*Zoological Studies* **46**(5): 609-621 (2007)

Zoological Studies

# Leaf Breakdown in a Subtropical Stream Riffle and Its Association with Macroinvertebrates

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*(Accepted May 3, 2007)*

**Sen-Her Shieh, Chorng-Bin Hsu, Chiao-Ping Wang, and Ping-Shih Yang (2007)** Leaf breakdown in a subtropical stream riffle and its association with macroinvertebrates. *Zoological Studies* **46**(5): 609-621. The relationships between the quality of leaves of 3 trees (*Machilus thunbergii*, *Schefflera octophylla*, and *Ficus erecta*) and the assemblages of macroinvertebrates were studied at a riffle section of a 3rd-order subtropical forest stream in northern Taiwan. Macroinvertebrate taxon richness and density that colonized bags of leaves of the 3 tree species did not significantly differ. Macroinvertebrate assemblages were dominated by collectors, such as non-Tanypondinae Chironomidae, *Prosimulium* spp., and *Baetis* spp., which constituted > 79% of the total fauna. Results of a principal component analysis (PCA) showed that the macroinvertebrate assemblages were associated with the incubation time of the litter bags in the stream and the fine particulate organic matter (FPOM) trapped by the leaf bags, but not with the variables of leaf litter quality. Shredders, predominantly small nemourids, accounted for only 5.7%, 7.1% and 10.8% of the total macroinvertebrate assemblages on *M. thunbergii*, *S. octophylla*, and *F. erecta*, respectively, suggesting that macroinvertebrates played only a minor role in leaf litter breakdown in this subtropical 3rd-order stream. However, the density of shredders on *F. erecta*, as a function of the weight of the leaf litter remaining, was significantly higher than that of *M. thunbergii*, possibly because of the preference of shredders for high-quality food resources. In a comparison with the temperate zone systems, the dominant taxa of shredders that colonized the leaf litter were similar, but their relative abundances were much less in this subtropical forest stream riffle.
http://zoolstud.sinica.edu.tw/Journals/46.5/609.pdf

**Key words:** Leaf litter quality, Shredders, Collectors, Particulate organic matter (POM), Taiwan.

Low-order forested streams depend on inputs of leaf litter from terrestrial vegetation as the primary source of energy for their detritus-based food webs (Webster and Benfield 1986, Wallace et al. 1997). As leaf litter directly or indirectly falls into streams, it is colonized and decomposed by microbes and consumed by macroinvertebrate shredders (Gessner et al. 1999). The breakdown rates of leaf litter in streams, therefore, depend on the composition of the decomposer community: microbes (bacteria and fungi) and macroinvertebrate shredders. These processes lead to the production of fine particulate organic matter (FPOM), which is consumed by macroinvertebrate collectors. The shredders and collectors are thus the major primary consumers, providing the main link between the organic inputs and predators in stream ecosystems.

Information on leaf breakdown in tropical evergreen forest systems is limited (Pearson et al. 1989, Graça 1993 2001, Nolen and Pearson 1993, Benstead 1996), although there have been several recent studies on leaf litter processing in tropical streams (e.g. Mathuriau and Chauvet 2002, Cheshire et al. 2005, Gonçalves et al. 2006, Wantzen and Wagner 2006). Tropical forests dif-

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fer from temperate ones in that leaves fall throughout the year in the tropics (Stout 1980, Benson and Pearson 1993, Wantzen and Wagner 2006). Therefore, a large standing stock of leaf litter is present in the streambed in all seasons and is always available to stream fauna (Dudgeon 1982, Pearson et al. 1989), except after floods (Pearson 2004). In temperate forests, the input of litter to the stream only occurs in autumn, and a great deal of this material is processed during winter (Stout 1989). Moreover, species diversity of the riparian vegetation in tropical forests is much higher than that in temperate zones and may provide more-diverse food resources for animals feeding on them (Bastian et al. 2007).

The influence of shredders on leaf breakdown is well known in temperate streams (Graça 2001, Hieber and Gessner 2002) but is still being debated in tropical streams. In temperate streams, for example, Petersen and Cummins (1974) reported that 30% of the leaf litter converted to FPOM was attributed to shredder activity. Anderson and Sedell (1979) indicated that shredders may account for 25% of leaf breakdown. Hieber and Gessner (2002) documented that shredders accounted for > 50% of leaf-mass loss during leaf-litter breakdown. In tropical streams, however, some studies (Irons et al. 1994, Dobson et al. 2002, Gonçalves et al. 2006) suggested that shredders are few in or even absent from tropical streams and probably do not play important roles in leaf breakdown. Other studies (Pearson et al. 1989, Nolen and Pearson 1993, Crowl et al. 2001, Cheshire et al. 2005, Crowl et al. 2006) indicated that shredders, special shrimp, have an important role in leaf-litter breakdown in tropical streams. Moreover, most of those studies were performed in the Neotropics. Little information is available on the role of shredders in leaf breakdown in subtropical forested stream systems.

Leaf litter which has accumulated in streams has different macroinvertebrate assemblages associated with it according to the hydraulic characteristics (current velocity and streambed topography) in the channel (Kobayashi and Kagaya 2002 2004). Densities of stonefly shredders are highest in leaf litter in riffles, while those of caddisfly shredders are highest in stream pools (Kobayashi and Kagaya 2005). This study was conducted in a riffle section in a subtropical Taiwanese stream to examine the assemblages of macroinvertebrates that colonized the leaf litter of 3 tree species during its breakdown and to determine the relationships between the quality of the leaves of these 3 species and the assemblage of macroinvertebrates.

## MATERIALS AND METHODS

### Study area

The study was conducted in Hapen Creek, a 3rd-order stream in northern Taiwan (Fig. 1). The stream has a drainage area of about 6 km$^2$ at elevations of 500-1200 m and a channel length of about 5.7 km. The watershed is in a subtropical rainforest. The forest is composed of mixed subtropical evergreen hardwoods and is dominated by species of the Fagaceae and Lauraceae (Lin et al. 2001). The riparian vegetation of the creek consists mainly of *Machilus thunbergii*, *Schefflera octophylla*, *Castanopsis carlesii*, *Litsea acuminata*, *Ficus erecta*, *Phoebe formosana*, and *Villebrunea pedunculata* (Chang 1998, Peng 1999). Most of the tree species lose leaves continuously during the year, with an increase in leaf litterfall in spring, resulting from nutrient translocation of the vegetation, and in summer and fall due to typhoon disturbances (Peng 1999). The substrate at the study site is primarily composed of cobbles and boulders and is shaded by riparian vegetation.

The climate of the area is hot and humid. The annual mean temperature is 18.2°C with the lowest in Jan. (11.8°C) and highest in July (24.1°C)

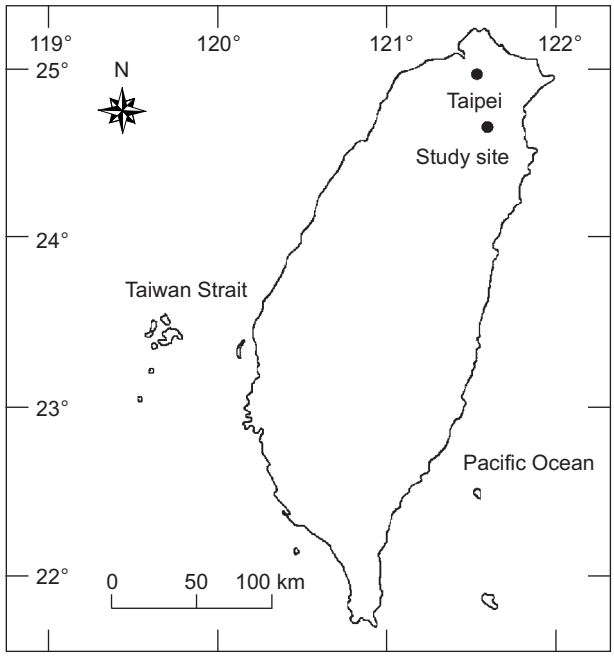


**Fig. 1.** Location of the study site in Taiwan.

(Lin et al. 2000). The area has an annual total precipitation of about 3660 mm and receives about 58% of its precipitation during May to Oct. and about 42% during Nov. to Apr. The annual mean relative humidity is 96%, with the lowest in July (94%) and highest in Feb. (98%) (Hsia and Hwong 1999). The soil of the area is a lithic dystrochrept with pH values ranging 3.8-5.0 (Lin et al. 1996). The study was conducted from 25 Jan. to 24 Mar. 2002 during which time water temperatures ranged 16.6-19.4°C (with an accumulative water temperature of about 1028°C), a stream width of 6.3-6.6 m, a water depth of 13-14 cm, and a current velocity of 32-47 cm/s. The conductivity of the stream water ranged 28.2-41.0 μs/cm, pH was 6.53-6.88, and dissolved oxygen was 8.46-9.83 mg/l.

**Litter processing**

Leaves of *M. thunbergii* (Lauraceae), *S. octophylla* (Araliaceae), and *F. erecta* (Moraceae) were used to determine the relationships between the quality of leaf litter and the assemblage of macroinvertebrates. Leaves of *M. thunbergii* are thick, tough, and glabrous and contain relatively low nitrogen (N) and phosphorus (P) concentrations and high C: N ratios. Leaves of *S. octophylla* and *F. erecta* possess relatively high N and P concentrations and low C: N ratios; leaves of *S. octophylla* are thick, soft, and glabrous and those of *F. erecta* are thin, soft, and hairy (Shieh's unpubl. data). Leaves were picked up from the ground at the study area soon after natural abscission, brought back to the laboratory and air-dried. About 5 g of air-dried material was weighed for placement into litter bags (20 x 35 cm) with a 10 mm mesh size. This mesh size was chosen to ensure that the water flow through the bags was sufficient to exclude the possibility of decomposition rates being affected by confinement and that invertebrate activity, especially that of shrimp, was not restricted. On 25 Jan. 2002, 30 litter bags of each species were transported to a riffle section of the stream. In order to secure these litter bags in the stream, 10 steel wires were strung perpendicularly across the stream at 3 m intervals. Each steel wire was secured to the stream bottom near the banks with 1 m long steel rods. The litter bags were randomly tied to the steel wires at about 50 cm intervals. These leaf bags were left in the stream for periods of 1, 3, 9, 23, 58, and 86 d. There were 5 replicates of each species for each sampling date. The leaf bags were retrieved by placing a fine-mesh sieve under the litter bag and cutting the attaching string. Litter bags were enclosed in a zip-loc plastic bag and kept on ice during transfer to the laboratory. At the beginning of the experiment, another 5 bags of each species were used to determine the initial leaf quality.

In the laboratory, the leaf litter in the bags was rinsed with tap water, and the associated macroinvertebrates and detritus were retained on a 45 μm mesh net. Leaves were placed in paper envelopes, oven-dried to a constant weight of 50°C, and weighed. The litter samples were ground (to < 0.5 mm) (Ball Mill, CMT, TI-100, Tokyo, Japan) for the elemental analysis. Two milligrams of ground-up litter was taken to determine the carbon (C) and nitrogen (N) concentrations using a CN elemental analyzer (EA, Thermo Finnigan NA 1500, North Chelmsford, MA, USA). Further 0.5 g subsamples were heated to 490°C for 3 h in a muffle furnace to determine the ash-free dry mass (AFDM), which was used to correct for the whole sample. The ash was mixed with a 2 N HCl solution, washed into a 50 ml flask with distilled and deionized water, and filtered (Munson and Nelson 1990). An inductively-coupled plasma (ICP) mass spectrometer (Jobin-Yvon Horiba group, JY 2000, Edison, NJ, USA) was used to determine phosphorus (P), sodium (Na), potassium (K), calcium (Ca), and magnesium (Mg) concentrations. However, the remaining litter of *S. octophylla* and *F. erecta* on day 86 was insufficient for the elemental analysis, so this paper reports the results of the first 58 d of incubation in the stream.

Macroinvertebrates were sorted and enumerated under a dissecting microscope, and preserved in 75% ethanol. Numbers of animals per bag and per the remaining AFDM were calculated. Macroinvertebrates colonizing the litter bags were assigned to functional feeding groups by checking the gut contents and comparing species with information contained in Merritt and Cummins (1996) and Thorp and Covich (1991). Detritus accumulated in the leaf bags was passed through a series of sieves to separate the coarse particulate organic matter (CPOM > 1 mm) and fine particulate organic matter (FPOM < 1mm). The AFDM of these organic matter categories was determined as for leaf samples.

**Data analysis**

One-way analysis of variance ( ANOVA) was used to test for differences in the initial mean con-

centrations of elements among the 3 leaf species. Temporal variations and differences in accumulated particulate organic matter (POM) of the leaf species and macroinvertebrate assemblages colonizing these leaf bags were analyzed by two-way repeated-measures ANOVA. Data for elemental concentrations, accumulated POM, and macroinvertebrate assemblages were transformed (using arcsine, square root, and logarithmic transformations, respectively) to respectively meet the assumptions of normality and constant variances (Zar 1999). Significance was accepted at the $p < 0.05$ confidence level. Following a significant ANOVA, Tukey's test was used to determine where the differences occurred. These analyses were performed using the statistical package SPSS for Windows 10.0 (SPSS, Chicago, IL, USA, 1999). A stepwise multiple regression was used to examine the relationships between the density of individual taxa and accumulated POM and leaf quality. In this analysis, density data were log(x+1)-transformed. The default entry and $p$ values were both 0.15. This analysis was conducted using SAS for Windows 9.1 (SAS Institute, Cary, NC, USA, 2006).

Ordination techniques were used to examine the relationship among accumulated POM, leaf quality, and macroinvertebrate assemblages in the leaf bags. The initial analysis of the macroinvertebrate dataset, using a detrended correspondence analysis (DCA), revealed that the dataset had a short gradient length (< 2 standard deviation units). Thus, the linear models were appropriate for further analysis (ter Braak 1995). A principal component analysis (PCA) was conducted with the computer software CANOCO 3.12 (ter Braak 1988 1990). Forward selection of 11 environmental variables (including 2 POM variables (CPOM and FPOM) accumulated in the leaf bags, 7 variables of leaf quality (i.e., the concentrations of C, N, P, Na, K, Ca, and Mg), and 2 nominal variables (incubation time and leaf types)) was used to ascertain the minimal set of variables that explained the data of the macroinvertebrate assemblages. The statistical significance ($p < 0.05$) of a variable was determined by means of a Monte Carlo permutation test. Taxa that occurred on only 1 sampling date and which constituted less than 0.01% of the total abundance were excluded from the analyses. In total, 19 taxa were included in the dataset, and the abundance data were $\log_{10}(x+1)$-transformed before the analyses.

## RESULTS

### Leaf litter quality

All elemental concentrations showed significant differences among the 3 leaf species (one-way ANOVA, $p < 0.05$) (Table 1). The initial C amount was highest for *M. thunbergii* (49.3%), 2nd for *S. octophylla* (48.2%), and lowest for *F. erecta* (37.6%). The initial N and P concentrations were lowest for *M. thunbergii*, intermediate for *F. erecta*, and highest for *S. octophylla*, at the respective concentrations of 1.45%, 1.65%, and 2.13% for N and 0.066%, 0.089%, and 0.160% for P. In terms of nutrient elements, therefore, the leaves of *S. octophylla* and *F. erecta* had higher resource quality attributes than those of *M. thunbergii*. The initial Na concentration of *S. octophylla* leaves was much higher than those of *M. thunbergii* and *F. erecta*. Leaves of *S. octophylla* had the highest initial concentrations of Mg and K and the least of Ca. In contrast, *M. thunbergii* had the lowest initial

**Table 1.** Mean initial concentrations of elements (± SD) ($n = 5$) for leaves of the 3 tree species. Values within an element with the same letter do not significantly differ ($p > 0.05$, one-way ANOVA and Tukey's test)

| | Tree species | | |
|---|---|---|---|
| Concentration (%) | *M. thunbergii* | *S. octophylla* | *F. erecta* |
| Carbon | $49.2800^{a} \pm 0.3800$ | $48.2400^{b} \pm 0.4200$ | $37.6000^{c} \pm 0.5000$ |
| Nitrogen | $1.4460^{a} \pm 0.0760$ | $2.1340^{b} \pm 0.1370$ | $1.6500^{c} \pm 0.1060$ |
| Phosphorus | $0.0658^{a} \pm 0.0085$ | $0.1596^{b} \pm 0.0101$ | $0.0894^{c} \pm 0.0048$ |
| Calcium | $1.2670^{a} \pm 0.2490$ | $0.8200^{b} \pm 0.0880$ | $4.3190^{c} \pm 0.2000$ |
| Potassium | $0.2244^{a} \pm 0.0612$ | $1.1690^{b} \pm 0.1061$ | $0.5470^{c} \pm 0.1553$ |
| Magnesium | $0.2114^{a} \pm 0.0332$ | $0.3846^{b} \pm 0.0310$ | $0.3772^{b} \pm 0.0271$ |
| Sodium | $0.0380^{a} \pm 0.0037$ | $0.4076^{b} \pm 0.0261$ | $0.0188^{c} \pm 0.0030$ |

concentrations of Mg and K.

**Macroinvertebrate assemblages**

In total, 46 macroinvertebrate taxa colonized the 3 leaf species during the experimental period (Table 2). There were 40, 36, and 31 taxa which colonized *M. thunbergii*, *S. octophylla*, and *F. erecta*, respectively, during the 58 d incubation (Fig. 2A). Average taxon richness did not differ among the leaf species (two-way ANOVA, $p > 0.05$). This indicated that the colonization rates of macroinvertebrate taxa on the 3 species of leaves were similar. In general, the taxon richness significantly increased with the time of incubation (two-way ANOVA, $p < 0.05$), with the exception of *M. thunbergii* on days 3 and 23, and *F. erecta* on day 3. The assemblage structure of macroinvertebrates on the 3 leaf species was similar (Table 2), being composed of Diptera (82.3% on *M. thunbergii*, 83.3% on *S. octophylla*, and 80.6% on *F. erecta*), Plecoptera (6.2%, 7.5%, and 11.1%), Ephemeroptera (5.2%, 3.9%, and 4.2%), and Trichoptera (2.2%, 1.7%, and 1.5%). These 4 taxa represented > 95% of the total numbers. Although there was no significant difference in macroinvertebrate densities per litter bag among the 3 leaf species (two-way ANOVA, $p > 0.05$), the mean density in the litter bags of *M. thunbergii* was lowest, *F. erecta* 2nd, and *S. octophylla* highest. Maximum mean densities reached 268 and 341 individuals per bag on day 58 for *M. thunbergii* and *F. erecta*, respectively, while the peak number of *S. octophylla* occurred on day 9 with 363 individuals per bag (Fig. 2B). In general, macroinvertebrate abundance significantly increased with the time of incubation (two-way ANOVA, $p < 0.05$), with the exception of *M. thunbergii* on days 9 and 23, *S. octophylla* on day 23, and *F. erecta* on day 3 (Fig. 2B).

Non-Tanypodinae Chironomidae predominated at 53.5%, 65.3%, and 61.9% for *M. thunbergii*, *S. octophylla*, and *F. erecta*, respectively, followed by *Prosimulium* spp. (25.2%, 14.8%, and 12.5%), *Amphinemura* sp. (4.1%, 5.2%, and 8.8%), and *Baetis* spp. (3.9%, 3.2%, and 3.5%) (Table 2). Changes in individual numbers of these 4 dominant taxa during the course of the study are shown in figure 3. In general, the number of non-Tanypodinae Chironomidae increased through the experimental period for the 3 leaf species, except for *M. thunbergii* on days 9 and 23, *S. octophylla* on day 23, and *F. erecta* on day 3. The number of the taxa increased to 164 individuals per bag after day 58 on *M. thunbergii*, 325 individuals per bag after day 9 on *S. octophylla*, and 227 individuals per bag after day 58 on *F. erecta*. *Prosimulium* spp. colonized the 3 leaf species very rapidly, with maximum densities found on day 3 for *M. thunbergii* and *S. octophylla*, and on day 1 for *F. erecta*, after which the numbers decreased. The number of *Amphinemura* sp. reached a maximum on day 23 and then decreased on day 58. The number of *Baetis* spp. reached a maximum on day 9 for *S. octophylla* and *F. erecta*, but it increased throughout the experimental period for *M. thunbergii*.

**Functional organization**

Macroinvertebrates were assigned to func-

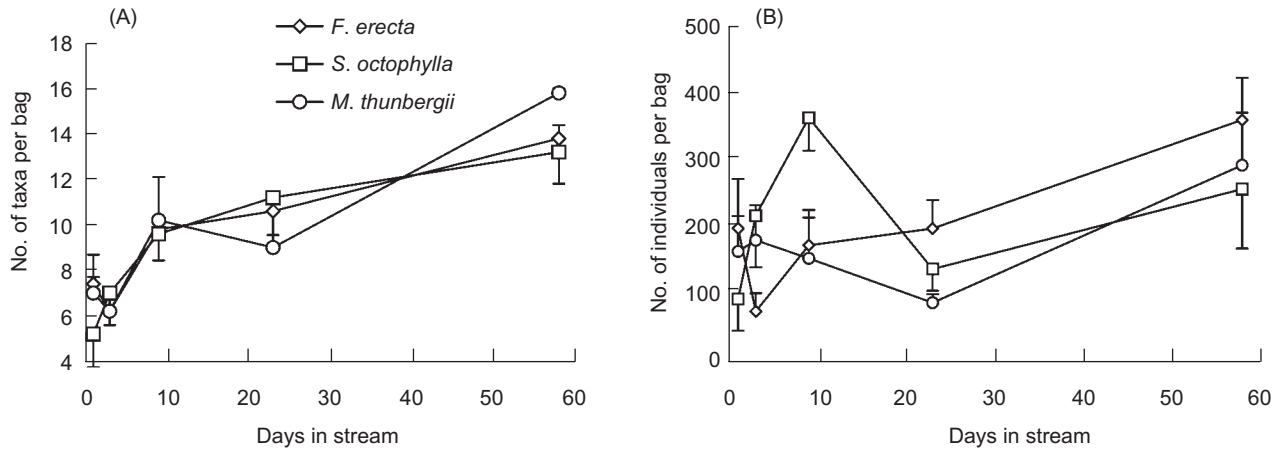


**Fig. 2.** Mean number of taxa (A) and total number of individuals per bag (B) colonizing litter bags containing leaves of 3 tree species during their breakdown in Hapen Creek, Taiwan. Vertical lines indicate 1 standard error.

**Table 2.** Relative abundances of macroinvertebrate taxa associated with bags containing leaves of 3 tree species (% of total numbers accumulated over the study period). CO, collectors, SC, scrapers, SH, shredders, P, predators, PI, piercers, -, absent. An asterisk (*) indicates that the data were not used in the principal component analysis

| Taxa | FFG | Abbr. | *M. thunbergii* | *S. octophylla* | *F. erecta* |
|---|---|---|---|---|---|
| Ephemeroptera | | | | | |
| *Afronurus* sp. | SC | * | - | 0.02 | - |
| *Baetiella* sp. | CO | Bal | 0.50 | 0.39 | 0.31 |
| *Baetis* spp. | CO | Bae | 3.88 | 3.22 | 3.54 |
| *Caenis* sp. | CO | * | - | 0.08 | 0.04 |
| *Choroterpes taiwanensis* | CO | * | 0.02 | - | - |
| *Eburella brocha* | CO | * | 0.12 | 0.04 | - |
| *Electrogena fracta* | SC | * | 0.05 | - | - |
| *Epeorus erratus* | SC | Epe | 0.31 | 0.08 | 0.02 |
| *Rhithrogena ampla* | SC | * | 0.10 | 0.02 | 0.02 |
| *Torleya glareosa* | CO | Tor | 0.17 | 0.02 | 0.27 |
| Plecoptera | | | | | |
| *Amphinemura* sp. | SH | Amp | 4.05 | 5.17 | 8.82 |
| *Kamimuria* sp. | P | * | 0.02 | 0.08 | - |
| *Neoperla* sp. | P | Neo | 0.60 | 0.56 | 0.41 |
| *Protonemura* sp. | SH | Pro | 1.49 | 1.70 | 1.80 |
| *Togoperla* sp. | P | * | 0.02 | - | 0.04 |
| Odonata | | | | | |
| *Calopterys* sp. | P | * | - | - | 0.04 |
| *Mnais* sp. | P | * | 0.02 | 0.04 | - |
| Trichoptera | | | | | |
| *Anisocentropus* sp. | SH | * | 0.02 | - | - |
| *Ceraclea* sp. | CO | * | - | 0.02 | - |
| *Cheumatopsyche* sp. | CO | * | 0.05 | 0.08 | 0.04 |
| *Dipseudopsis* sp. | CO | * | 0.02 | 0.04 | 0.04 |
| *Goerodes* sp. | SH | * | 0.05 | 0.10 | 0.04 |
| *Hydropsyche* sp. | CO | Hyd | 0.12 | 0.10 | 0.08 |
| *Hydroptila* sp. | PI | Hyt | 0.41 | 0.56 | 0.77 |
| *Leptocerus* sp. | SH | * | 0.02 | 0.02 | 0.00 |
| *Oecetis* sp. | P | * | - | 0.02 | - |
| *Psychomyia* sp. | CO | * | 0.12 | 0.04 | 0.02 |
| *Rhyacophila* sp. | P | * | 0.05 | - | 0.06 |
| *Setodes* sp. | CO | * | 0.05 | - | - |
| *Stenopsyche* sp. | CO | Ste | 1.25 | 0.75 | 0.41 |
| Coleoptera | | | | | |
| *Eubrianax niger* | SC | * | 0.02 | - | - |
| *Grouvellinus* sp. | CO | Gro | 0.07 | 0.06 | 0.10 |
| *Mataeopsephus esakii* | SC | * | 0.02 | - | - |
| *Psephenoides* sp. | SC | * | 0.02 | - | - |
| *Zaitzevia* sp. | CO | Zai | 0.07 | 0.06 | 0.10 |
| Diptera | | | | | |
| *Antocha* sp. | CO | Ant | 0.86 | 0.66 | 0.52 |
| *Athrix* sp. | P | * | 0.02 | - | 0.04 |
| *Hemerodromia* sp. | P | Hem | 1.10 | 0.46 | 0.87 |
| Non-Tanypodinae Chironomidae | CO | Chi | 53.52 | 65.32 | 61.90 |
| *Nymphomyia* sp. | SC | * | - | 0.02 | - |
| *Prosimulium* spp. | CO | Sim | 25.16 | 14.75 | 12.45 |
| Tanypodinae | P | Tap | 1.65 | 2.04 | 4.83 |
| Decapoda | | | | | |
| *Macrobrachium asperulum* | CO/SH/P | Mac | 0.02 | 0.10 | 0.10 |
| Acari | P | Aca | 3.88 | 3.37 | 2.26 |
| Gastropoda | SC | * | 0.05 | 0.02 | 0.04 |
| Oligochaeta | CO | * | - | 0.04 | - |

tional feeding groups. The overall functional compositions of the macroinvertebrate assemblages on the 3 leaf species were similar. The 3 leaf species were dominated by collectors (86.0% for *M. thunbergii*, 85.6% for *S. octophylla*, and 79.8% for *F. erecta*), mainly due to the presence of non-Tanypodinae Chironomidae. Shredders represented only 5.7%, 7.1%, and 10.8% on *M. thunbergii*, *S. octopylla*, and *F. erecta*, respectively. The dominant shredders were nemourid stoneflies, *Amphinemura* sp. and *Protonemura* sp. Three taxa of caddisfly larvae, *Anisocentropus* sp., *Goerodes* sp., and *Leptocerus* sp., and 1 omnivorous shrimp, *Macrobrachium asperulum*, were less abundant. Shredder densities per litter bag showed significant increases with the time of incubation (two-way ANOVA, $p < 0.05$) with the exception of *M. thunbergii* and *F. erecta* on day 3 and *S. octophylla* and *F. erecta* on day 58 (Fig. 4A). They reached maxima on day 23 for *S. octophylla* and *F. erecta* and on day 58 for *M. thunbergii* (Fig. 4A). Although the shredder density was highest for *F. erecta*, followed by *S. octophylla* and *M. thunbergii*, there was no significant difference in the number of shredders per bag among the 3 leaf species (two-way ANOVA, $p > 0.05$). However, the number of shredders/g of leaf AFDM remaining among the 3 leaf species showed significant differences (two-way ANOVA, $p < 0.05$) (Fig. 4B). The number of shredders colonizing *F. erecta* was significantly higher than that on *M. thunbergii*, but there were no significant differences between *M. thunbergii* and *S. octophylla* or between *S. octophylla* and *F. erecta* (Tukey's test, $p > 0.05$).

### Accumulated POM, leaf litter quality, and macroinvertebrate assemblages

In general, the amount of all POM categories which accumulated in the leaf bags significantly increased with the time of incubation except for CPOM on day 3 and FPOM on day 23 (two-way ANOVA, $p < 0.05$). However, there was no significant difference in the amount of the 2 POM categories which accumulated in leaf bags among the 3 leaf species except for the amount of FPOM of *F. erecta* which was significantly higher than those of *M. thunbergii* and *S. octophylla* (two-way ANOVA, $p < 0.05$).

In the stepwise multiple regressions, the resulting best-fit model for each major taxa was significant ($p < 0.05$) (Table 3). The variables that

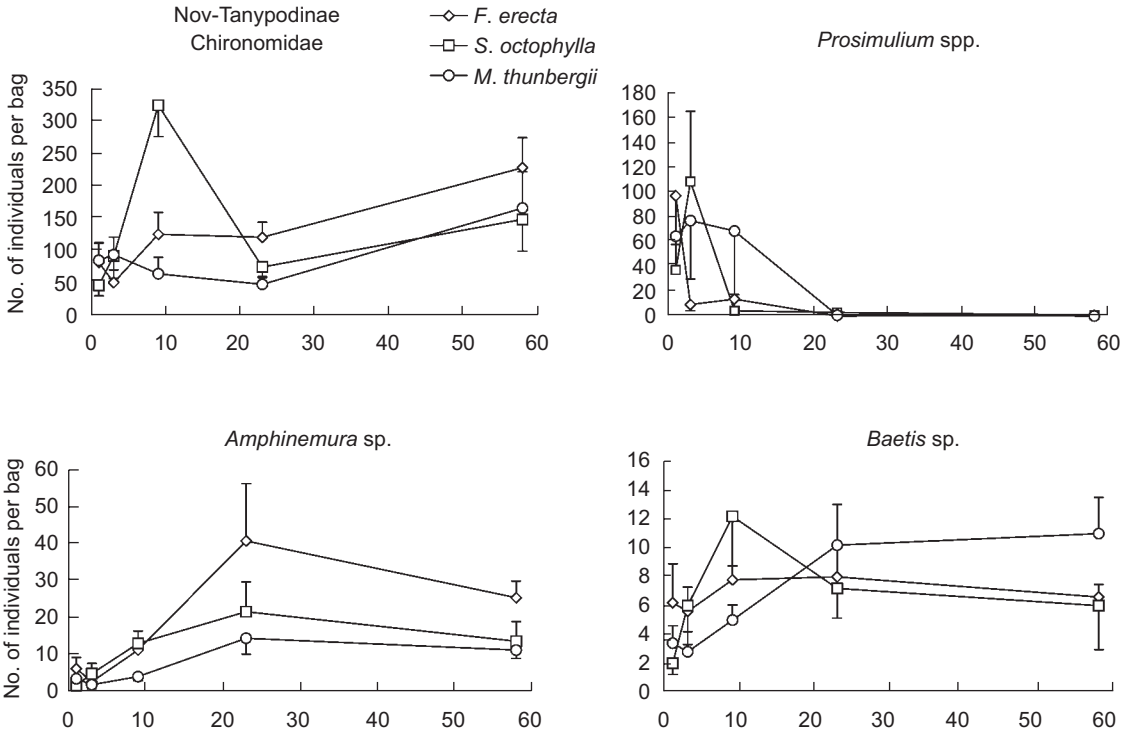


**Fig. 3.** Numbers of 4 major taxa colonizing litter bags containing leaves of 3 tree species during their breakdown in Hapen Creek, Taiwan. Vertical lines indicate 1 standard error.

best explained the colonization of *Baetis* spp. and *Amphinemura* sp. on the leaf bags were the N and K concentrations of the leaf litter and the FPOM that accumulated in the leaf bags. They explained 13% and 41%, respectively, of the variance of their abundances in the leaf bags. Only the incubation time of the leaf bags in the stream was selected by the analysis as influencing non-Tanypodinae Chironomidae and the total density colonizing the leaf bags, and it accounted for 15% and 9% of the variances, respectively. The FPOM that accumulated in the leaf bags explained 34% of the variance in the abundance of *Prosimulium* spp. The abundances of shredders were best explained by the N and K concentrations of leaf litter, as they together accounted for 38% of the variance.

The ordination results of the PCA on the relative importances of environmental variables to the macroinvertebrate assemblages are given in table 4. Eigenvalues for the 1st 4 axes were 0.414, 0.261, 0.077, and 0.056, respectively, indicating that the 2-dimensional diagram of the PCA was proper for presenting the dataset. The 1st 2 PCA axes explained 67.5% of the total variance in the macroinvertebrate assemblages. Neither of the 1st 2 PCA axes correlated with the number of taxa, number of individuals, or number of shredders.

The result of the PCA indicated the relative importance of accumulated POM and leaf litter quality to the macroinvertebrate assemblages that colonized the leaf bags (Fig. 5). In figure 5A, the samples are separated along axis 1 with samples collected in the early period of the experiment located to the left, and samples collected in the later period located to the right. This pattern reflects changes in the taxonomic composition of macroinvertebrates with incubation time of leaf bags in the stream.

Only 2 (incubation time of leaf bags in the stream and accumulated FPOM in the leaf bags) of 11 variables were selected by the Monte Carlo permutation test to explain the macroinvertebrate

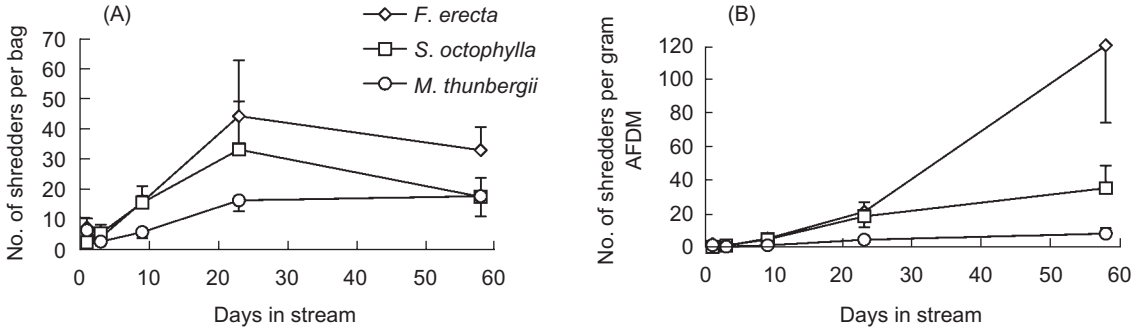


**Fig. 4.** Number of shredders per leaf bag (A) and per gram of the ash-free dry mass (AFDM) remaining in the litter bags (B) containing leaves of 3 tree species during their breakdown in Hapen Creek, Taiwan. Vertical lines indicate 1 standard error.

**Table 3.** Regression coefficients, *F*-values of the best-fit model, and adjusted $R^2$ for the results of the stepwise multiple regression. Densities of dominant taxa were used as the dependent variable. Various elements of the leaf litter (C, N, P, Na, K, Ca, and Mg), fine particulate organic matter (FPOM) and coarse POM (CPOM) accumulated in the leaf bags, and the time the leaf bags were in the stream (Exposure) were used as independent variables ($n$ = 75)

| Taxa | C | N | P | Na | K | Ca | Mg | FPOM | CPOM | Exposure | Intercept | *F*-value | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Baetis* spp. | ns | 0.1063* | ns | ns | -0.0395* | ns | ns | 0.7496* | ns | ns | 0.5384*** | 3.61** | 0.1324 |
| *Amphinemura* sp. | ns | 0.2327* | ns | ns | -0.0549* | ns | ns | 3.0169*** | ns | ns | ns | 16.12*** | 0.4052 |
| Non-Tanypodinae Chironomidae | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.0059* | 1.3656*** | 6.28** | 0.1484 |
| *Prosimulium* spp. | ns | ns | ns | ns | ns | ns | ns | -4.0038** | ns | ns | 1.2063*** | 18.32*** | 0.3372 |
| Shredders | ns | 0.2186** | ns | ns | -0.0586** | ns | ns | ns | ns | ns | 0.3545* | 13.74*** | 0.3673 |
| Total density | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.0066*** | 1.9768*** | 7.56*** | 0.0938 |

*$p$ < 0.15, **$p$ < 0.05, ***$p$ < 0.01, ns : not significant

data (dashed lines in Fig. 5B). The orientation of the line reflects the direction of the changes in the maximum of that variable, while the length of the line is proportional to the rate of change in that direction and reflects the proportion of variance that might explain the macroinvertebrate data. In this study, the exposure time of leaf bags in the stream was the variable which was most strongly related to the macroinvertebrate assemblages, followed by FPOM. The variables of leaf litter quality

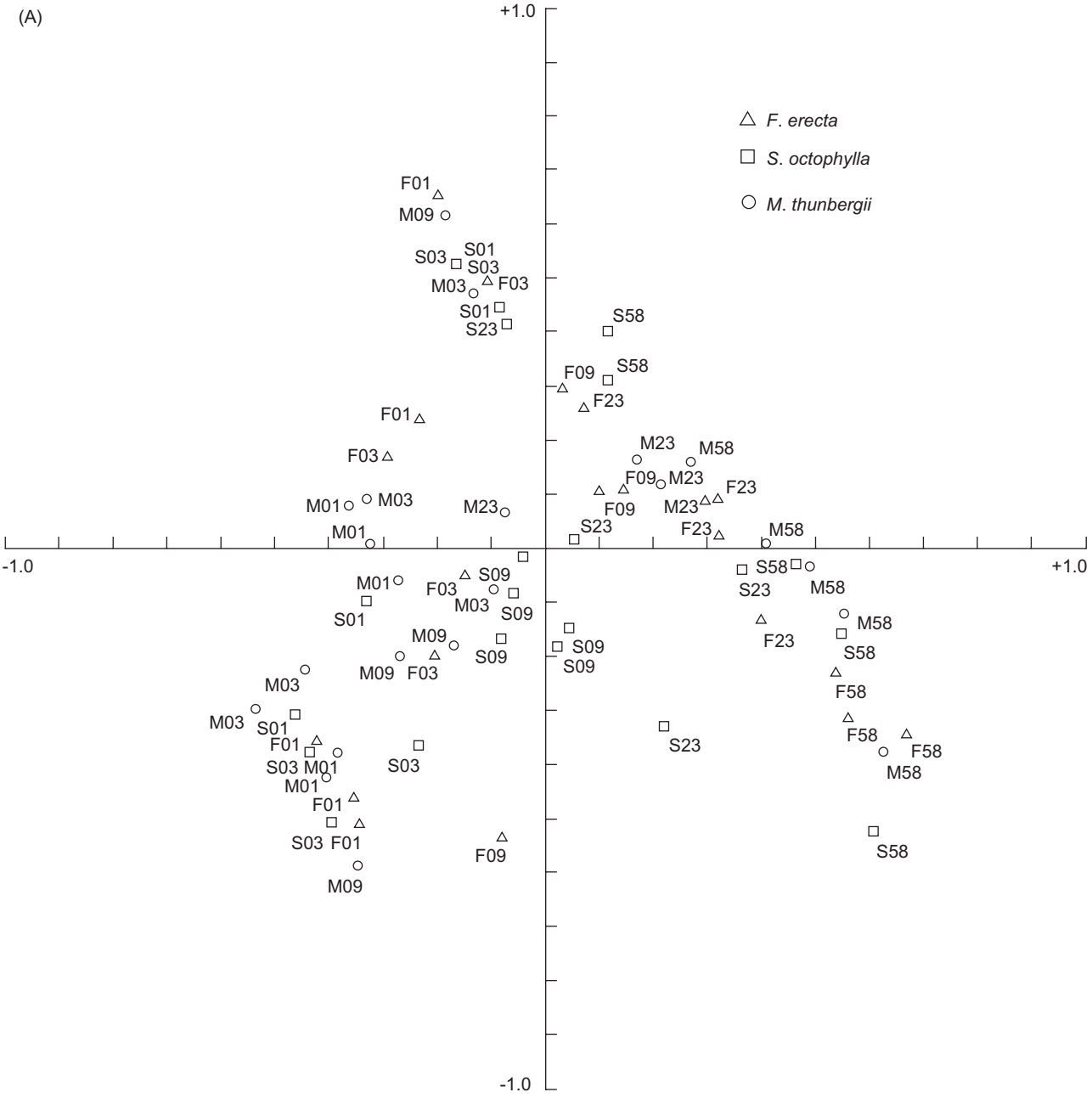


**Fig. 5.** Principal component analysis (PCA) ordination diagrams of sample scores (A) and selected environmental variables and macroinvertebrate taxa (B) on litter bags containing leaves of 3 tree species during the experiment. Environmental variables are shown as dashed lines (Exposure, incubation time in the stream; FPOM, fine particulate organic matter). Macroinvertebrate taxa are shown as solid lines (see table 2 for taxonomic abbreviations). Samples are labeled with a letter and 2-digit numbers. The letter represents the species leaf (M, *Machilus thunbergii*; S, *Schefflera octophylla*; F, *Ficus erecta*) and the 2-digit number represents the incubation time of the leaf bag in the stream. For example, M01 indicates that the sample is the leaf bag of *M. thunbergii* taken on day 1. The Eigenvalues for the 1st 4 axes are 0.414, 0.261, 0.077, and 0.056, respectively.

might not have been important in determining the macroinvertebrate assemblages colonizing the litter bags. The 1st axis of the PCA was positively correlated with the exposure time and accumulated FPOM in the litter bags in the stream. The 2nd axis suggested no significant environmental gradient.

In figure 5B, the orientation of the taxon line indicates the direction of change of the maximum of each taxon, while the length of the line reflects the proportion of variance that might explain the taxon data. Lines pointing in different directions indicate that individual taxa differed from each other in their responses to the environmental variables. The abundances of most taxa increased with the time of incubation, such as non-Tanypodinae Chironomidae, Tanypodinae, *Hemerodromia* sp., *Amphinemura* sp., *Baetis* spp., *Neoperla* sp., and *Protonemura* sp. However, *Prosimulium* spp., *Baetiella* sp., and *Epeorus eratus* had maximum abundances on days 1 or 3.

## DICUSSION

Macroinvertebrates rapidly colonized the leaf litter. This was in accordance with observations made by Dudgeon (1982) in Hong Kong and Mathuriau and Chauvet (2002) in southwestern Colombia. On day 1, there were about 150 invertebrate individuals colonizing the leaf bags of the 3 leaf species. Three of 4 dominant taxa (i.e., non-Tanypodinae Chironomidae, *Prosimulium* spp., and *Baetis* spp.), which constituted > 79% of the

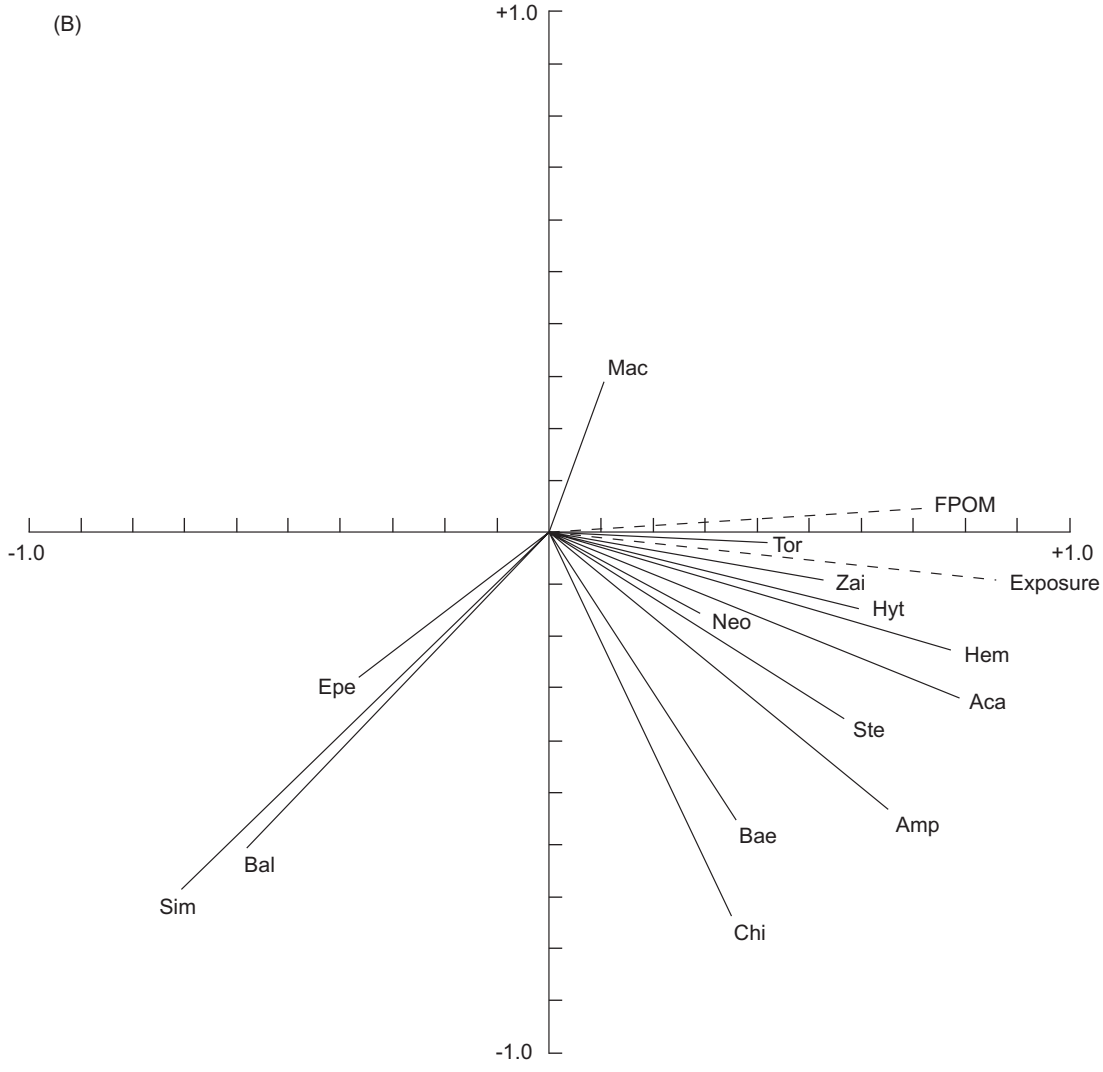


**Fig. 5.** Cont.

total fauna colonizing the 3 leaf species, belonged to the collector group. Wantzen and Wagner (2006) suggested that the number of macroinvertebrate collectors which possess generalized and opportunistic feeding strategies will increase in tropical streams containing leaves of tropical tree species which are recalcitrant and being disturbed by frequent spates which interfere with biotic leaf degradation. These collectors, which feed on FPOM, did not directly participate in the rapid breakdown of the leaves and probably used the litter bags primarily as a habitat. Dudgeon and Wu (1999) and Mathurian and Chauvet (2002) suggested that leaf litter in the stream offers a short-lived habitat for certain stream macroinvertebrates. In this study, FPOM accumulated in the litter bags from 2 potential sources: the leaf material in the bag itself as it was processed, and FPOM being transported which was filtered from the water column by the litter bag. Thus FPOM represented a potential food source for collectors which inhabited the bags. Therefore as Short et al. (1980) suggested, collector colonization of leaf bags may be a function of the amount of FPOM present. Dangles et al. (2001) also found that the colonization of macroinvertebrates on litter bags was directly linked with the quantity of accumulated POM. The results of the PCA in this study supported the relationship of the number of collectors being related to the amount of FPOM present in the leaf bags.

Macroinvertebrate density, as a function of the remaining leaf mass, did not statistically differ among the 3 leaf species, so there was no preference for leaf species. However, the high occurrence of shredders appeared to be associated with N concentrations of the leaf litter (Table 3). Pearson and Tobin (1989) suggested that the decomposition rates of leaf litter in streams reflect differences in the initial nutrient contents of the leaves as well as changes in nutrient levels associated with the decomposition process. Leaf litter of *S. octophylla* and *F. erecta* contained high N concentrations (Table 1), exhibited rapid breakdown, and supported higher colonization by shredders (Fig. 4B). The colonization of litter bags by shredders suggested that they have a preference for *F. erecta* over *M. thunbergii*. This preference is probably related to differences in leaf quality. This result indicates that leaves of *F. erecta* are probably more palatable to shredders than are those of *M. thunbergii*. Stout (1989) indicated that *Ficus* leaves have low levels of condensed tannins and high palatability for benthic invertebrates. Lin et al. (2002) reported that *M. thunbergii* leaf litter was thought to be slowly processed due to its low nutrient quality. The nutrients of this leaf litter did not become available to invertebrates until it has been conditioned for a longer period. Therefore, this litter provided a more-durable substrate for the benthic fauna and supported more-diverse macroinvertebrate assemblages on day 58 (Fig. 2A). According to the shredder response model of Cummins et al. (1989), the 50% breakdown point should be when leaves are most palatable to shredders and, therefore, should be the period of maximum shredder colonization. This model applies to this study for *S. octophylla* and *F. erecta* for which shredder abundances reached maxima on day 23 and for *M. thunbergii* on day 58 (Fig. 4A).

Breakdown rates of leaf litter in streams are influenced by the density and species richness of shredders (Short et al. 1980, Jonsson et al. 2001). In temperate streams, the most typical shredder taxa are gammarid amphipods, nemourid plecopterans, limmephilid and lepidostomatid trichopterans, and some tipulid dipterans (Graça 2001). Their relative abundances are reported to range from 5% to 62% of the total macroinvertebrate abundance (Imbert and Pozo 1989, Robinson et al. 1998, Fleituch 2001, Graça et al. 2001, Gonçalves et al. 2006). In tropical streams, the most typical shredder taxa are replaced by

**Table 4.** Eigenvalues, cumulative percentage variance explained by the macroinvertebrate taxa, cumulative percentage variance explained by the taxon-environment relationship, and taxon-environment correlation coefficients for the 1st 4 axes of the principal component analysis

| | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|---|---|---|---|---|
| Eigenvalues | 0.414 | 0.261 | 0.077 | 0.056 |
| Cumulative % variance explained by taxa data | 41.4 | 67.5 | 75.2 | 80.8 |
| Cumulative % variance explained by taxa- environmental relationship | 88.1 | 90.2 | 96.2 | |
| Taxa-environment correlation coefficients | 0.894 | 0.172 | 0.543 | 0.311 |

crabs, shrimp, nemourid plecopterans, and leptocerid and calamocertid trichopterans (Dudgeon 1982, Pearson et al. 1989, Covish et al. 2003, Crowl et al. 2006, Wantzen and Wagner 2006) and they account for 0.2%-32.4% of the total macroinvertebrate assemblages (Benstead 1996, Dudgeon and Wu 1999, Mathuriau and Chauvet 2002, Cheshire et al. 2005). In this study, shredders were dominated by nemourid plecopterans with a few calamoceratid, lepidostomatid, and leptocerid trichopterans. This subtropical stream thus exhibited similarities to both temperate and tropical streams.

Shredders in this study were mainly represented by nemourid plecopterans. This is in consent with the suggestion of Kobayashi and Kagaya (2005) that shredders in fast-flowing riffles are dominated by small-sized stoneflies. The dominant shredder taxa were similar to those in the riffle sections reported from boreal (Haapala et al. 2001), temperate (Short et al. 1980), and tropical (Dudgeon 1982) regions, but differed from those from Neotropical (Mathurian and Chauvet 2002, Wantzen and Wagner 2006) and tropical Australian (Pearson et al. 1989) regions. In Neotropical and tropical Australian regions, shredders are dominated by large-sized caddisfly larvae, such as calamocertids and leptocerids, although those studies were conducted in riffle sections. Furthermore, our study was conducted in a riffle reach in a subtropical stream, and shredders accounted for only 5.7%, 7.1%, and 10.8% of the total macroinvertebrate assemblages on *M. thunbergii*, *S. octophylla*, and *F. erecta* leaves, respectively. High processing rates of leaf litter are usually associated with larger shredder taxa (Short et al. 1980, Robinson et al. 1998). The low proportion and small body size of shredders in this study indicated that they only weakly influenced the breakdown of the 3 leaf species. Therefore, the breakdown of leaf litter in this study might be mainly attributed to microbial decomposition and physical fragmentation (Shieh's unpubl. data).

**Acknowledgments:** We are grateful to the Taiwan Forest Research Institute, Taipei, Taiwan for offering facilities and accommodations, Mr. Chun-Hsiun Chen for assisting in the collection of leaf litter, colleagues of the Laboratory of Insect Conservation, National Taiwan University, Taipei, Taiwan for helping with the fieldwork and the anonymous reviewers for providing valuable comments on this manuscript. This study was supported by the National Science Council of Taiwan (NSC90-2621-B-126-001-A10).

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