(1) Title: Ecological functions of persistent Japanese cedar litter in structuring stream macroinvertebrate assemblages

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Abstract

Stream macroinvertebrate assemblages are expected to be affected by the abundance and constitution of litter from surrounding forests. We compared forest floor cover, overland flow, stream environment, and stream macroinvertebrate assemblages between the catchments of a Japanese cedar plantation (CP) and a primary deciduous forest (DF). Both systems experience excessive deer browsing. Understory vegetation cover was higher in the DF than in the CP in summer, although cover was low (<20%), likely because of excessive deer browsing. Litter cover was much higher in the CP than in the DF in summer as a result of the long abscission period, low breakdown rate, and low dispersal rate of Japanese cedar litter compared to deciduous litter. Monthly overland flow was always lower in the CP than in the DF, and substrate size was smaller in the DF stream. In the CP, cedar litter accumulated in the stream, probably because of its low breakdown rate and morphology, and abundant shredder taxa characterized the macroinvertebrate assemblage. In contrast, abundant burrower taxa characterized the macroinvertebrate assemblage in the DF stream. These results imply that Japanese cedar litter functions in structuring the macroinvertebrate assemblage by supplying persistent food resources for detritivores, and by buffering fine sedimentation via overland flow under excessive deer browsing.

Key words

Denudation・Forest floor cover・Overland flow・Sediment runoff・Shredders

Introduction

In lotic ecosystems, allochthonous organic matter such as terrestrial litter and autochthonous organic matter such as algae are vital basic food resources (Dodds 2002). Litter from riparian forests constitutes a higher proportion of available food for macroinvertebrates in headwater streams than in downstream areas (Vannote et al. 1980). Riparian forests influence stream ecosystems by providing terrestrial invertebrates as food for fish (Nakano and Murakami 2001), controlling water temperature (Sugimoto et al. 1997; Richardson and Danehy 2007), purifying water by filtering it through complex networks of soil and roots (Peterjohn and Correll 1984; Pinay and Decamps 1988), and creating diverse habitats via woody debris (Inoue and Nakano 1998; Richardson and Danehy 2007).

Forest type (e.g., deciduous broad-leaf, evergreen coniferous) is one of the main terrestrial conditions within catchments, and ecological properties tend to vary with forest type. The biomass and diversity of understory vegetation are generally higher in deciduous forests (Barbier et al. 2008), whereas annual litter input (Gregory et al. 1991) and standing stock of accumulated litter (Augusto et al. 2002) tend to be higher in coniferous systems. These ecological properties affect hydrological processes on slopes (Sidle et al. 2007) as well as stream environments and macroinvertebrates (Gregory et al. 1991). For example, Friberg (1997) noted that both the standing stock of detritus and the abundance of shredders in streams are greater in coniferous than in deciduous catchments.

Nearly 27% of the land in Japan is covered by evergreen coniferous plantations (Nagaike et al. 2006). Japanese cedar (*Cryptomeria japonica*) is one of the most

important plantation species in Japan (Ota 2007), covering about 4.5 million hectares. In contrast to deciduous trees, litterfall of Japanese cedar continues from winter to early spring, and cedar litter has a much narrower dispersal range (Kanasashi and Hattori 2011). Japanese cedar litter breaks down at a slower rate than deciduous litter in both terrestrial and aquatic systems (Nakane 1995; Hisabae et al. 2010). Therefore, litter is expected to remain on the forest floor and in streams for longer periods in Japanese cedar plantations than in deciduous forests. This may result in particular stream macroinvertebrate assemblages characteristic of cedar plantations (Yoshimura and Maeto 2006; Yoshimura 2007).

We studied the effects of Japanese cedar litter accumulation on stream macroinvertebrate assemblages by comparing forest floor cover, overland flow, stream environment, and macroinvertebrate assemblages between a Japanese cedar plantation and a deciduous forest. Both of the systems experience excessive deer browsing characterized by the denudation of vegetation. We expected to find characteristic differences in macroinvertebrate assemblages between these systems, particularly because cedar litter provides better protection against soil erosion and should help reduce erosion of denuded forest floors.

Materials and methods

Study site

The study area is located at the Ashiu Forest Research Station of the Field Science Education and Research Center, Kyoto University (35°20’N, 135°45’E; Fig. 1). Average

annual precipitation at the site was 2298 mm and mean annual temperature was 11.9°C from 1976 to 2005. Maximum snow depth in winter generally exceeds 2 m, and snow cover typically exists from mid-December to early April. The geological components of the area are sandstone, mudstone, and shale of the Tanba Belt of the Mesozoic. Most of the soil is brown forest soil. Excessive deer browsing has caused drastic decreases in the abundance and diversity of understory plants since the late 1990s (Kato and Okuyama 2004; Tanaka et al. 2008). Soil erosion via denudation by deer has increased sediment runoff and subsequent sandy sedimentation of streambeds in deciduous forests (Sakai et al. 2012).

The study was conducted in a 74-year-old Japanese cedar plantation catchment (CP; area, 1.33 ha) and a primary deciduous forest catchment (DF; area, 1.66 ha), both draining first-order streams of the Yura River (Fig. 1). The two catchments were located close to one another. The DF comprised primary cool-temperate deciduous forest and was dominated by *Fagus crenata* (dominance in basal area, 74.0%), *Acer mono* (10.6%), *Acer japonicum* (5.0%), and *Carpinus tschonoskii* (2.1%), whereas the CP was dominated by *Cryptomeria japonica* (85.3%), *Quercus crispula* (7.8%), and *Aesculus turbinata* (2.3%).The two streams were topographically similar and typical colluvial valleys (Bisson et al. 2006), where riffle-pool structures are rarely observed. A 30-m study reach in the lower section of each stream was established for surveying macroinvertebrates. The two reaches had perennial flow, and similar channel slope, width, and depth (Table 1).

Forest floor cover and overland flow

Because forest floor cover is a good predictor of soil erosion potential (e.g., Lyon and Sagers 1998; Wear et al. 1998; Heartsill-Scalley and Aide 2003), we evaluated coverage of understory vegetation and litter as well as water runoff along the slopes of each catchment to examine the effect of soil inflow on stream substrate and macroinvertebrate assemblages, following Sakai et al. (2012). One belt transect (1-m wide) was established from the valley floor to 20 m up the upper slope on the right and left banks of each catchment. These transects were located in areas where the most overland flow entering the streams was likely to be generated. Coverage (%) of vegetation within 30 cm of the ground was visually estimated by one individual in 1 × 2-m plots equally spaced along each transect (10 plots per bank). The survey was conducted in June and August 2008. In August 2011, 10 quadrats (40 × 40 cm) were also randomly located on the lower, middle, and upper slopes of each catchment, and litter coverage (%) within the quadrats was visually estimated by one individual. We also evaluated the standing stock of litter in the riparian zone. We collected litter from four randomly located quadrats (40 × 40 cm) along the 30-m study reach in each catchment in August and November 2009. Collected litter was dried at 60°C for 1 week and then weighed.

Plots for measuring water runoff (0.5 × 2.0 m) were established on the midslopes of each catchment near the vegetation transect (Fig. 1). The coverage of understory vegetation and litter in the plots was representative of other midslope locations for each catchment. Plastic borders were inserted about 5 cm into the soil along all sides of the plots, and a trough was inserted several centimeters into the soil (parallel to the slope

direction) to collect storm runoff. Runoff from these plots was routed to a rain gauge (Davis Instruments, Rain Collector II) to estimate discharge per month. Overland flow was monitored from July to November 2010.

Stream environment

Channel slope was measured at 6 points at 5 m intervals using a laser surveying instrument (Laser Technology, Trupulse 200), and stream width was measured at 7 transects located at 5 m intervals in each study reach in July 2010. Water depth and current velocity were also measured at 10 points in the centers of the streams in each study reach in July 2010. The current velocities of the surface and bottom water (about 0–2 cm above the streambed) were calculated by averaging three repeated 5-s measurements from an electromagnetic current meter (Kenek, VE10). The measurements were done under base-flow conditions. Litter coverage (%) in six quadrats (40 × 40 cm) randomly located on the streambed in each study reach was visually estimated by one individual in August 2011.

To evaluate grain-size distribution, we randomly collected three samples of stream substrates (1000 ml) by shovel, according to Grost et al. (1991) and Zweig and Rabení (2001), in each study reach. The substrate samples were sieved into 10 grain sizes: >31.5, 31.5–16, 16–8, 8–4, 4–2, 2–1, 1–0.5, 0.5–0.25, 0.25–0.125, and 0.125–0.063 mm. The substrates of each size were dried at 105°C for 24 h and weighed, and we determined the effective grain size (D_{50}) of each substrate sample. This survey was conducted in December 2010.

To evaluate the amount of organic matter of fine deposition, we collected one

sample of sandy deposition (300 ml) by shovel in each study reach in July 2010. The samples were sieved into six fractions: >2, 2–1, 1–0.5, 0.5–0.25, 0.25–0.125, and 0.125–0.063 mm, and dried at 105°C for 24 h. Organic material was decomposed by adding hydrogen peroxide at 90°C for 3 days according to Dane and Topp (2002) and samples were then reweighed. The amount of organic matter was calculated for each fraction.

Hemispherical photographs were taken at 6 points at 6 m intervals in each study reach in August 2008 and April 2009 to determine light conditions above the streambed. Photographs were taken with a digital camera (Nikon, E995) equipped with a fish-eye lens (Nikon, FC-E8) that was fixed horizontally at 1 m above the streambed. Photosynthetically active radiation (PAR; mol m^{-2} day^{-1}) was estimated from the photographs, and we determined relative photosynthetically active radiation (rPAR %) to the open environment using Gap Light Analyzer version 2.0 (Frazer et al. 1999).

Periphyton

Because fine sediment may affect macroinvertebrates by reducing periphyton, algal abundance was estimated in each study reach in August, September, and October 2008. Periphyton was sampled from four randomly-collected submerged rocks (maximum diameter, 13–26 cm) by brushing 4 cm^2 of the upper surface of the rocks and filtering the water through glass microfiber filters (Whatman, GF/F). These samples were ground in 90% acetone and then centrifugally separated (Hitachi, CF16RXII) after being dried and frozen. The absorbance of the periphyton samples was measured at 630, 647, 664,

and 750 nm (Hitachi, U-1800). The amount of chlorophyll *a* was calculated by substituting the measured values into the formula of Jeffrey and Humphrey (1975).

Macroinvertebrates

Macroinvertebrates were sampled every month from May to November 2008 and in April 2009 in each study reach. Four samples per stream were collected using a Surber net (25 × 25 cm, 1-m length, 0.5-mm mesh) on each sampling occasion. Sampling points were randomly selected among locations where the channel width was >50 cm. Samples were preserved in 70% ethanol in the field and returned to the laboratory.

Macroinvertebrates were sorted by eye and identified to the lowest possible taxonomic level using a stereomicroscope (Nikon, SMZ800), following Kawai and Tanida (2005) and Merritt et al. (2008). Identified macroinvertebrates were classified by life-form type (burrowers, clingers, crawlers, side-swimmers, or swimmers) and functional feeding group (collector-filterers, collector-gatherers, grazers, predators, or shredders) based on Takemon (2005), Merritt et al. (2008), Kobayashi et al. (2010) and our unpublished data.

Statistical analyses

Student's t-tests were used to determine the differences between the CP and DF in understory coverage on the forest floor (June, August), litter cover on the forest floor (lower, middle, upper slope), litter quantity in the riparian zone (August, November), channel slope, stream width, water depth, current velocity (surface, bottom), litter

coverage in the stream, D_{50} of stream substrate, rPAR (April, August), and algal abundance (August, September, October). A Friedman test was used to test for differences between the CP and DF in monthly overland flow during the monitoring period.

To test for differences between the CP and DF in the total abundance and taxa richness of macroinvertebrates and the abundance of each of the most dominant taxa (>1% of the individuals in all samples), a two-way analysis of variance was performed using stream (n = 2) and month (n = 8) as factors. When the stream × month interaction was significant, the difference between streams in each month was tested using Fisher's protected least significant difference test.

Proportional data were arcsine-transformed, and abundance data were log-transformed to normalize distributions and standardize variance structures prior to statistical analyses.

Results

Forest floor cover and overland flow

Vegetation cover on hillslopes was two to three times lower in the CP than in the DF in June and August, whereas litter cover at any position on the hillslopes was three to five times higher in the CP than in the DF in August (Table 1). Litter in the riparian zone was also significantly more abundant in the CP than in the DF in August, although not in November (Table 1). Monthly overland flow was significantly lower in the CP than in the DF from July to November (Fig. 2, $P < 0.05$).

Stream environment

Mean channel slope, stream width, and water depth in July were largely similar between the CP and DF (Table 1). Current velocities of both surface and bottom water were slower in the CP than in the DF in July (Table 1). Litter cover in streams was more than 30 times higher in the CP than in the DF in August (Table 1 and Fig. 3). The D_{50} of stream substrate was significantly higher in the CP than in the DF in December (Table 1). Fine particulate organic matter (>0.25 mm) was more abundant in the CP than in the DF in July (Table 1). Except for rPAR in April, which was lower in the CP, rPAR and algal abundance did not differ significantly between the catchments.

Macroinvertebrates

A total of 4465 macroinvertebrate individuals representing 100 taxa in 13 orders, 49 families, and 78 genera were collected. Total abundance and taxa richness of the samples did not differ between the CP and DF, or among months (Table 2), although the stream × month interaction was significant; total abundance in November and taxa richness in October were higher in the DF than in the CP.

Forest type had a significant effect on the abundance of 13 of the 26 dominant taxa. The abundances of *Gammarus nipponensis*, *Nemoura* spp., *Amphinemura* spp., *Geothelphusa dehaani*, and *Lepidostoma crassicorne* were significantly greater in the CP than in the DF (Table 2). The abundances of Lumbriculidae gen. spp., *Caroperla pacifica*, *Ecdyonurus tigris*, Chironominae spp., Ceratopogonidae gen. spp., *Psilotreta*

kisoensis, *Niponiella limbatella*, and Tabanidae gen. spp. were significantly greater in the DF than in the CP (Table 2). The site × month interaction was significant for *Ga. nipponensis*, *Nemoura* spp., *E. tigris*, *Amphinemura* spp., Chironominae spp., *L. crassicorne*, *Epoicocladius* sp.1, Ceratopogonidae gen. spp., and *P. kisoensis* (Table 2). If a significant difference between the streams was detected in some months, *Ga. nipponensis*, *Nemoura* spp., *Amphinemura* spp., and *L. crassicorne* were always more abundant in the CP, whereas *Epoicocladius* sp.1, Ceratopogonidae gen. spp., and *P. kisoensis* were always more abundant in the DF (Table 3). *E. tigris* and Chironominae spp. were more abundant in the CP in April but in the DF in other months (Table 3).

Discussion

In summer, vegetative cover on hillslopes was lower in the CP than in the DF, whereas litter cover at any position along the hillslope and standing stock of litter in the riparian zone were higher in the CP. The lower amount of understory vegetative cover in the CP may be attributed to the low light intensity at the forest floor beneath the dense canopy of cedar plantations (Katagiri et al. 1985). However, understory cover was very low (<20%) even in the DF compared to an adjacent deciduous forest where deer are excluded (Sakai et al. 2012). The forest floor in the CP would be covered with more abundant litter at least in summer because Japanese cedar litter exhibits a long period of abscission, low breakdown rate, and low dispersal compared to deciduous litter (Nakane 1995; Inagaki et al. 2004; Kanasashi and Hattori 2011). Overland flow runoff was always lower in the CP. Generally, understory vegetation and litter protect the soil infiltration capacity against rain drop impact (Onda and Yukawa 1994) and prevent

overland flow from discharging soil (Miura et al. 2002; Sidle et al. 2007; Gomi et al. 2008). Our results suggest that an abundance of litter is more important than understory cover in buffering runoff of overland flow in forests experiencing excessive deer browsing.

Litter cover in the streambed was also higher in the CP than in the DF in summer. Japanese cedar litter breaks down at a slower rate than deciduous litter in streams (Hisabae et al. 2010) as well as on the forest floor, and accumulates as complex structures composed of shoot or twig litter within streams. These structures persist for a prolonged period, probably buffering current velocity in the CP. The D_{50} of substrate was higher in the CP. Sakai et al. (2012) reported that higher runoff of overland flow induced fine sedimentation in the streambed in the DF compared to the deer-excluded catchment. The reduced overland flow protected the CP stream from fine sedimentation. Although fine sedimentation may affect periphyton (Yamada and Nakamura 2002), algal abundance did not differ between the CP and DF.

We observed differences in total abundance and taxa richness of macroinvertebrate assemblages between the DF and CP, but only in some seasons. In contrast, we observed differences in the structure of macroinvertebrate assemblages between the streams throughout the year. Yoshimura and Maeto (2006) demonstrated that the structure, but not the abundance or taxa richness, of macroinvertebrate assemblages in streams varied between a Japanese cedar plantation and a natural broad-leaf forest. In Europe, several studies have documented negative effects of coniferous plantations on the abundance, diversity, and biomass of macroinvertebrate assemblages (Ormerod et al. 1993; Thomsen and Friberg 2002). However, Collier and Halliday (2000) reported higher richness and diversity of macroinvertebrate assemblages in coniferous plantations

compared to deciduous forests in New Zealand and suggested that slower breakdown rates of conifer litter provide increased habitat for invertebrates.

All dominant shredder taxa (*Ga. nipponensis*, *Nemoura* spp., *Amphinemura* spp., and *L. crassicorne*) were more abundant in the CP than in the DF. The strong dominance of *Ga. nipponensis* has also been reported in other streams that drain Japanese cedar plantations in Japan (Hisabae et al. 2010). Japanese cedar litter is generally considered an unsuitable food for invertebrates because of its toughness and low nutritive quality (Hisabae et al. 2010). However, cedar litter should provide a constantly available food resource for shredder invertebrates due to its long period of abscission, low breakdown rate, and low dispersal. The advantage of slow-decaying litter for shredders has also been reported by Friberg and Jacobsen (1994). The shredders that were abundant in the CP suggest that Japanese cedar litter supplies persistent and abundant organic matter. In contrast, the abundances of burrowers (Lumbriculidae gen. spp., *Epoicocladius* sp.1, Ceratopogonidae gen. spp., and Tabanidae gen. spp.) were greater in the DF, where the increased level of fine sediments should provide more suitable habitats for burrower invertebrates.

In conclusion, the macroinvertebrate assemblages in a first-order stream draining a Japanese cedar plantation differed from those in a first-order stream draining a deciduous forest under excessive deer browsing. Our findings suggest that Japanese cedar litter functions in structuring macroinvertebrate assemblages by supplying persistent food resources for detritivores, and by buffering fine sedimentation via overland flow. The latter function might also be important in systems that have not experienced excessive deer browsing because litter may prevent soil erosion more effectively than understory vegetation (Miura et al. 2002).

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Table 1 Comparisons of environmental characteristics between the CP and DF. Differences between the catchments in litter cover, understory vegetation cover, quantity of litter at the bottom of the slope, channel slope, litter cover in the stream, stream width, water depth, current velocity, D_{50} of stream substrate, relative photosynthetically active radiation, and algal abundance were tested using Student's t-tests.

Variable		CP	DF	*t* value	Degrees of freedom	*P*
Forest type		Japanese cedar plantation	Deciduous forest			
Catchment area (ha)		1.31	1.66			
Cover of litter (%): Bottom slope		90.50 ± 2.33	25.75 ± 2.06	14.813	38	**<0.0001**
: Middle slope		84.50 ± 2.78	26.50 ± 3.44	10.842	38	**<0.0001**
: Upper slope		78.00 ± 2.20	13.05 ± 1.77	18.011	38	**<0.0001**
Cover of understory vegetation (%)	Jun.	6.18 ± 2.12	15.20 ± 4.29	2.307	38	**0.027**
	Aug.	5.50 ± 2.17	16.62 ± 3.99	2.865	38	**0.007**
Quantity of litter at bottom slope (g m^{-2})	Aug.	802.87 ± 125.14	294.87 ± 73.23	3.504	6	**0.013**
	Nov.	876.72 ± 125.54	611.53 ± 210.73	1.081	6	0.321
Channel slope (degrees)		12.75 ± 1.57	11.13 ± 1.75	0.688	10	0.507
Cover of litter in stream (%)		66.00 ± 3.93	2.00 ± 1.11	15.138	10	**<0.0001**
Stream width (m)		1.00 ± 0.11	1.17 ± 0.27	0.591	12	0.571
Water depth (cm)		4.79 ± 0.29	4.44 ± 0.40	0.712	18	0.486
Current velocity (cm s^{-1}): Surface water		10.83 ± 0.75	13.80 ± 0.53	3.220	18	**0.002**
: Bottom water		4.08 ± 0.46	12.19 ± 0.61	10.601	18	**<0.0001**
Effective grain size (D_{50}) (cm)		15.94 ± 0.69	6.34 ± 0.86	8.726	4	**0.001**
Quantitiy of organic matter (mg ml^{-1}): 2 mm		0.41	0.22			
: 1 mm		1.25	0.43			
: 0.5 mm		1.60	0.16			
: 0.25 mm		1.04	0.30			
: 0.125 mm		0.20	0.26			
: 0.063 mm		0.15	0.16			
Relative photosynthetically active radiation (%)	Apr.	16.15 ± 1.14	42.68 ± 1.50	13.760	10	**<0.0001**
	Aug.	19.41 ± 1.46	22.74 ± 2.59	1.096	10	0.299
Algal abundance (mg Chl. *a* cm^{-2})	Aug.	0.24 ± 0.14	0.19 ± 0.07	0.303	6	0.772
	Sep.	0.21 ± 0.07	0.08 ± 0.01	1.749	6	0.179
	Oct.	0.10 ± 0.03	0.07 ± 0.02	1.189	6	0.279

Values are means ± standard errors.
Bold characters indicate statistical significance (< 0.05).

Table 2 Results of analyses of variance testing for effects of stream and month on total abundance, taxa richness, and abundance of the 26 most dominant macroinvertebrate taxa.

					Factors					
			Mean		Stream		Month		Stream × month	
Variable	LFT	FFG	CP	DF	*F*	*P*	*F*	*P*	*F*	*P*
Total abundance	-	-	72.28	67.25	0.63	0.432	1.11	0.374	3.22	**0.007**
Taxa richness	-	-	17.09	17.59	0.25	0.618	1.21	0.317	3.06	**0.010**
Abundance of each taxon										
Gammarus nipponensis	SS	S	16.34	0.25	211.94	**<0.0001**	4.64	**0.001**	4.02	**0.002**
Ephemera japonica	B	C/G	5.16	9.31	3.16	0.082	2.22	**0.049**	0.85	0.553
Nemoura spp.	Cr	S	8.84	4.31	10.47	**0.002**	11.37	**<0.0001**	2.74	**0.018**
Paraleptophlebia japonica	B	C/G	2.91	4.66	0.50	0.485	2.81	**0.016**	1.59	0.163
Lumbriculidae gen. spp.	B	C/G	2.31	5.00	9.40	**0.004**	2.24	**0.047**	1.76	0.118
Caroperla pacifica	Cr	P	2.38	4.88	5.37	**0.025**	5.73	**<0.0001**	1.16	0.342
Orthocladiinae spp.	B	C/G, G	1.81	3.75	0.89	0.352	0.24	0.406	0.89	0.526
Ecdyonurus tigris	Cr	G	1.63	3.38	8.34	**0.006**	4.53	**0.001**	4.82	**0.000**
Amphinemura spp.	Cr	S	3.97	0.91	14.84	**0.000**	4.98	**0.000**	2.41	**0.034**
Chironominae spp.	B	C/F, C/G	0.47	3.63	12.26	**0.001**	4.33	**0.001**	5.09	**0.000**
Geothelphusa dehaani	Cr	C/G	3.31	0.66	42.82	**<0.0001**	1.07	0.396	0.79	0.603
Togoperla limbata	Cr	P	1.97	1.75	0.76	0.388	1.27	0.284	0.90	0.515
Lepidostoma crassicorne	Cr	S	2.69	0.75	13.68	**0.001**	3.98	**0.002**	3.52	**0.004**
Baetis yoshinensis	S	G	1.59	1.34	0.14	0.707	1.81	0.108	1.41	0.224
Diamesinae spp.	B	C/G, G	1.00	1.88	3.63	0.063	10.10	**<0.0001**	1.20	0.320
Hydropsyche sp.	Cl	C/F, C/G	1.88	0.78	3.42	0.071	2.28	**0.044**	0.76	0.625
Epoicocladius sp.1	B	C/G	0.66	1.78	3.81	0.057	19.89	**<0.0001**	5.53	**0.000**
Perissoneura paradoxa	Cr	C/G	0.72	1.41	3.17	0.081	0.69	0.677	2.17	0.054
Ceratopogonidae gen. spp.	B	C/G	0.50	1.50	11.62	**0.001**	6.73	**<0.0001**	3.22	**0.007**
Psilotreta kisoensis	Cr	C/G	0.00	1.97	48.98	**<0.0001**	3.29	**0.006**	3.29	**0.006**
Epoicocladius sp.2	B	C/G	1.22	0.72	0.91	0.345	6.39	**<0.0001**	1.21	0.318
Paralichas sp.	B	C/G	0.91	1.00	0.18	0.674	1.08	0.078	0.66	0.706
Niponiella limbatella	Cr	P	0.38	1.47	17.05	**0.000**	5.91	**<0.0001**	0.65	0.717
Tabanidae gen. spp.	B	P	0.00	1.81	41.79	**<0.0001**	0.69	0.678	0.69	0.678
Rhyacophila sp.	Cr	P	0.97	0.66	1.39	0.244	0.62	0.734	0.89	0.525
Dolophilodes sp.DB	Cl	C/F, C/G	0.72	0.69	0.03	0.870	1.76	0.117	2.05	0.068

df = 1,48 for effects of stream, and 7,48 for month and stream × month.
Bold characters indicate statistical significance (< 0.05).
Life form type (LFT); B: Burrower, Cl: Clinger, Cr: Crawler, S: Swimmer, SS: Side swimmer.
Functional feeding group (FFG); C/F: Collector-filterer, C/G: Collector-gatherer, G: Grazer, P: Predator, S: Shredder.

Table 3 Results of Fisher's protected least significant difference test for difference between streams in each month in total abundance, taxa richness and abundance of the 9 macroinvertebrate taxa, in which interaction between stream and month in analysis of variance were significant. The stream (CP or DF) that showed greater abundance or richness is denoted if significant difference was detected ($P < 0.05$).

Variable	May	Jun.	Jul	Aug.	Sep.	Oct.	Nov.	Apr.
Total abundance	-	-	-	-	-	-	DF	-
Taxa richness	-	-	-	-	-	DF	-	-
Abundance of each taxon								
Gammarus nipponensis	CP	CP	CP	CP	CP	CP	CP	CP
Nemoura spp.	-	CP	-	CP	-	-	CP	-
Amphinemura spp.	-	CP	-	CP	-	-	-	-
Lepidostoma crassicorne	-	-	-	CP	-	-	CP	-
Epoicocladius sp.1	-	-	-	DF	DF	DF	-	-
Ceratopogonidae gen. spp.	-	-	DF	-	-	DF	-	-
Psilotreta kisoensis	-	-	DF	DF	DF	DF	-	DF
Ecdyonurus tigris	-	-	-	-	DF	DF	-	CP
Chironominae spp.	-	DF	DF	-	-	-	-	CP

Figure legends

Fig. 1 The study site in the Ashiu Research Forest Station, Kyoto Prefecture, Japan.

Fig. 2 Monthly runoff of overland flows (mm) for the cedar plantation and deciduous forest catchments.

Fig. 3 Landscapes (a, c) and close-up views of streams (b, d) in the cedar plantation and deciduous forest catchments.

Fig. 1 (Sakai et al.)

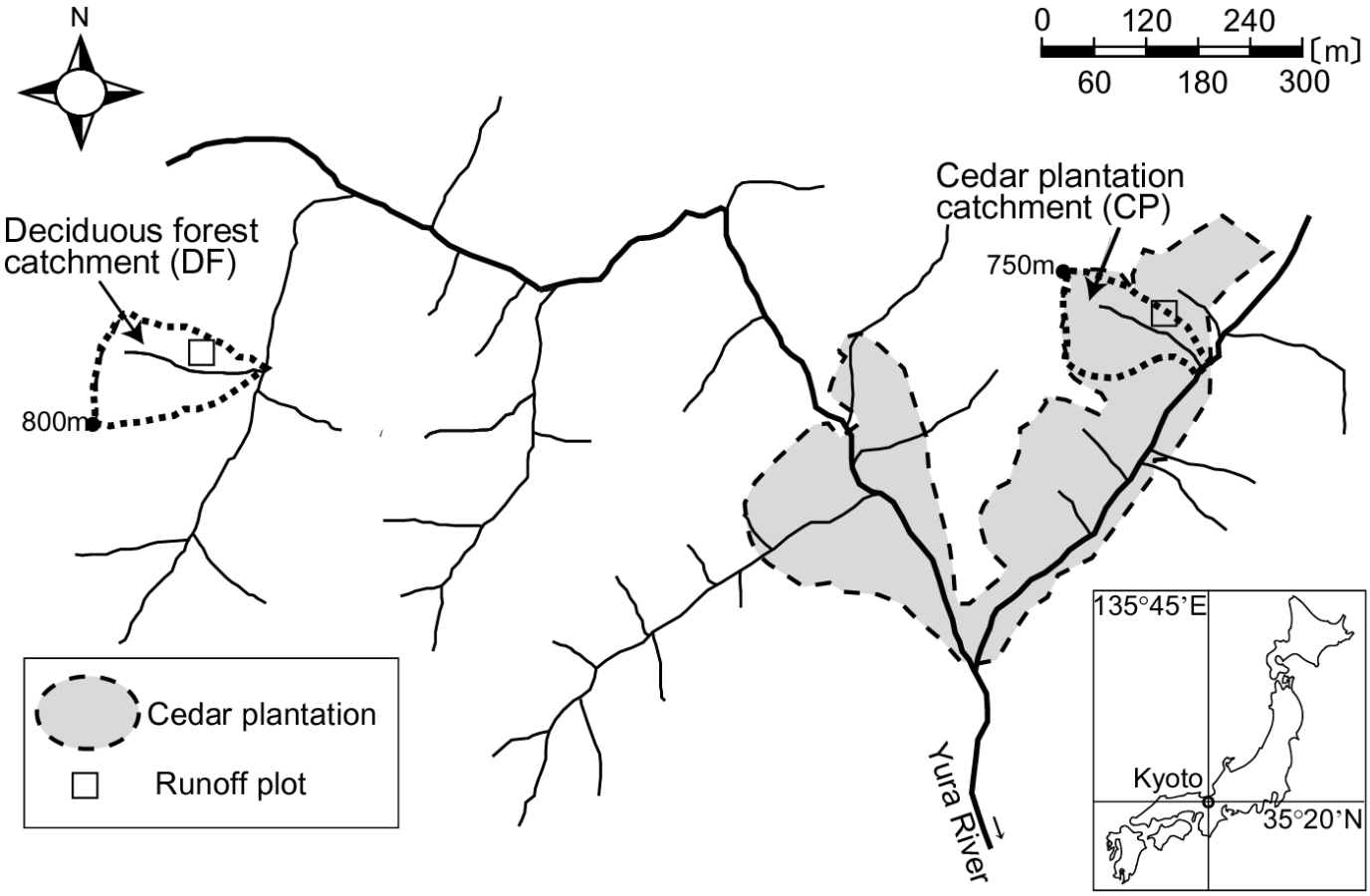


Fig. 2 (Sakai et al.)

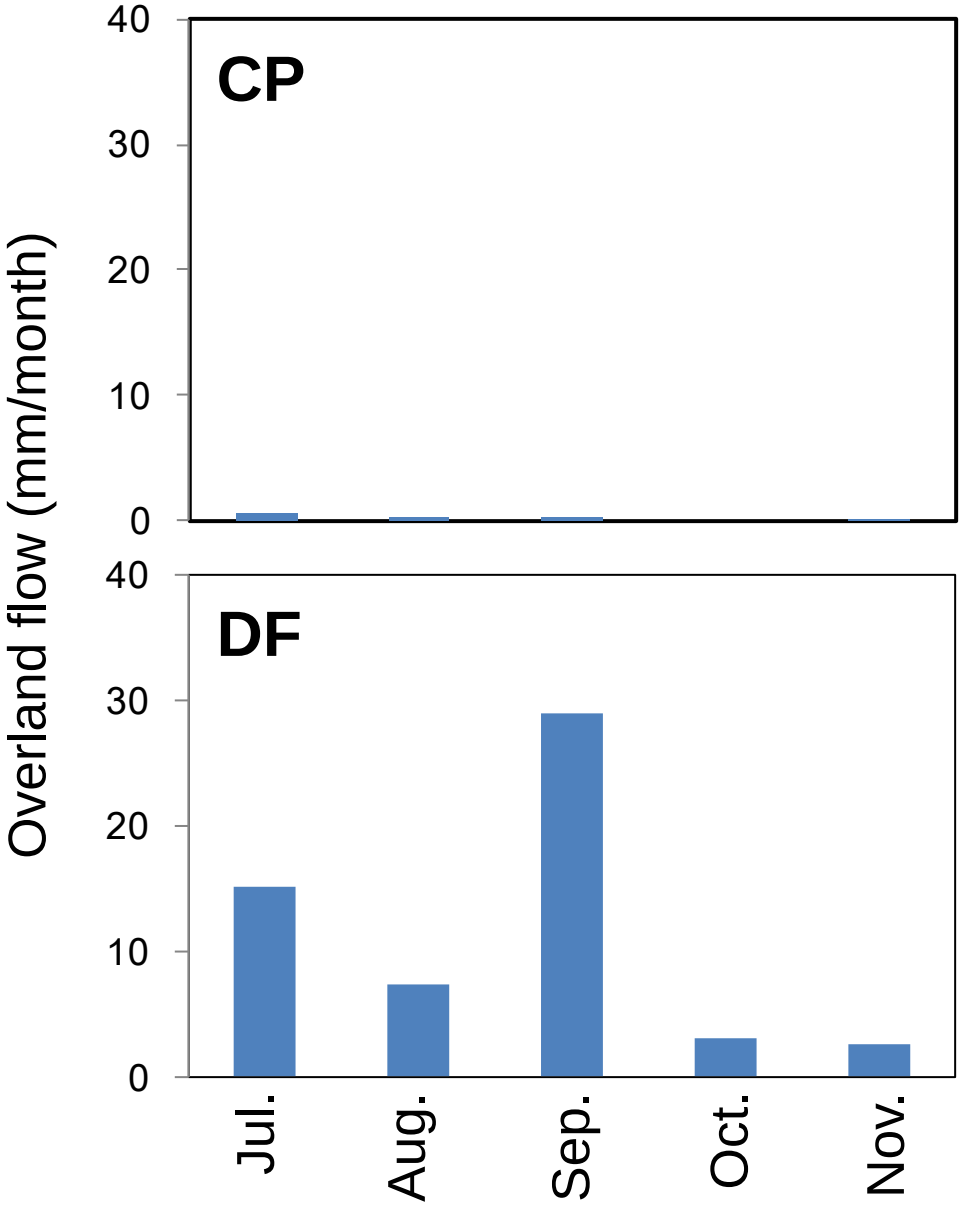
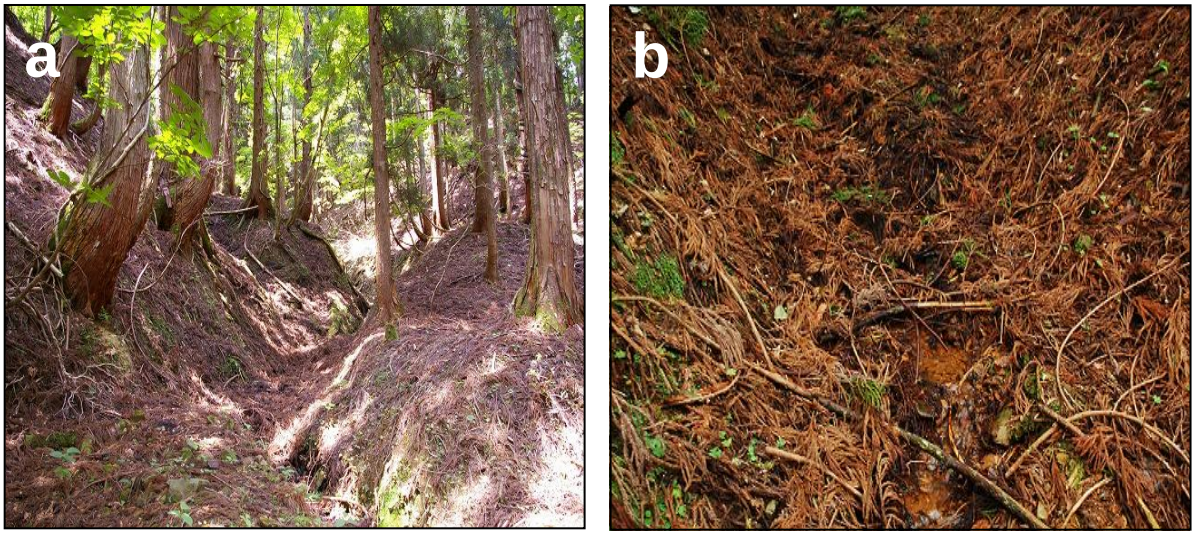


Fig. 3 (Sakai et al.)

Cedar plantation catchment (CP)



Deciduous forest catchment (DF)