle litter during decomposition. Long-term decomposition in a Scots pine forest. – Can. J. Bot. **60:** 1310–1319.

Blair, J. M., Parmelee, R. W. & Baere, M. H. (1990): Decay rates, nitrogen fluxes and decomposer communities in single and mixed species foliar litter. – Ecology **71:** 1976–1985.

Boulton, A. J. & Boon, P. I. (1991): A review of methodology used to measure leaf litter decomposition in lotic environments: Time to turn over a new leaf? – Aust. J. Mar. Freshwater Res. **42:** 1–43.

Choi, K. H. & Dobbs, F. C. (1999): Comparison of two kinds of Biolog microplates (GN and ECO) in their ability to distinguish among aquatic microbial communities. – J. Microbiol. Methods **36:** 203–213.

Cornelissen, J. H. C. & Thompson, K. (1997): Functional leaf attributes predict litter decomposition rate in herbaceous plants. – New Phytol. **135:** 109–114.

Duffy, J. E., Macdonald, K. S., Rhode, J. M. & Parker, J. D. (2001): Grazer diversity, functional redundancy, and productivity in seagrass beds: An experimental test. – Ecology **82:** 2417–2434.

Eaton, A. D., Clesceri, L. S. & Greenberg, A. E. (1995): Standard methods for the examination of water and wastewater, 19th. Ed. – APHA, Washington D. C.

Egglishaw, H. J. (1968): The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. – J. Appl. Ecol. **5:** 731–740.

Findlay, S., Carreiro, M., Krischic, V. & Jones, C. J. (1996): Effects of damage to living plants on leaf litter quality. – Ecol. Appl. **6:** 269–275.

Gartner, T. B. & Cardon, Z. G. (2004): Decomposition dynamics in mixed-species leaf litter. – Oikos **104:** 230–246.

Griffiths, B. S., Ritz, K., Wheatley, R., Kuan, H. L., Boag, B., Christensen, S., Ekelund, F., Sorensen, S. J., Muller, S. & Bloem, J. (2001): An examination of the biodiversity-ecosystem function relationship in arable soil microbial communities. – Soil Biol. Biochem. **33:** 1713–1722.

Grime, J. P., Cornelissen, J. H. H. C., Thompson, K. & Hodgson, J. G. (1996): Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. – Oikos **77:** 489–494.

Haldeman, D. L. & Amy, P. S. (1993): Diversity within a colony morphotype: implications for ecological research. – Appl. Environm. Microbiol. **59:** 933–935.

Hanson, R. A. & Coleman, D. C. (1998): Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acrai: Oribatida) in litterbags. – Appl. Soil Ecol. **9:** 17–23.

Hattori, T., Mitsui, H., Hattori, R., Shikano, S., Gorlach, K., Kasahara, Y. & El-Beltagy, A. (1997): Analysis of the bacterial community according to colony development on solid medium. – In: Rangger, A. & Insam, I. (eds): Microbial Communities: functional versus structural approaches. – Springer, Berlin, pp. 229–235.

Gessner, M. O. & Chauvet, E. (1994): Importance of stream microfungi in controlling breakdown rates of leaf litter. – Ecology **75:** 1807–1817.

Heal, O. W., Anderson, J. W. & Swift, M. J. (1997): Plant litter quality and decomposition: an historical overview. – In: Cadisch, G. & Giller, K. E. (eds): Driven by nature: plant litter quality and decomposition. – CAB International, Wallingford, pp. 3–45.

Jonsson, M. & Malmqvist, B. (2003): Importance of species identity and number for process rates within different stream invertebrate functional feeding groups. – J. Anim. Ecol. **72:** 453–459.

Kitching, R. L. (2001): Food webs in phytotelmata: "Bottom-up and top-down explanations for community structure. – Annu. Rev. Entomol. **46:** 729–760.

Loreau, M., Naeem, S. & Inchausti, P. (2002): Biodiversity and ecosystem functioning: Synthesis and perspectives. – Oxford University Press, Oxford.

Mikola, J., Yeates, G. W., Wardle, D. A., Barker, G. M. & Bonner, K. I. (2001): Response of soil food-web structure to defoliation of different plant species combinations in an experimental grassland community. – Soil Biol. Biochem. **33:** 205–214.

Minshall, G. W. (1967): Role of allochthonous detritus in the trophic structure of a woodland springbrook community. – Ecology **48:** 139–149.

Newman, J. A., Bergelson, J. & Grafen, A. (1997): Blocking factors and hypothesis tests in ecology: is your statistics text wrong? – Ecology **78:** 1312–1320.

Palumbo, A. V., Zhang, C. L., Liu, S., Scarborough, S. P., Pfiffner, S. M. & Phelps, T. J. (1996): Influence of media on measurement of bacterial populations in the subsurface – Numbers and diversity. – Appl. Biochem. Biotech. **57:** 905–914.

Petchey, O. L., Morin, P. J., Hulot, F. D., Loreau, M., McGrady-Steed, J. & Naeem, S. (2002): Contributions of aquatic model systems to our understanding of biodiversity and ecosystem functioning. – In: Loreau, M., Naeem, S. & Inchausti, P. (eds): Biodiversity and ecosystem functioning. – Oxford University Press, Oxford, pp. 127–138.

Rich, P. H. & Wetzel, R. G. (1978): Detritus in the lake ecosystem. – Amer. Nat. **112:** 57–71.

Richardson, J. S., Shaughnessy, C. R. & Harrison, P. G. (2004): Litter breakdown and invertebrate association with three types of leaves in a temperate rainforest stream. – Arch. Hydrobiol. **159:** 309–325.

Schädler, M., Jung, G., Auge, H. & Brandl, R. (2003): Palatability, decomposition and insect herbivory: Patterns in a successional old-field community. – Oikos **103:** 121–132.

Swift, M., Heal, O. W. & Anderson, J. M. (1979): Decomposition in terrestrial systems. – Blackwell Science, Oxford.

Walker, E. D., Kaufman, M. G., Ayres, M. P., Riedel, M. H. & Merritt, R. W. (1997): Effects of the variation and quality of leaf detritus on growth of the eastern treehole mosquito, *Aedes triseriatus* (Diptera: Culicidae). – Can. J. Zool. **75:** 706–718.

Wardle, D. A. (2002): Communities and ecosystems: Linking the aboveground and belowground components. – Princeton University Press, Princeton.

WARDLE, D. A., BONNER, K. I. & NICHOLSON, K. S. (1997): Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. – Oikos **79:** 247–258.

WARDLE, D. A. & VAN DER PUTTEN, W. H. (2002): Biodiversity, ecosystem functioning and soil decomposer foodwebs. – In: LOREAU, M., NAEEM, S. & INCHAUSTI, P. (eds): Biodiversity and ecosystem functioning. – Oxford University Press, Oxford, pp. 155–168.

WEBSTER, J. R. & BENFIELD, E. F. (1986): Vascular plant breakdown in freshwater ecosystems. – Annu. Rev. Ecol. Syst. **17:** 567–594.

WESTERGAARD, K., MÜLLER, A. K., CHRISTENSEN, S., BLOEM, J. & SORENSEN, S. J. (2001): Effects of tylosin as a disturbance on the soil microbial community. – Soil Biol. Biochem. **33:** 2061–2071.

WOLTERS, V. (2001): Biodiversity of soil animals and its function. – Eur. J. Soil Biol. **37:** 221–227.

Submitted: 30 June 2004; accepted: 28 December 2004.