

Primary Research Paper

Leaf decomposition in an extremely acidic river of volcanic origin in Indonesia

Ansje J. Löhr*, Jinze Noordijk, Kelik Lrianto, Cornelis A.M. Van Gestel
& Nico M. Van Straalen

Faculty of Earth and Life Sciences, Department of Animal Ecology, Institute of Ecological Science, Vrije Universiteit,
De Boelelaan 1085, 1081 HV, Amsterdam, The Netherlands

(*Author for correspondence: Fax: +31-20-5987123, E-mail: ansje.lohr@ou.nl)

Received 21 October 2004; in revised form 21 September 2005; accepted 2 October 2005

Key words: leaf decomposition, low pH, rivers, macroinvertebrates, microbial activity, Indonesia

Abstract

Functional processes in freshwater ecosystems are highly influenced by acidic conditions. Foodwebs are affected and macroinvertebrate species diversity is decreased. This study aims to investigate leaf decomposition at very low pH in the acidic Banyupahit–Banyuputih river originating from the acidic crater lake Kawah Ijen in Indonesia. Leaf decomposition experiments were carried out for 200 days in the acidic river at pHs of approximately 0.7, 2.3 and 3.0 and in the neutral Kali Sengon river, using leaves from teak, *Tectona grandis*, and bamboo, *Bambusa* sp. Two different types of leaf packs were used: fine mesh size packs were used to exclude macroinvertebrates and coarse mesh size packs allowed macroinvertebrate colonization. Clear differences in decomposition rate were observed between the neutral Kali Sengon and the acidic Banyupahit–Banyuputih river with decomposition in the Kali Sengon river proceeding significantly faster for both leaf types. In the Kali Sengon k values (d^{-1}) over 46 days were 0.0202 for fine teak, 0.0236 for coarse teak, 0.0114 for fine bamboo and 0.0151 for coarse bamboo. No significant differences were observed between the three sites in the acidic Banyupahit–Banyuputih river with k values of 0.0034–0.0066 for fine teak, 0.0002–0.0057 for coarse teak, 0.0029–0.0054 for fine bamboo and 0.0000–0.0068 for coarse bamboo. Moreover, no clear adaptation of macroinvertebrates or microbes to low pH conditions could be detected. The coarse mesh leaf packs in the neutral Kali Sengon river revealed that macroinvertebrates are important in the breakdown process. Fine mesh packs revealed that microbial activity is depressed under acidic conditions. Based on this evidence, we conclude that the toxicity at low pH conditions, and probably also the precipitation of metals on the leaf material, seriously affects leaf decomposition.

Introduction

Leaf litter decomposition is a key ecosystem-level process in most aquatic systems (Hieber & Gessner, 2002) and riparian vegetation constitutes a major food and energy source (Giller & Malmqvist, 1998). In acidic aquatic systems the pH has a great effect on the structure and functioning of the ecosystem (Clements & Newman, 2002). Accumulation of organic material in acidic waters has been demonstrated in several studies (Maltby,

1996) and the depression of leaf litter decomposition under acidic conditions causes a reduction of energy flow through the ecosystem (Mulholland et al., 1987).

Three processes lead to leaf litter breakdown: shredders break down litter by their feeding activity; fungi and bacteria mineralize litter, and physical processes like leaching and abrasion contribute to litter mass loss (Niyogi et al., 2003). These processes are affected at low pH conditions and lead to a decrease in leaf litter decomposition.

At low pH the toxicity of both high H^+ concentrations and high dissolved metal concentrations often leads to a decrease of both microbial and macroinvertebrate diversity (Gerhardt, 1993; Tuchman, 1993; Rothschild & Mancinelli, 2001). Nevertheless, it is difficult to indicate what exactly causes the stress under low pH conditions since these features frequently co-occur (Allen & Hansen, 1996; Orendt, 1999). Lower microbial activity can indirectly lead to a decrease in macroinvertebrate diversity due to reduced food quality (Groom & Hildrew, 1989; Dangles & Guérol, 2001) and a decrease in palatability of decomposing leaves (Kok & Van der Velde, 1994). Differences in ecosystem functioning have been observed depending on the origin and age of acidic aquatic systems. Dangles et al. (2004b), for example, found no differences in taxonomic richness of benthic invertebrates between old natural acidic streams ($pH > 3.97$) and neutral streams in Sweden. However, lower diversity was found for a relatively young acidic system, subjected to recent anthropogenic acidification as a result of atmospheric deposition (Dangles et al., 2004b).

Systems impacted by acid rain have a $pH > 4$, and the more acidic brown water systems, with high concentrations of organic acids derived from decomposing vegetation (Winterbourn & Mc Diffet, 1996), rarely result in environments with pH values below 3 (Gross & Robbins, 2000). More acidic systems include waters of anthropogenic origin, e.g. acid mine drainage (AMD), or of natural origin, like volcanic lakes and streams. Natural volcanic acidic systems and AMD are both characterized by extremely low pH, accompanied by high concentrations of metals and other elements that have evident impacts on local community structure (Townsend et al., 1983). Few investigations have focused on leaf litter decomposition in extremely acidic aquatic systems of natural origin, although several studies on leaf litter decomposition in AMD systems have been carried out (Carpenter et al., 1983; Niyogi et al., 2001). Although acidic systems of volcanic origin chemically relate to AMD systems, they are generally much older which may lead to selection for unusual functional adaptations (Dangles et al., 2004a). Macroinvertebrates and microbes thus may show a higher level of adaptation possibly resulting in a higher diversity

and significant effects on leaf litter decomposition.

The aim of this study was to investigate the impact of extremely acidic water of volcanic origin on leaf decomposition rate in an acidity gradient, $pH 0.52$ – 3.83 . Experiments were carried out at three sites (Liwung, Blawan and Paltuding) in the Banyupahit–Banyuputih river, a natural acidic river originating from the acidic crater lake Kawah Ijen in East Java, Indonesia. The neutral river Kali Sengon was used as a reference. To evaluate the role of macroinvertebrate communities in the decomposition of different leaf species, the decomposition rate of two common leaf types of the area, bamboo (*Bambusa* sp.; Poaceae) and teak (*Tectona grandis*; Verbenaceae), were studied, using coarse and fine mesh-size packs.

Material and methods

Research area

The Banyupahit–Banyuputih river is a 50 km long acidic river in East Java, Indonesia, originating from seepage water from the Kawah Ijen crater lake, the World's largest natural reservoir of extremely acid ($pH < 0.3$) volcanic water. Experiments were carried out at three sites with varying pH in the Banyupahit–Banyuputih river, designated by their local names as Paltuding, Blawan and Liwung (Fig. 1). A reference site was chosen in the nearby neutral Kali Sengon river which is located 1 km from the confluence with the Banyupahit–Banyuputih river. For a detailed description of the research area, see Löhr et al. (2005).

Water quality parameters

At each site, on all sampling dates, pH (SenTix 41, WTW), temperature (SenTix 41, WTW), conductivity (TetraCon 325), oxygen concentration (Cellox 325) and redox potential (SenTix ORP) of the river water were measured using the Multi-line P4 (WTW) aquatic field kit. To ensure maximum reliability of pH measurement, the pH electrode was calibrated in between each measurement at the most acidic sites. An extensive physico-chemical description of the research area is also given in Löhr et al. (2005).

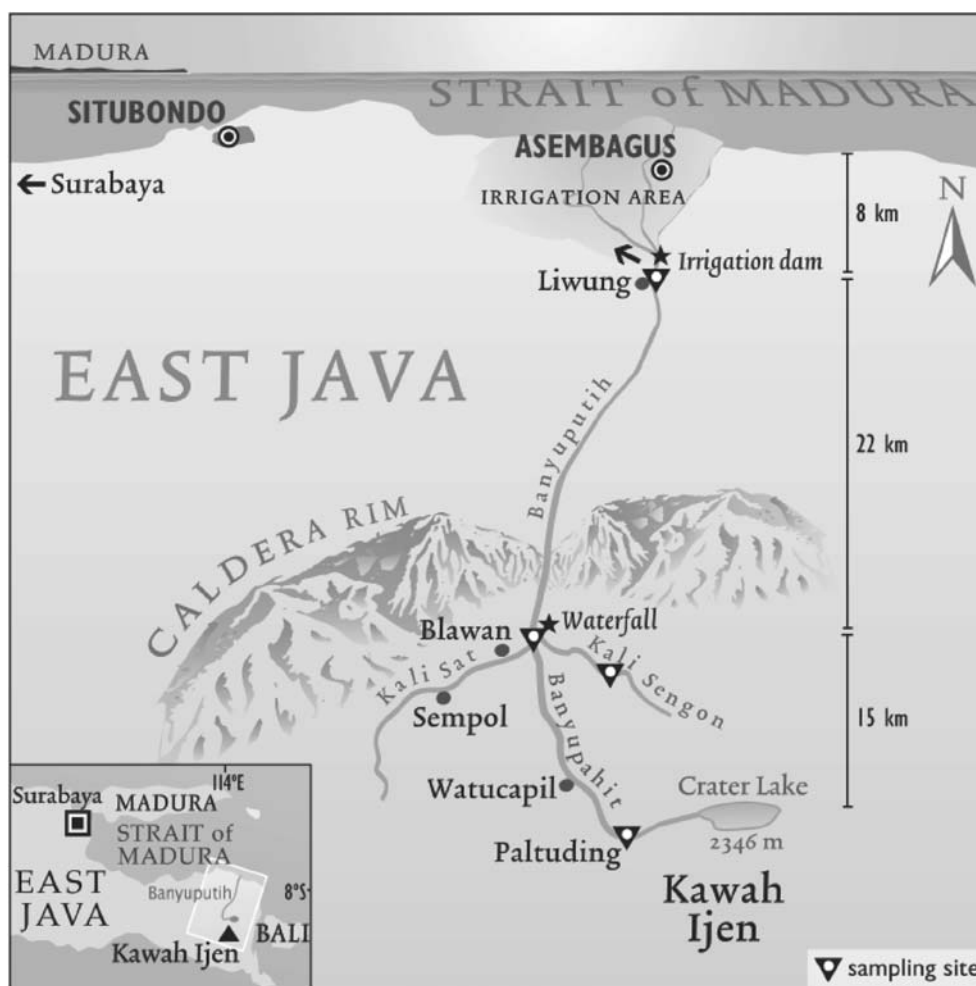


Figure 1. Map of the Ijen ecosystem, showing the crater lake Kawah Ijen, the acidic Banyupahit–Banyuputih river and the neutral river Kali Sengon. The triangles indicate the litter incubation sites in the acidic river (Paltuding, Blawan, and Liwung) and in the neutral Kali Sengon.

Leaf decomposition

Leaves of teak (*Tectona grandis*; Verbenaceae) and bamboo (*Bambusa sp.*; Poaceae), two common species in the research area (Perum Perhutani, 1998), were used in the experiment. Teak and bamboo leaves were collected from trees near Liwung, on the banks of the Banyupahit–Banyuputih river, in March 2002. Only undamaged leaves were picked. After collection the leaves were air-dried to constant weight for one day. For the leaf packs, teak leaves were cut into ribbons but bamboo leaves were used complete. Teak leaves were weighed to portions with a final weight of

7 g, bamboo leaves to a final weight of 5 g. Both leaf types were placed into two types of packs: coarse-mesh packs (mesh size 5 mm) and fine-mesh packs (mesh size <1 mm).

Four different pack types were tied together resulting in 4-pack-units consisting of coarse teak (CT), coarse bamboo (CB), fine teak (FT) and fine bamboo (FB). An additional 10 packs of each pack type were used to estimate the initial dry weight. The line to which the packs were attached was tied to pegs driven in the river bank. At each site 15 4-pack units were submerged at three different locations about 3 m apart, with five replicates per location. One of the replicates at each location per

site was collected after 2, 14, 32, 46 and 200 days, respectively. Prior to analysis the coarse packs were placed in 70% ethanol; fine packs were put into plastic bags and stored at 4 °C. Remaining leaf mass was determined for every pack. The leaves were gently washed with water in the lab, dried for 72 h at 60 °C and weighed.

Dried leaves were transported to the Netherlands, pulverized using a Retsch S2 ball mill and carbon: nitrogen ratios were determined with an elemental analyser (Carlo Erba model 1106). To determine ash weight, the pulverized leaves were transferred to crucibles, placed in a stove at 100 °C for 14 h and weighed. Subsequently, crucibles were placed in a furnace for 1 h at 200 °C, 1 h at 350 °C and 6 h at 500 °C and weighed again.

Macroinvertebrates

During the washing of the leaves from the coarse-mesh packs, macroinvertebrates were separated from the leaves and preserved again in 70% ethanol. Macroinvertebrates were identified to the lowest possible taxonomic level according to De Pauw & Vannevel (1991) and Tachet et al. (2000).

Data analysis

Dry weight loss was calculated for each leaf pack and expressed as a percentage of the initial weight.

Leaf decomposition rates (k) per day were calculated from linear regression of $\ln W$ (W =dry weight) against exposure time (days) with initial weight (W_i) fixed. To compare the results, a generalized likelihood ratio test (GLM) was used to test for differences in the slope parameters of the different sites for each different leaf pack. Since temperature may affect litter decomposition rates, decomposition rates were also calculated on a basis of physiological times, assuming that no decomposition takes place at a temperature below zero. By plotting $\ln W$ as a function of physiological times (degree days), leaf decomposition rates (k) per degree day were calculated for the different sites and also compared using the GLM as described above. Calculations were run in SYSTAT® 5.2.1. on a MacIntosh computer.

Results

Water chemistry

Chemical and physical data of the Banyupahit–Banyuputih and the Kali Sengon river water during the research period are given in Table 1. pH was very low at the most acidic site Paltuding (between 0.52 and 0.73). The dilution with the two neutral tributaries caused an increase in pH, at Blawan (between 2.15 and 2.67) after the

Table 1. Physicochemical characteristics and element concentrations of the Banyupahit–Banyuputih and Kali Sengon river water of incubation of the leaf material in the decomposition experiment (data are ranges measured at days 2, 14, 32, 46 and 200)

Parameter	Paltuding	Blawan	Liwung	Kali Sengon
pH	0.52–0.73	2.15–2.67	2.26–3.83	7.33–7.74
Conductivity (mS/cm)	101–125	2.54–4.69	1.18–2.39	0.97–1.03
Temperature (°C)	18.2–22.7	21.6–23.5	21.6–25.8	21.8–24.3
Redox potential (mV)	455–469	483–530	396–547	107–148
SO ₄ * (mg/l)	29,600–37,300	966–1270	800–967	246–297
Cl* (mg/l)	7300–10,200	237–367	180–247	70.3–123
F* (mg/l)	274–498	8.11–17.7	5.89–11.2	1.38–2.05
Al* (mg/l)	2740–3570	78.1–124	47.9–68.4	0.240–0.689
Fe* (mg/l)	1450–1780	17.9–42.1	2.52–21.4	0.00–0.04
Zn* (mg/l)	1.83–2.77	0.11–0.33	0.15–0.31	0.02–0.24
Cu* (ug/l)	558–707	26.7–36.5	11.5–25.0	1.81–10.6
Dissolved oxygen* (mg/l)	7.23–7.72	7.38–8.26	7.83–8.46	7.50–8.56
Discharge* (m ³ /s)	0.1	3.12		1.21
Average flow velocity* (m/s)	0.64	1.39	1.39	0.94

* From Löhner et al. (2005).

confluence with the Kali Sat and at Liwung (between 2.26 and 3.83) after the confluence with the Kali Sengon (between 7.33 and 7.74). Conductivity values were very high for Paltuding (101–125 mS/cm) and decreased with increasing pH. The same pattern was observed for redox potential values. Water temperatures did not vary much but were slightly lower at the acidic site Paltuding when compared to the other three sites. No differences were observed in oxygen levels between the four sites. Element concentrations are given in Löhner et al. (2005) and summarized in Table 1. In general, extremely high concentrations of sulphate, chloride, fluoride, aluminium and other elements were found at the most acidic site, and concentrations decreased with increasing pH. Discharge was small at Paltuding (0.1 m³/s), greater in the Kali Sengon (1.21 m³/s) and greatest in Blawan (3.12 m³/s). Flow velocities were highest in Blawan and Liwung, followed by the Kali Sengon and lowest in Paltuding. There was no obvious trend of

changes in water chemistry during the incubation of leaf packs.

Leaf decomposition

Leaf weights decreased to 30% (teak at Kali Sengon) or to 80% (bamboo at Paltuding) of the initial weight over 46 days (Table 2). Despite variability, linear regression applied to ln dry weight showed significant differences in decomposition rate for the two leaf types; bamboo leaves had lower decomposition rates than teak leaves in each leaf pack type (Fig. 2). Also great differences between the acidic sites and the neutral Kali Sengon were observed for each pack-type.

Decomposition rate k over 46 days was fastest in the neutral river Kali Sengon for all pack types (Table 3). Decomposition rates k at the acidic sites were two to three times lower than in the neutral Kali Sengon river, a difference that was significant ($X^2_3 > 7.84$; $p < 0.05$). No significant differences

Table 2. Per cent (%) DW loss (average (\pm SD) of 3 replicates) for the four different pack types over 200 days in the Banyupahit–Banyuputih river (Paltuding, Blawan and Liwung) and in the Kali Sengon river (if no SD is given there was only 1 replicate)

	Time (days)				
	2	14	32	46	200
<i>Coarse Bamboo</i>					
Paltuding	16 \pm 1.81	17 \pm 6.03	13 \pm 6.03	17 \pm 2.13	36 \pm 2.19
Blawan	14 \pm 2.68	16 \pm 5.99	23 \pm 4.67	25 \pm 6.53	29
Liwung	9 \pm 1.97	16 \pm 1.47	22 \pm 2.11	34 \pm 3.74	45 \pm 13.9
Kali Sengon	14 \pm 8.36	34 \pm 7.46	48 \pm 1.90	57 \pm 0.20	97
<i>Coarse Teak</i>					
Paltuding	39 \pm 2.50	41 \pm 9.65	31 \pm 4.21	43 \pm 4.00	47 \pm 10.1
Blawan	32 \pm 7.03	28 \pm 14.4	47 \pm 15.1	40 \pm 11.0	42
Liwung	29 \pm 14.3	52 \pm 2.66	44 \pm 2.99	51 \pm 1.29	59 \pm 13.6
Kali Sengon	27 \pm 11.5	48 \pm 11.6	61 \pm 12.9	76	84
<i>Fine Bamboo</i>					
Paltuding	7 \pm 4.53	13 \pm 2.66	12 \pm 0.58	20 \pm 7.35	29 \pm 12.9
Blawan	3 \pm 4.33	16 \pm 5.27	19 \pm 6.50	25 \pm 3.38	20
Liwung	3 \pm 2.36	10 \pm 3.35	21 \pm 1.18	16	39
Kali Sengon	14 \pm 4.02	30 \pm 2.73	41 \pm 4.17	49 \pm 4.53	76
<i>Fine Teak</i>					
Paltuding	18 \pm 3.51	44 \pm 2.21	44 \pm 1.81	37 \pm 2.61	45 \pm 0.32
Blawan	24 \pm 15.9	35 \pm 17.5	49 \pm 3.90	30 \pm 1.82	22
Liwung	16 \pm 0.52	44 \pm 4.33	38 \pm 10.4	43 \pm 3.65	56 \pm 5.11
Kali Sengon	8 \pm 4.72	46 \pm 21.1	48 \pm 14.9	67 \pm 5.34	64

Table 3. Decomposition rates of bamboo and teak leaves in coarse and fine bags in the acidic Banyupahit–Banyuputih river (Paltuding, Blawan and Liwung) and the neutral river Kali Sengon

Site	Coarse Bamboo		Fine Bamboo		Coarse Teak		Fine Teak	
	$k (d - 1)$	r ²	$k (d - 1)$	r ²	$k (d - 1)$	r ²	$k (d - 1)$	r ²
A								
Paltuding	0.0049	0.71	0.0052	0.21	0.0138	0.59	0.0146	0.15
Blawan	0.0072	0.44	0.0067	0.89	0.0149	0.17	0.0133	0.03
Liwung	0.0090	0.90	0.0052	0.70	0.0186	0.09	0.0149	0.35
Kali Sengon	0.0196	0.92	0.0159	0.87	0.0313	0.90	0.0242	0.88
B								
Paltuding	0.0000	0.00	0.0029	0.80	0.0002	0.00	0.0050	0.14
Blawan	0.0032	0.98	0.0054	0.91	0.0050	0.49	0.0034	0.15
Liwung	0.0068	0.96	0.0037	0.67	0.0057	0.40	0.0066	0.46
Kali Sengon	0.0151	0.99	0.0114	0.98	0.0236	0.98	0.0202	0.87
C								
Paltuding	0.0002	0.68	0.0002	0.66	0.0007	0.59	0.0007	0.15
Blawan	0.0003	0.44	0.0003	0.90	0.0007	0.17	0.0006	0.03
Liwung	0.0004	0.90	0.0002	0.70	0.0007	0.09	0.0006	0.35
Kali Sengon	0.0008	0.92	0.0007	0.87	0.0013	0.90	0.0010	0.88
D								
Paltuding	0.0000	0.00	0.0001	0.80	0.0000	0.00	0.0003	0.29
Blawan	0.0001	0.98	0.0002	0.91	0.0002	0.49	0.0002	0.15
Liwung	0.0003	0.96	0.0001	0.67	0.0002	0.40	0.0003	0.46
Kali Sengon	0.0006	0.99	0.0005	0.99	0.0010	0.98	0.0009	0.87

Estimates of k were obtained by linear regression of natural logarithm of remaining dry weight versus time. (r²=r squared values of linear regression trendline).

A: values calculated using all data over 46 days.

B: values calculated omitting t = 0 data.

k values based on physiological time (degree days).

C: A: values calculated using all data over 46 days.

D: values calculated omitting t = 0 data.

in decomposition rates for all leaf pack type were observed for the three acidic sites ($X^2_2 < 5.99$). Another interesting feature is the large weight loss of especially coarse teak observed already after 2 days of incubation at all 4 sites. When compensated for initial weight loss over the first 2 days fit clearly increased (Table 3) and decomposition rates k at the acidic sites were two to six times lower than in the neutral Kali Sengon river (Table 3). For both coarse packs from Paltuding k was much lower which is caused by the relatively higher initial loss when compared to the fine packs at Paltuding. Correcting for temperature

differences by expressing time as degree days did not affect the difference in decomposition rates between the acidic sites and the neutral Kali Sengon (Table 3).

In addition weight loss data after 200 days are given (Table 2). No large differences were observed in % DW loss of bamboo between the coarse and fine mesh size packs over 200 days for the acidic sites Paltuding, Blawan and Liwung. For the neutral river Kali Sengon also no large differences were observed for the first 46 days but % DW loss differed significantly (t -test, $p < 0.005$) after 200 when it was 97% for CB and 76% for

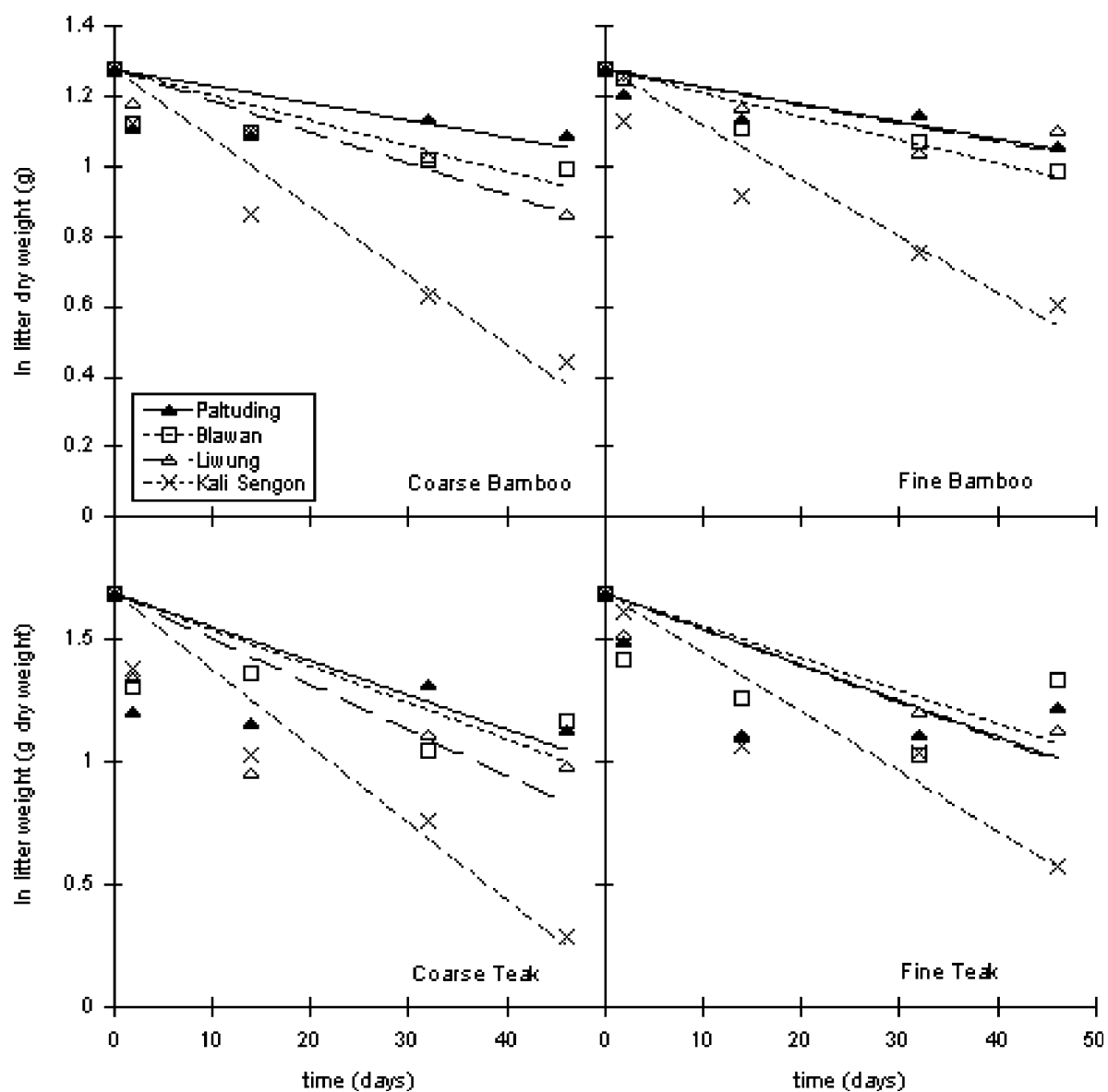


Figure 2. Decomposition expressed as the dry weight (In DW (g)) loss with time of bamboo and teak leaves enclosed in coarse and fine meshpacks and incubated in the acidic Banyupahit-Banyuputih river and the neutral Kali Sengon river for 46 days.

FB. Also no large differences were observed in % DW loss between CT and FT for the acidic sites Paltuding, Blawan and Liwung, but teak decomposition was higher for coarse mesh packs over 200 days at the Kali Sengon when % DW loss was 84% for CT and 64% for FT. From Table 2, it may also be concluded that except for bamboo in the Kali Sengon, litter weight loss over the period between 46 and 200 days was low compared to

that in the first 46 days. In some cases, no further weight loss was recorded in the last incubation period.

Upon visual inspection, leaf packs from Blawan and especially Liwung seemed to get covered with some precipitation of metal oxides. To determine a possible effect of this on mass loss measurements, ash-weight of litter samples was determined by combustion of the dry litter at

500 °C. In the Kali Sengon, litter ash weights fluctuated with time and so did ash-weight of all coarse teak at the acidic sites. For the other three litter types, ash-weight in the acidic sites did show a consistent increase with time over the first 32 days from 15–20% to 26–27%, but stabilized or decreased again after 46 days. However, when *k*'s were compensated for this no large differences were observed.

Carbon/ nitrogen ratios

C:N ratios measured at the start of the experiment were 20.9 (SD 0.78; $n=10$) for teak leaves and 17.6 (SD 0.55; $n=10$) for bamboo leaves. C:N ratios of teak leaves slightly decreased in the first two weeks but remained fairly constant later on. C:N ratios of bamboo leaves showed a slight increase with time. No differences were observed between sites or leaf pack types.

Macroinvertebrate colonization of leaf packs

Already after 2 days, colonization of coarse leaf packs was observed in the neutral Kali Sengon river. At all sampling dates macroinvertebrate densities were less than 100 specimens per 2 or 3 packs. Chironomids (family Chironomidae) were the most dominant group found in both the teak (74–96%) and bamboo (65–95%) leaf packs. Few specimen of other macroinvertebrate taxa were found: in teak packs members of the orders Coleoptera and Ephemeroptera and of the families Lymnaeidae, Talitridae, Potamonidae, Elminthidae, Perlodidae, Hydropsychidae, Culicidae and Limoniidae were found; in bamboo packs members of the orders Oligochaeta and Ephemeroptera and of the families Lymnaeidae, Talitridae, Potamonidae, Perlodidae, Hydropsychidae, and Limoniidae were found. No large differences in colonization of macroinvertebrate species or numbers were observed between teak and bamboo packs. In sharp contrast, no colonization of leaf packs was observed for the most acidic site Paltuding and the acidic site Blawan. At Liwung some chironomids were found but in very low numbers and two specimen of the order Coleoptera in the teak leaf packs.

Discussion

Our results clearly show that leaf litter decomposition is slower at the acidic sites in the Banyupahit–Banyuputih river in comparison to the neutral Kali Sengon river. This is in accordance with other extreme acidic systems, e.g., AMD, where leaf litter decomposition is depressed (Carpenter et al., 1983; Niyogi et al., 2001; Siefert & Mutz, 2001). Dry weight loss in the first two days was fast, which is in agreement with other studies with pre-dried leaves showing 5–30% DW loss in the first 2 days, probably caused by leaching (Maltby, 1996; Giller & Malmqvist, 1998).

The decomposition rates of bamboo are low and are in the range of values found for other members of the grass family Poaceae (Giller & Malmqvist, 1998), although the decomposition rates in the neutral river were rather high. On average, decomposition was two to three times slower in the acidic Banyupahit–Banyuputih river than in the neutral Kali Sengon river and slightly lower when initial loss due to leaching was taken into account. Despite differences in pH and metal concentrations, no significant differences were observed between the three acidic sites.

Decomposition rates for both leaf types at low pH were still fairly high when compared to other acidic systems (Siefert & Mutz, 2001; Niyogi et al., 2001). The decomposition rate for bamboo leaves was lower than for teak leaves but these differences are in accordance with variances in decomposition rates between plant species (Mills et al., 2001).

In the Kali Sengon river a larger difference in decomposition rates between the fine mesh packs and coarse mesh packs was observed for both leaf types when compared to the acidic sites. Bamboo and teak leaf packs in the neutral Kali Sengon river were colonized by several macroinvertebrate taxa, among which chironomid larvae were dominant. However no density increase in macroinvertebrate abundance over time was observed, which differs from the results of Dudgeon & Wu (1999). No large differences were observed between the coarse and fine packs from the acidic sites and we therefore conclude that the differences in *k* rates between coarse and fine mesh packs in the neutral Kali Sengon river can be explained by the decomposition activity of macroinvertebrates.

In contrast to the neutral Kali Sengon, only chironomids were found in very low numbers at Liwung and no macroinvertebrates were present at Blawan and, obviously, at Paltuding, the most acidic site. Lower macroinvertebrate diversity, and the absence of shredders, are common in acidic streams (Wren & Stephenson, 1991; Gerhardt, 1993; Dangles & Guérol, 1998) although macroinvertebrate species have been found in environments with pHs lower than 3 (Winterbourn & Mc Diffet, 1996). Results from an extended macroinvertebrate survey in the Banyupahit–Banyuputih river reported chironomids from both Blawan and Liwung. These chironomids were identified as belonging to the genus *Polypedilum* (subfamily Chironominae) at both Blawan and Liwung; at Blawan members of the genus *Chironomus* sp. (subfamily Chironominae) and *Rheocricotopus* sp. (subfamily Orthocladiinae) were also found. Members of the genus *Polypedilum* were not found earlier in acidic streams (Orendt, 1999), but members of the genus *Chironomus* were (Green & Kramadibrata, 1988). Chironomids may be the only shredders present in acidic environments as was observed at pH 4.0 (Tuchman, 1993). However, the chironomids collected earlier at Blawan and Liwung were sediment dwelling organisms and it is unclear if they belong to the shredder functional group. So the influence of shredders in the coarse packs at the three acidic sites is probably insignificant. The hypothesis that macroinvertebrates may have adapted to the old acidic environment, in particular shredders involved in leaf litter decomposition, cannot be confirmed by our results.

In acidic environments microbial activity can be depressed (Groom & Hildrew, 1989; Birmingham et al., 1996), and fungal growth as well as bacterial activity are often depressed under acidic conditions (Gross & Robbins, 2000). Low pH does not always relate to microbial respiration rate, as was reported from AMD streams (Niyogi et al., 2001). However, a cultivation-independent fingerprinting method revealed lower microbial diversity for the Banyupahit–Banyuputih river than for the Kali Sengon river (Löhr, unpublished data). Also metabolic capacity, e.g. the capability to use carbon sources measured using Biolog EcoPlates, was much lower at the most acidic site Paltuding than at Blawan and Liwung. We therefore conclude

that the differences in microbial composition and activity caused the higher decomposition rate in the Kali Sengon river in the fine leaf packs. It was expected that breakdown rates at the moderately acidic sites would be faster than at the extremely acidic site, because of the higher microbial activity found with the Biolog EcoPlates, but differences were small. It is known that microbial respiration can be affected by the deposition of metal oxides (Niyogi et al., 2001) and ferric hydroxide affects microbial colonization, especially aquatic hyphomycetes, at pH 2.8 (Siefert & Mutz, 2001). Along the entire stretch of the Banyupahit–Banyuputih river solid phases may precipitate in response to changes in pH. A whitish suspension is formed between the Kali Sat and Kali Sengon that consists mainly of an amorphous aluminium hydroxysulfate precipitate (Delmelle & Bernard, 2000). This precipitate may settle under quiet conditions, but part of it will also be transported downstream in suspension. Below the junction with the Kali Sengon a reddish veneer is frequently observed to cover rocks and pebbles in the riverbed, suggesting that much of the dissolved iron is precipitated as (oxy)hydroxide compounds. It is therefore possible that the precipitation at Blawan and Liwung inhibits the settlement of microorganisms, which resulted in leaf litter decomposition rates comparable to those at Paltuding.

The lower microbial activity might also partly explain the low abundance of shredders at Blawan and Liwung since they prefer leaves that are colonized by microorganisms, i.e. conditioned leaves, which are more palatable (Barlöcher & Kendrick, 1975; Giller & Malmqvist, 1998). In an AMD study at low pH, 72% of leaf litter breakdown related to metal oxides and increased concentrations of Zn (Niyogi et al., 2001). Although zinc concentrations are lower in the Banyupahit–Banyuputih river than from the AMD, high metal concentrations also play an important role in the regulation of the aquatic community in the Banyupahit–Banyuputih river. We conclude that the aquatic community of this volcanogenic river is impacted by multiple stress factors. Its functioning is directly or indirectly affected by these factors as is observed from the leaf litter breakdown experiments. Moreover, the low pH and high load of metals have serious effects on the energy supply of the river ecosystem. Leaf decomposition rates were lower in the acidic

Banyupahit–Banyuputih river than in the neutral Kali Sengon river and differences between the three acidic sites were small. The differences in decomposition rates can be explained by a decrease of shredders in the coarse leaf packs and by reduced microbial activity at low pH.

Acknowledgements

We would like to thank Rik Zoomer for his assistance with the C:N ratio analyses, Rudo Verweij for his assistance with lab measurements, and Janita Löhr and Wouter Meijer for their assistance during the fieldwork. This work was supported by The Netherlands Foundation for the Advancement of Tropical Research (WOTRO), residing under the Netherlands Organization for Scientific Research (NWO) (project number WAE 84–465).

References

- Allen, H. E. & D. J. Hansen, 1996. The importance of trace metal speciation to water quality criteria. *Water Environmental Research* 68: 42–53.
- Barlöcher, F. & B. Kendrick, 1975. Leaf-conditioning by microorganisms. *Oecologia* 20: 359–362.
- Birmingham, S., L. Matlby & R. C. Cooke, 1996. Effects of coal mine effluent on aquatic hyphomycetes. I. Field study. *The Journal of Applied Ecology* 33: 1311–1321.
- Carpenter, J., W. E. Odum & A. Mills, 1983. Leaf litter decomposition in a reservoir affected by acid mine drainage. *Oikos* 41: 165–172.
- Clements, W. H. & M. C. Newman, 2002. *Community Ecotoxicology*. John Wiley & Sons, Chichester.
- Dangles, O. & F. Guérol, 1998. A comparative study of beech leaf breakdown, energetic content, and associated fauna in acidic and non-acidic streams. *Archiv für Hydrobiologie* 144: 25–39.
- Dangles, O. & F. Guérol, 2001. Linking shredders and leaf litter processing: insights from an acidic stream study. *Internationale Revue der Gesamten Hydrobiologie* 86: 395–406.
- Dangles, O., M. O. Gessner, F. Guérol & E. Chauvets, 2004a. Impacts of stream acidification on litter breakdown: implications for assessing ecosystem functioning. *Journal of Applied Ecology* 41: 365–378.
- Dangles, O., B. Malmqvist & H. Laudon, 2004b. Naturally acid freshwater ecosystems are diverse and functional evidence from boreal streams. *Oikos* 104: 149–155.
- Delmelle, P. & A. Bernard, 2000. Downstream composition changes of acidic volcanic waters discharged into the Banyupahit stream, Ijen caldera, Indonesia. *Journal of Volcanology and Geothermal Research* 97: 55–75.
- De Pauw, N. & R. Vannevel, 1991. Macro-invertebraten en Waterkwaliteit. Stichting Leefmilieu, Antwerpen.
- Dudgeon, D. & K. J. Wu, 1999. Leaf litter in a tropical stream: food or substrate for macroinvertebrates? *Archiv für Hydrobiologie* 146: 65–82.
- Gerhardt, A., 1993. Review of impact of heavy metals on stream invertebrates with special emphasis on acid conditions. *Water, Air and Soil Pollution* 66: 289–314.
- Giller, P. S. & B. Malmqvist, 1998. *The Biology of Streams and Rivers*. Oxford University Press.
- Green, J. & H. Kramadibrata, 1988. A note on Lake Goang, an unusual acid lake in Flores, Indonesia. *Freshwater Biology* 20: 195–198.
- Groom, A. P. & A. G. Hildrew, 1989. Food quality for detritivores in streams of contrasting pH. *Journal of Animal Ecology* 58: 863–881.
- Gross, S. & E. I. Robbins, 2000. Acidophilic and acid-tolerant fungi and yeasts. *Hydrobiologia* 433: 91–109.
- Hieber, M. & M. O. Gessner, 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass determinations. *Ecology* 83: 1026–1038.
- Kok, C. J. & G. Van der Velde, 1994. Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf material in alkaline and acid still water. *Freshwater Biology* 31: 65–75.
- Löhr, A. J., T. A. Bogaard, A. Heikens, M. R. Hendriks, S. Sumarti, M. J. van Bergen, C. A. M. van Gestel, N. M. van Straalen, P. Z. Vroon & B. Widianarko, 2005. Natural pollution caused by the extremely acid crater lake Kawah Ijen, East Java, Indonesia. *Environmental Science & Pollution Research* 12: 89–95.
- Maltby, L., 1996. Chapter 4. Heterotrophic microbes. In Petts, G. & P. Calow (eds.), *River Biota: Diversity and Dynamics*. Blackwell Science, Oxford, UK: 145–167.
- Mills, G. L., J. V. McArthur, C. Wolfe, J. M. Aho & R. B. Rader, 2001. Changes in fatty acids and hydrocarbon composition of leaves during decomposition in a southeastern blackwater stream. *Archiv für Hydrobiologie* 152: 315–328.
- Mulholland, P. J., A. V. Palumbo, J. W. Elwood & A. D. Rosemond, 1987. Effects of acidification on leaf decomposition in streams. *Journal of the North American Benthological Society* 6: 147–158.
- Niyogi, D. K., W. M. Lewis & D. Mc Knight, 2001. Litter breakdown in mountain streams affected by mine drainage: biotic mediation of abiotic controls. *Ecological Application* 11: 506–516.
- Niyogi, D. K., K. S. Simon & C. R. Townsend, 2003. Breakdown of tussock grass in streams along a gradient of agricultural development in New Zealand. *Freshwater Biology* 48: 1698–1708.
- Orendt, C., 1999. Chironomids as bioindicators in acidified streams: a contribution to the acidity tolerance of chironomid species with a classification in sensitivity classes. *Internationale Revue Hydrobiologie* 84: 439–449.
- Perum Perhutani, 1998. A glance at Perum Perhutani (state-owned forest enterprise) Indonesia, Jakarta.

- Rothschild, L. J. & R. L. Mancinelli, 2001. Life in extreme environments. *Nature* 409: 1092–1101.
- Siefert, J. & M. Mutz, 2001. Processing of leaf litter in acid waters of the post-mining landscape in Lusatia, Germany. *Ecological Engineering* 17: 297–306.
- Tachet, H., P. Richoux, M. Bournaud & P. Usseglio-Polatera, 2000. *Invertébrés d'eau douce, systématique, biologie, écologie*. CNRS Editions, Paris.
- Townsend, C. A., A. G. Hildrew & J. Francis, 1983. Community structure in some southern English streams: the influence of physicochemical factors. *Freshwater Biology* 13: 315–327.
- Tuchman, N. C., 1993. Relative importance of microbes versus macroinvertebrate shredders in the process of leaf decay in lakes of differing pH. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2707–2712.
- Winterbourn, M. J. & W. F. M. McDiffet, 1996. Benthic faunas of streams of low pH but contrasting water chemistry in New Zealand. *Hydrobiologia* 341: 101–111.
- Wren, C. D. & G. L. Stephenson, 1991. The effect of acidification on the accumulation of metals to freshwater invertebrates. *Environmental Pollution* 71: 205–241.