

Breakdown and macroinvertebrate colonization of needle and leaf litter in conifer plantation streams in Shikoku, southwestern Japan

Mayu Hisabae · Shin Sone · Mikio Inoue

Received: 24 December 2009 / Accepted: 5 June 2010 / Published online: 29 June 2010
© The Japanese Forest Society and Springer 2010

Abstract Breakdown and macroinvertebrate colonization of conifer needles (*Cryptomeria japonica*) and deciduous broadleaves (*Euptelea polyandra*) were investigated using litter bags in two study sites in streams flowing through a conifer plantation of *C. japonica* in Shikoku, southwestern Japan (one site with conifer canopy and another with mixed conifer and broadleaved canopy). Breakdown rates and macroinvertebrate densities were compared between litter species (conifer needle vs broadleaf) and between the two sites (conifer vs mixed canopy) to determine (1) whether breakdown rate of broadleaves is higher than conifer needles, (2) whether macroinvertebrates prefer broadleaves to conifer needles, and (3) whether the difference in riparian canopy is reflected in macroinvertebrate abundance. The results indicated that breakdown rates of broadleaves were higher than those of conifer needles, suggesting poorer quality of the latter as food for macroinvertebrates. Differences in macroinvertebrate density between needles and broadleaves were generally consistent with those in breakdown rates: broadleaves tended to have higher densities than needles, suggesting that conifer needles were not preferred by macroinvertebrates. However, total macroinvertebrate density in the conifer site was not significantly different from that in the mixed site, although the dominant shredder taxon differed (conifer site: gammarids; mixed site: lepidostomatids). Although conifer needles are low-quality food for macroinvertebrates, this may offer some advantages. Conifer needles remain on the streambed for

longer periods owing to their lower breakdown rates, being a constantly available resource. In addition, accumulations of conifer litter may effectively trap and retain particulate organic matter.

Keywords Coarse particulate organic matter · Fusa-zakura *Euptelea polyandra* · Riparian forest · Shredder · Sugi *Cryptomeria japonica*

Introduction

Riparian forests play important roles in structure and functioning of stream ecosystems (Gregory et al. 1991). For example, headwater streams receive various allochthonous resources from surrounding vegetation, such as woody debris, leaf litter, and terrestrial invertebrates. Input of coarse woody debris alters channel morphology and flow patterns, affecting organic matter retention and habitat structure for fishes and invertebrates (Wallace et al. 1995; Inoue and Nakano 1998). Leaf litter and terrestrial invertebrates from riparian canopy are major energy sources for aquatic communities in forested streams (Wallace et al. 1999; Nakano and Murakami 2001). Quantity and quality of such allochthonous resources can vary depending on riparian vegetation types (e.g., Pozo et al. 1997; Wipfli 1997). Therefore, changes in riparian vegetation can strongly affect stream communities.

In Japan, 40% of the total forested areas (i.e., a quarter of the total land area of Japan) is covered by plantation forests, which consist of monotonic, even-aged stands of conifers (typically sugi *Cryptomeria japonica*, or hinoki *Chamaecyparis obtusa*) (Nagaike et al. 2006). Although plantation forestry in Japan had been established by the nineteenth century (Totman 1998), it was

M. Hisabae · S. Sone · M. Inoue (✉)
Department of Biology, Faculty of Science, Ehime University,
2-5 Bunkyo-cho, Matsuyama 790-8577, Japan
e-mail: inom@sci.ehime-u.ac.jp

not until the 1960s that intensive conversion from natural forests or coppices to conifer plantations became widely prevalent. Potential vegetation of the present plantation areas is, in most cases, deciduous or evergreen broad-leaved forests, both of which were very different from coniferous forests in various ecological aspects (e.g., seasonal pattern of litterfall, litter quality). The extensive and drastic changes of forest vegetation to conifer plantations during the past several decades may have had a great impact on stream biota. In Japan, research activities on forest–stream interactions rapidly grew during the 1990s (see Inoue and Nakamura 2004 for a review). Nevertheless, effects of conifer plantations on stream communities and ecological processes have been examined by only a few studies (Abe et al. 2006; Yoshimura and Maeto 2006; Yoshimura 2007). Consequently, knowledge of ecological effects of plantation forestry on streams is still largely lacking, despite the wide prevalence of conifer plantations.

In headwater streams, conifer plantations may affect macroinvertebrate communities through quantity and quality of their food. In streams, fallen litter is colonized by microorganisms, and then fed by macroinvertebrate consumers (i.e., shredders) and converted into fine particulate organic matter (FPOM), which is available to other consumers (i.e., collectors) (Allan 1995). For consumers, litter quality differs between conifer and broadleaved species. In general, conifer needles have higher C/N ratio and decay much slower than leaves (Sedell et al. 1975; Webster and Benfield 1986; Maloney and Lamberti 1995), suggesting their relatively poor quality as food for macroinvertebrates. On the other hand, owing to their low decomposition rate, conifer needles can be a stable resource. Needles may persist in streams for longer periods, being a constantly available energy source, while fast-decaying leaf litter rapidly disappears.

In this study, we compared breakdown rates and macroinvertebrate colonization between conifer needles and deciduous broadleaves to provide fundamental information on ecological effects of plantation forestry. We used two study sites in headwater streams flowing through a conifer plantation of *C. japonica*. Riparian canopy at one site consisted entirely of *C. japonica*, whereas that at another site also included deciduous broadleaved species. Such a difference resulted in differences in the composition of in-stream litter patches. Our specific objectives were to determine (1) whether breakdown rate of leaves is higher than that of conifer needles, (2) whether macroinvertebrates prefer leaves to conifer needles, and (3) whether the difference in riparian canopy (i.e. conifer vs mixed), a major source of terrestrial litter, is reflected in the abundance of macroinvertebrates in litter patches.

Materials and methods

Study site

The study was conducted in headwater streams of the Ishite River (near the Forest Research Center of Ehime University), a tributary of the Shigenobu River in Shikoku, southwestern Japan (Ehime Prefecture). Headwater catchments of the Ishite River are underlain by granite and covered by forests, most of which are conifer plantations of sugi (*C. japonica*) or hinoki (*Ch. obtusa*). The climate is warm-temperate and potential vegetation is evergreen (elevation <700 m) or deciduous (>700 m) broadleaved forests. Annual precipitation is about 1,800 mm, with wet season in summer. Two study sites (i.e., 200-m stream reaches), one with conifer canopy (conifer site) and another with mixed conifer and broadleaved canopy (mixed site), were established in two 1st- and 2nd-order streams in close proximity (one site per stream; 1st-order for conifer site, 2nd-order for mixed site) (33°55'N, 132°54'E, 530 m in elevation). These two streams join and the downstream ends of conifer and mixed sites were located at 200 and 100 m upstream from the confluence of the two streams, respectively. Riparian zones of both sites were *C. japonica* stands of a plantation (approximately 42 years old). Although the stream banks at the mixed site had been colonized by natural vegetation (deciduous broadleaved trees; density of trees with diameter at breast height >5 cm: 42 trees per 200 m reach), streamside vegetation of the conifer site consisted entirely of planted *C. japonica* (no broadleaved tree with DBH >5 cm was found at the site). Major broadleaved species at the mixed site included fuzazakura (*Euptelea polyandra*), yama-guwa (*Morus australis*), shiromoji (*Lindera triloba*) and maples (*Acer* spp.). The stream channels at the two sites were similar in size and channel morphology, being boulder-dominated, step-bed channels with 2–3 m wetted width. Most litter patches in the conifer site were accumulations of conifer-derived litter (twigs with needles) and these were abundant throughout a year. In the mixed site, such accumulations were less abundant, and leaf-dominated patches were common, especially in autumn and winter.

Litter bag experiments

Litter bag experiments were conducted to examine differences in breakdown rates and macroinvertebrate colonization between conifer needle (*C. japonica*) and broadleaf litter. Leaf litter was represented by a single species, *E. polyandra*, which is a typical riparian species and has been used by previous litter-breakdown studies in other regions (Kagaya 1990; Kochi 2002; Kobayashi and Kagaya 2005). Mesh bags (20 × 20 cm, 1-cm mesh of hexagonal

pattern), filled with weighted litter of a single species (*C. japonica* or *E. polyandra*), were placed in streams at each site for 77 days from 6 December 2002 (winter experiment) and for 69 days from 22 July 2004 (summer experiment) to allow breakdown and macroinvertebrate colonization.

In the winter experiment, freshly abscised (senescent) leaves of *E. polyandra* and needles of *C. japonica* were collected from the forest floor near the study sites. These needles and leaves were air-dried, weighed and placed into the mesh bags (13.3 ± 2.1 g for *C. japonica* bag; 4.5 ± 0.3 g for *E. polyandra* bag in air-dried weight). In each site, 50 bags were placed at 5 locations (5 pools: 15–30 cm in water depth; <5 cm/s in current velocity), with 10 bags (5 needle bags and 5 broadleaf bags) being tied to a metal stake hammered into the streambed at each location. The five locations were set 10–50 m apart within the 200-m sites. On days 20, 43, and 77, one bag for each species was sampled from each location (2 species \times 5 locations \times 3 occasions per site; 20 bags were not used). The summer experiment was conducted using the same design, but fresh green leaves picked from the foliage of *E. polyandra* were used for broadleaf bags to simulate natural summer input of broadleaves. In summer, although litter patches of senescent needles (*C. japonica*) were commonly found on the streambed, senescent broadleaves were rare; broadleaves are usually provided as green leaves owing to storm events. Sixty bags filled with needles (6.3 ± 0.8 g in air-dried weight) or leaves (3.9 ± 0.6 g) were placed at five locations (6 needle bags and 6 broadleaf bags) at each site and one bag for each species per location was sampled on days 6, 21, 44, and 69 (20 bags were not used).

In the laboratory, needles or leaves in the bags were gently washed to remove macroinvertebrates, trapped particulate organic matter, and fragments of needles and leaves (<10 mm in size were considered as broken-down materials), and then dried at 60°C for 48 h and weighed. The removed materials were sifted through 5- and 1-mm mesh sieves, and macroinvertebrates were sorted from the materials >1 mm and preserved in 70% ethanol for identification. Coarse particulate organic matter (CPOM) sifted on the 5-mm mesh sieve (i.e., >5 mm) except woody materials (e.g., twigs) was dried at 60°C for 48 h, and weighed. Materials on the 1-mm mesh sieve (i.e., 1–5 mm), which may include inorganic materials, were dried at 60°C for 48 h, weighed, and ashed at 500°C for 4 h to quantify CPOM (1–5 mm) as ash-free dry mass (AFDM).

During the winter experiment, the maximum and minimum water temperatures recorded using maximum–minimum thermometer were 9.0 and 2.0°C, respectively, at both sites. The maximum and minimum water temperatures during the summer experiment were 20.0 and 16.0°C at the conifer site, and 19.0 and 14.0°C at the mixed site. The

discharge was stable during the winter, whereas occasional high-flow events occurred during the summer experiment. Owing to the high flows in the summer, all bags at one location of each site were lost during the period between days 6 and 21; between days 21 and 44, all bags of another location at the conifer site were also lost. In winter, one sample from day 43 (a leaf sample in the mixed site) was lost by our mistake during sampling.

Data analysis

Litter breakdown rates (k) were assessed using an exponential decay model (Petersen and Cummins 1974): $W_t = W_0 e^{-kt}$, where W_t is litter dry weight at time t , and W_0 is the initial dry weight. Initial dry weight (oven-dried at 60°C) was estimated from air-dried weight by correcting for water content and treatment loss. At the time of the preparation of litter bags, five sub-samples of air-dried litter were weighed, dried at 60°C for 48 h, and then reweighed to determine water content (winter experiments, needle: 6.6%, leaf: 6.5%; summer experiments, needle: 10.7%, leaf: 68.8%). Treatment loss (the weight of loss during transportation from the laboratory to the field) was estimated using 10 litter bags that were transported to the field but were not placed instream (winter experiments, needle: 4.0%, leaf: 0.2%; summer experiments, 0% for both). The time t in the above function was expressed by both days and degree days. The latter was calculated by multiplying days by the mid-value between the maximum and minimum water temperatures (i.e., 5.5°C for both sites in winter; 18.0 and 16.5°C for conifer and mixed sites, respectively, in summer). This estimation of degree day is a rough approximation; to obtain accurate values, daily mean temperatures should be used. In our study, the breakdown rate k based on degree day was used for reference, to be compared with that measured in other regions. Breakdown rate based on degree day, which corrects for temperature differences, is useful for regional comparisons (e.g., Riipinen et al. 2010), because breakdown rates generally increase with water temperature (Webster and Benfield 1986).

For the calculation of the breakdown rate k in the summer experiment, samples from days 44 and 69 were omitted because broadleaf samples of most bags were completely broken down by day 44 (see Fig. 2). As a result, the range of the time t for the calculation of k largely differed between the winter and summer experiments in terms of days (within 77 vs 21 days), but similar in terms of degree days (within 424 vs 378 degree days) (see Fig. 2). The k was calculated for each species in each season by pooling samples from the two sites, and was compared between species within each season and between seasons for each species using analysis of covariance

(ANCOVA). In the ANCOVA, $\ln(W_t)$ was used as a dependent variable, species or season as a factor, and time t as a covariate; differences in the k (slope) were assessed by the interaction effect (species or season \times time t). This statistical comparison was not conducted on the k based on degree day, because strict comparisons of rough approximations are not so informative.

Macroinvertebrate abundance in the litter bags was compared by litter species and sites to examine whether macroinvertebrates prefer broadleaves to needles, and whether macroinvertebrate abundance differs between the two sites. Samples from day 43 (winter) and day 21 (summer), when macroinvertebrates sufficiently colonized (Fig. 1) and a large portion of original litter still remained (Fig. 2), were used for this analysis. Macroinvertebrate density was expressed by the number of individuals per CPOM weight, which included original litter (i.e., needles or leaves; mean \pm SD percentages in total CPOM weight were 74.3 ± 24.6 and $73.9 \pm 22.3\%$ in winter and summer, respectively) and other CPOM (>5 and 1–5 mm combined) except woody materials. Densities of total macroinvertebrates and numerically abundant taxa at the family level (i.e., >10% in number in either of the sites: Gammaridae, Lepidostomatidae, Chironomidae, Leptophlebiidae, and Nemouridae; see Figs. 3 and 4 for their percentages) were compared using analysis of variance (ANOVA) with site (conifer vs mixed) and litter (needle vs broadleaf) as between-subject and within-subject factors, respectively, and the locations of litter bags as a block factor nested within site. Although we set five locations (blocks) in each site, the number of block was four for the mixed site in winter and both sites in summer, owing to the losses of samples by our mistake and the high flows. Macroinvertebrate densities were \log_{10} -transformed prior to analysis.

It was assumed that litter effect in the ANOVA reflected differences in litter preference by macroinvertebrates, because needle and broadleaf bags were placed at the same

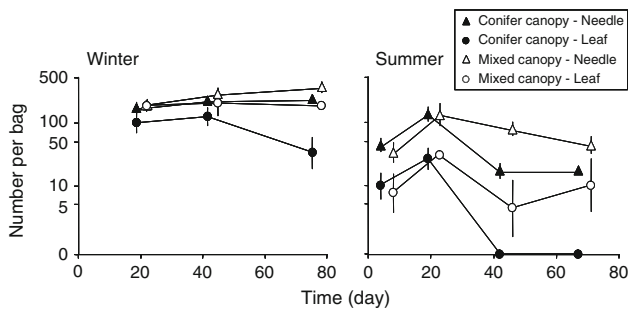


Fig. 1 Temporal changes in the number of total macroinvertebrates (mean and SE) per bag during the experiments (days 20, 43 and 77 in winter, and days 6, 21, 44 and 69 in summer). Symbols for the conifer and mixed sites are offset for clarity (arranged not to overlap). The vertical axes are logarithmic scale

locations in pairs. Site effect in the ANOVA was assumed to indicate between-site differences in macroinvertebrate abundance, because macroinvertebrate abundance in the

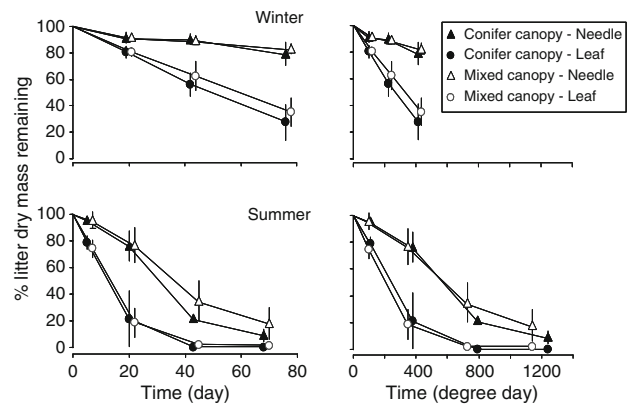


Fig. 2 Percent litter mass (mean and SD) remaining over time expressed as days (left) and degree days (right). Symbols for the conifer and mixed sites are offset for clarity

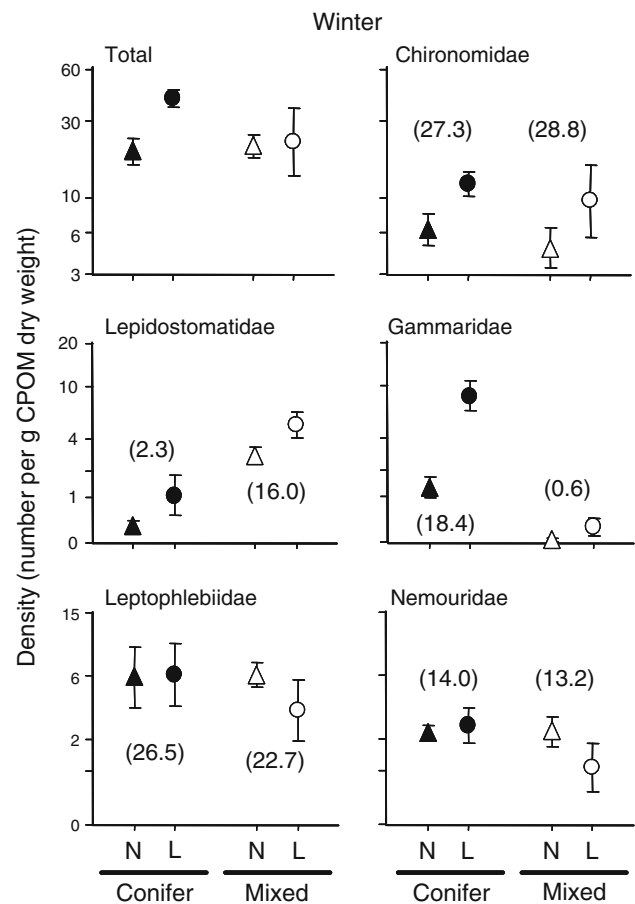


Fig. 3 Comparisons of macroinvertebrate densities (mean and SE) by site and litter in the winter experiment (on day 43). N Needle, L broadleaf. Relative abundance (%) of each taxon in each site is indicated in parentheses. The vertical axes are logarithmic scale

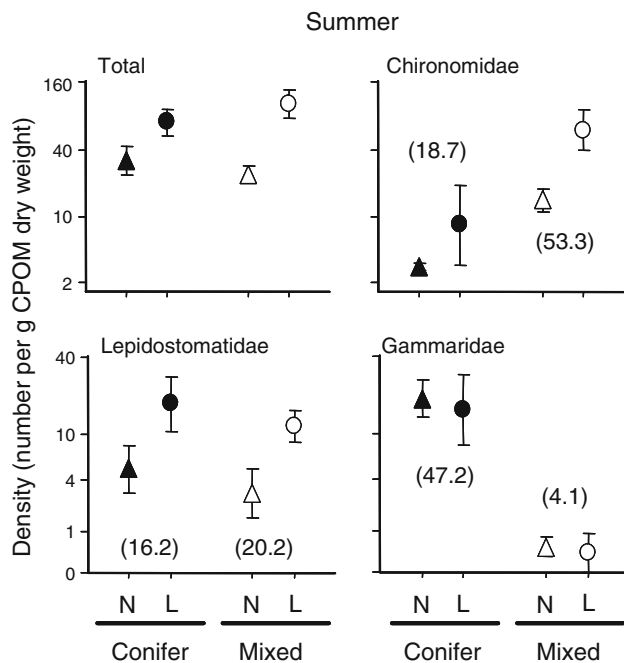


Fig. 4 Comparisons of macroinvertebrate densities (mean and SE) by site and litter in the summer experiment (on day 21). *N* Needle, *L* broadleaf. Relative abundance (%) of each taxon in each site is indicated in parentheses. The vertical axes are logarithmic scale

litter bags reflects their ambient abundance (litter bags can be regarded as a sampler; e.g., Murphy et al. 1998). Among the five taxa examined, gammarid amphipods, lepidostomatid caddisflies and nemourid stoneflies were generally considered as shredders (e.g., Kagaya 1990; Kobayashi and Kagaya 2004; Kochi and Yanai 2006). Leptophlebiid mayflies and many chironomid midges are generally categorized as collector-gatherers. All analyses were conducted using SPSS (ver 13; SPSS).

Results

Breakdown rate k of *E. polyandra* leaves was significantly higher than that of *C. japonica* needles in both winter ($F_{1,114} = 68.63$, $P < 0.001$) and summer ($F_{1,100} = 114.13$, $P < 0.001$) (Table 1). In winter, 80–90% of conifer needles still remained by the end of the experiment (day 77), whereas *E. polyandra* leaves were reduced to <40% (Fig. 2). Similarly, in summer, 70–80% of needles remained on day 21, whereas broadleaves were reduced to around 20%. Both needles and leaves were more rapidly reduced in summer (needles: $F_{1,106} = 7.11$, $P = 0.009$; leaves: $F_{1,108} = 167.56$, $P < 0.001$); most leaf samples had been completely broken down by day 44, and needles were lost to around 20% by the end.

In winter, chironomids and leptophlebiids numerically dominated in the litter bag assemblages at both sites,

Table 1 Litter breakdown rates (k) for needles and leaves with coefficient of determination (R^2) and significance (P) of each exponential decay model

	Winter			Summer		
	k	R^2	P	k	R^2	P
Based on days						
Needle (<i>C. japonica</i>)	0.0028	0.10	0.018	0.0132	0.37	<0.001
Leaf (<i>E. polyandra</i>)	0.0156	0.80	<0.001	0.0885	0.78	<0.001
Based on degree days						
Needle (<i>C. japonica</i>)	0.0005	0.10	0.018	0.0008	0.38	<0.001
Leaf (<i>E. polyandra</i>)	0.0028	0.80	<0.001	0.0051	0.79	<0.001

together making up more than 50% (Fig. 3). Dominant shredder taxa in winter differed between the two sites, with gammarids and lepidostomatids dominating at the conifer and mixed sites, respectively. ANOVA on the winter densities indicated that neither site nor litter had a significant effect on densities of total macroinvertebrates, chironomids, leptophlebiids and nemourids (Table 2; Fig. 3). Both site and litter effects were detected on lepidostomatid density. Their density was higher in leaves than in needles and, accordingly, higher at the mixed site than at the conifer site. For gammarids, site, litter and their interaction effects were significant. Their density was higher in leaves than in needles, but lower at the mixed site than at the conifer site. At the mixed site, although gammarid density was higher in leaves than in needles, the difference was much smaller than that at the conifer site, owing to the low density at the mixed site; such a difference in litter effect on gammarid density between the two sites was detected as the significant interaction effect.

In summer, litter bag assemblages at the conifer and mixed sites were dominated by gammarids and chironomids, respectively, with each making up about 50% (Fig. 4). ANOVA on summer densities indicated that only a litter effect was significant on total density, with leaves having higher density than needles (Table 2; Fig. 4). A similar litter effect was found for lepidostomatids. A site effect was detected for chironomids, with their density being higher at the mixed site than at the conifer site. In contrast, gammarid density at the conifer site was significantly greater than that at the mixed site.

Discussion

Our results showed that breakdown rate k of *C. japonica* needles was lower than that of *E. polyandra* leaves, as expected from a general trend that conifer needles decay more slowly than broadleaves (Sedell et al. 1975; Webster and Benfield 1986; Maloney and Lamberti 1995). The

Table 2 Results of ANOVAs testing for effects of site and litter on macroinvertebrate density, using locations of litter bags as a block factor nested within site

	Site		Litter		Site × litter		Block (site)	
	F	P	F	P	F	P	F	P
Winter								
Total density	1.18	0.314	2.01	0.199	0.99	0.354	0.48	0.825
Chironomidae	1.17	0.316	2.91	0.132	0.01	0.927	0.28	0.941
Lepidostomatidae	29.19	0.001	5.89	0.046	0.06	0.807	0.96	0.521
Gammaridae	68.55	<0.001	22.37	0.002	12.92	0.009	1.02	0.491
Leptophlebiidae	0.25	0.634	0.81	0.398	1.07	0.336	3.44	0.063
Nemouridae	2.94	0.130	0.63	0.452	1.38	0.279	0.42	0.861
Summer								
Total density	0.05	0.830	17.26	0.006	1.37	0.286	0.89	0.557
Chironomidae	13.56	0.010	4.95	0.068	0.32	0.593	0.77	0.624
Lepidostomatidae	0.54	0.489	27.20	0.002	0.00	0.953	5.95	0.024
Gammaridae	25.01	0.002	0.42	0.540	0.04	0.845	4.57	0.043

df = 1,7 for effects of site, litter, and their interaction, and 7,7 for block effect nested within site in winter; *df* = 1,6 for effects of site, litter, and their interaction, and 6,6 for block effect nested within site in summer

Bold characters indicate statistical significance (<0.05)

lower breakdown rates of conifer needles have been explained by its higher toughness, the presence of secondary compounds that inhibit decomposition, and lower nutritive quality (e.g., higher C/N ratio) (Sedell et al. 1975; Webster and Benfield 1986; Maloney and Lamberti 1995). Although we did not measure litter quality, C/N ratio of *C. japonica* litter has been reported by several studies as 50–90 (Nioh et al. 1989; Oyanagi et al. 2002; Abe et al. 2006; Joo et al. 2006), which are much higher than that of *E. polyandra* litter (green leaves: C/N ratio = 21–26) reported by Kochi (2002). It has frequently been reported that litter types with higher C/N ratio have lower breakdown rates (Yanai and Terazawa 1995; Ostrofsky 1997).

Euptelea polyandra, as a typical riparian species, has often been used for instream litter-breakdown studies in Japan (Kagaya 1990; Kobayashi and Kagaya 2005; Kochi 2002). Breakdown rates *k* of *E. polyandra* leaves in our study were higher than those reported by such previous studies. Winter breakdown rates (based on day) of senescent leaves of this species were reported as 0.002–0.008 in headwater streams of the Ara-kawa River, central Japan (Saitama Prefecture), whereas ours was 0.0156 (Table 1). Summer breakdown rates of green leaves (based on day) measured in central Japan (Nagano Prefecture) by Kochi (2002) was 0.0509, which is also lower than ours (0.0885). These differences were attributable, at least in part, to regional differences in thermal regimes. Water temperature during winter experiments by Kagaya (1990) and Kobayashi and Kagaya (2005) was reported as 1–5°C, and that during the summer experiment by Kochi (2002) was 10–14°C. Water temperature in our streams in southwestern

Japan (Ehime Prefecture) was higher than those (2–9°C in winter, 14–20°C in summer). In Kochi (2002), breakdown rates for green leaves of *E. polyandra* are also provided on the basis of degree day. When compared in terms of degree day, our result from the summer experiment (*k* = 0.0051) is similar to that by Kochi (2002) (*k* = 0.0042). In Japan, like the studies referred to above, study sites where litter breakdown rates were measured are biased toward regions with relatively cool climate (in addition to the above studies: Yanai and Terazawa 1995; Kochi and Yanai 2006 in Hokkaido). Our results indicate that, in southwestern Japan, autumn-shed leaves would decompose and disappear more rapidly than those described in such previous studies in Japan.

The lower breakdown rates of *C. japonica* needles, a main result of our litter bag experiments, suggest their poorer quality as food for macroinvertebrates than deciduous broadleaves. Patterns in macroinvertebrate colonization were generally consistent with the results of breakdown rates. Litter effects were detected on densities of total macroinvertebrates in summer, lepidostomatids in both winter and summer, and gammarids in winter, with higher densities found in leaves than in needles for all these taxa, suggesting their preference for broadleaves over conifer needles. Although litter effect was not detected on some taxa (chironomids, nemourids, leptophlebiids), there was no case that exhibited higher densities in needles than in leaves. Similar trends have been reported in other regions of the world. Litter breakdown experiments conducted in Oregon streams by Sedell et al. (1975) reported lower invertebrate densities in Douglas-fir and hemlock

(*Pseudotsuga* and *Tsuga*) needles than in maple (*Acer*) leaves. Maloney and Lamberti (1995) compared litter bags of five species (four broadleaf and one conifer species) in a Michigan stream and showed that invertebrate density was lowest in hemlock needles. A laboratory experiment on food preference by caddisfly and gammarid shredders demonstrated that alder (*Alnus*) leaves were most preferred by both shredders while their least preferred food items were beech (*Fagus*) leaves and spruce (*Picea*) needles (Friberg and Jacobsen 1994). Our results suggest that *C. japonica* needles are generally not preferred by macroinvertebrate detritivores, like other conifer needles reported previously.

If *C. japonica* needles are not preferred by macroinvertebrates, it would be expected that litter-associated macroinvertebrates are more abundant in the mixed site than in the conifer site. However, a significant site effect was not detected on total density in either winter or summer (Table 2; Figs. 3, 4). This contradiction is largely attributable to the responses of gammarids to the site effect. Gammarid density in the conifer site was much higher than that in the mixed site in both winter and summer, despite conifer needles not being preferred by them. Although the reasons for the higher gammarid density in the conifer site are unclear, this may be explained by seasonal stability of conifer litter. As shown by our results, breakdown rate of needles is much lower than that of deciduous broadleaves, indicating that needles remain on the streambed for longer periods while broadleaves rapidly disappear. That is, needle litter is a low-quality, but constantly available, resource for shredders. Such an advantage of slow-decaying litter has also been pointed out by Friberg and Jacobsen (1994). In addition, it is likely that *C. japonica* litter effectively traps and retains POM that are otherwise lost downstream (see Molles 1982 for similar effects in coniferous forest streams), because *C. japonica* litter is provided as shoots or twigs with needles, rather than fragmented needles (Kaneko et al. 1997), accumulating as complex structures in streams. Such effects of slow-decaying litter to stabilize seasonal availability of resources may be more important for gammarids than for aquatic insects (larvae/nymphs), because the former spend all of their lives in streams whereas many of the latter use instream habitats seasonally.

Overall, our results suggest that *C. japonica* needles have relatively poor quality as food for stream macroinvertebrates. This can be regarded as a negative aspect of conifer monocultures, which may have been intuitively inferred by stream ecologists. However, our between-site comparison showed similar total densities of macroinvertebrates, indicating little detrimental effect of *C. japonica* canopy at least in terms of total density, although some differences in taxonomic composition were found. Our study design cannot fully assess effects of conifer

plantations, because we did not have a true reference site (i.e., streams flowing through natural broadleaved forests), lacked site replication, and did not quantify differences in litter abundance between the two sites (site effects were assessed on the basis of density per CPOM weight, without considering between-site differences in CPOM abundance). However, our results suggest that conifer plantations may not cause drastic declines of macroinvertebrates, despite lower nutritive quality of conifer litter (see also Yoshimura and Maeto 2006; Riipinen et al. 2010 for weaker than expected effects of conifer plantations). To assess effects of conifer plantations on stream ecosystems, well-designed comparisons between streams with conifer plantations and those with natural forests are needed (e.g., Riipinen et al. 2010). In addition, we feel that effects of *C. japonica* litter should be evaluated not only from its nutritive quality but also from its seasonal stability and role as a retention device.

Acknowledgments We are grateful to Yumiko Akamine, Masanobu Miyayoshi, and Hiroshi Miyata for their help in the field and/or laboratory. We also thank the staff of the Forest Research Center of Ehime University for providing information in the field. Helpful comments from two reviewers greatly improved the manuscript. This research was partly supported by Grants-in-Aid for Scientific Research from JSPS (18915007 to S. Sone, 19580174 to M. Inoue) and a Special Fund for Education and Research by the Japanese Ministry of Education, Culture, Sports and Technology.

References

- Abe T, Nunokawa M, Fujieda M (2006) Organic matter derived from forests and mountain stream ecosystems. *Water Sci* 50:1–23 (in Japanese)
- Allan JD (1995) *Stream ecology: structure and function of running waters*. Chapman & Hall, London
- Friberg N, Jacobsen D (1994) Feeding plasticity of two detritivore-shredders. *Freshw Biol* 32:133–142
- Gregory SV, Swanson FJ, Mckee WA, Cummins KW (1991) An ecosystem perspective of riparian zones: focus on links between land and water. *Bioscience* 41:540–551
- Inoue M, Nakamura F (2004) Freshwater fishes and forests in Japan. In: Northcote TG, Hartman GF (eds) *Fishes and forestry: worldwide watershed interactions and management*. Blackwell, Oxford, pp 560–580
- Inoue M, Nakano S (1998) Effects of woody debris on the habitat of juvenile masu salmon (*Oncorhynchus masou*) in northern Japanese streams. *Freshw Biol* 40:1–16
- Joo SJ, Yim MH, Nakane K (2006) Contribution of microarthropods to the decomposition of needle litter in a Japanese cedar (*Cryptomeria japonica* D. Don) plantation. *For Ecol Manag* 234:192–198
- Kagaya T (1990) Processing and macroinvertebrate colonization of leaf detritus in a mountain forest stream in Japan. *Bull Tokyo Univ For* 82:157–176 (in Japanese with English abstract)
- Kaneko N, Katagiri S, Yamashita H, Kitaoka N, Tominaga A (1997) A long term observation of litterfall of Japanese red cedar in Sanbe Experimental Forest of Shimane University. *Bull Fac Life Environ Sci Shimane Univ* 2:7–13 (in Japanese with English abstract)

- Kobayashi S, Kagaya T (2004) Litter patch types determine macroinvertebrate assemblages in pools of a Japanese headwater stream. *J N Am Benthol Soc* 23:78–89
- Kobayashi S, Kagaya T (2005) Hot spots of leaf breakdown within a headwater stream reach: comparing breakdown rates among litter patch types with different macroinvertebrate assemblages. *Freshw Biol* 50:921–929
- Kochi K (2002) Decomposition of fresh leaves and colonization by shredders in a small mountain stream. *Jpn J Ecol* 52:331–342 (in Japanese with English abstract)
- Kochi K, Yanai S (2006) Shredder colonization and decomposition of green and senescent leaves during summer in a headwater stream in northern Japan. *Ecol Res* 21:544–550
- Maloney DC, Lamberti GA (1995) Rapid decomposition of summer-input leaves in a northern Michigan stream. *Am Midl Nat* 133:184–195
- Molles MC Jr (1982) Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. *Ecology* 63:1–6
- Murphy JF, Giller PS, Horan MA (1998) Spatial scale and the aggregation of stream macroinvertebrates associated with leaf packs. *Freshw Biol* 39:325–337
- Nagaike T, Masaki T, Ito S (2006) Special feature: ecology and management of conifer plantations in Japan: control of tree growth and maintenance of biodiversity. *J For Res* 11:215–216
- Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc Natl Acad Sci USA* 98:166–170
- Nioh I, Haruta Y, Kawakami H (1989) Chemical and microbial changes of leaf litter of Japanese cedar (*Cryptomeria japonica*) decomposed in a pot. *Bull Tokyo Univ For* 81:21–37 (in Japanese with English abstract)
- Ostrofsky ML (1997) Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *J N Am Benthol Soc* 16:750–759
- Oyanagi N, Chihara M, Haibara K, Toda H (2002) Nitrogen and carbon mineralization characteristics of different decomposition stages in forest floor of some tree species. *Jpn J Soil Sci Plant Nutr* 73:363–372 (in Japanese with English abstract)
- Petersen RC, Cummins KW (1974) Leaf processing in a woodland stream. *Freshw Biol* 4:343–368
- Pozo J, González E, Díez JR, Molinero J, Elósegui A (1997) Inputs of particulate organic matter to streams with different riparian vegetation. *J N Am Benthol Soc* 16:603–611
- Riipinen MP, Fleituch T, Hladyz S, Woodward G, Giller P, Dobson M (2010) Invertebrate community structure and ecosystem functioning in European conifer plantation streams. *Freshw Biol* 55:346–359
- Sedell JR, Triska FJ, Triska NS (1975) The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. *Verh Int Ver Limnol* 19:1617–1627
- Totman C (1998) The green archipelago: forestry in pre-industrial Japan. Ohio University Press, Athens
- Wallace JB, Webster JR, Meyer JL (1995) Influence of log additions on physical and biotic characteristics of a mountain stream. *Can J Fish Aquat Sci* 52:2120–2137
- Wallace JB, Eggert SL, Meyer JL, Webster JR (1999) Effects of resource limitation on a detrital-based ecosystems. *Ecol Monogr* 69:409–442
- Webster JR, Benfield EF (1986) Vascular plant breakdown in freshwater ecosystems. *Annu Rev Ecol Syst* 17:567–594
- Wipfli MS (1997) Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Can J Fish Aquat Sci* 54:1259–1269
- Yanai S, Terazawa K (1995) Varied effects of the forest on aquatic resources in a coastal mountain stream, in southern Hokkaido, northern Japan (II): autumn leaf processing of nine deciduous trees along the stream. *J Jpn For Sci* 77:563–572 (in Japanese with English abstract)
- Yoshimura M (2007) Comparison of stream benthic invertebrate assemblages among forest types in the temperate region of Japan. *Biodivers Conserv* 16:2137–2148
- Yoshimura M, Maeto K (2006) Comparison of an aquatic invertebrate assemblage between an old-growth natural forest and planted coniferous forest basins in a Japanese temperate region: the Kuroson stream in the Shimanto River basin. *Landsc Ecol Eng* 2:81–89