Hydrobiologia (2011) 669:183–197
DOI 10.1007/s10750-011-0682-8

PRIMARY RESEARCH PAPER

Longitudinal and seasonal changes in the origin and quality of transported particulate organic matter along a gravel-bed river

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Received: 29 January 2010 / Revised: 3 February 2011 / Accepted: 11 March 2011 / Published online: 26 March 2011

Abstract Particulate organic matter (POM) plays an important role in nutrient dynamics in river ecosystems, but little is known about changes in the origin and quality of POM in relation to physical and seasonal changes along rivers. Using stable isotope and stoichiometric analyses, we investigated the changes in origin and quality of POM of three different size fractions (fine [FPOM], 1.2–100 μm; medium [MPOM], 100–250 μm; and coarse [CPOM], 250–1,000 μm) at 14 sites along a gravel-bed river over four seasons. FPOM and MPOM accounted for 90% of all POM at all study sites. At each site, the δ^{13}C level was lower for FPOM (range: −29.0 to −21.1‰) than for MPOM (−26.9 to −17.2‰) and CPOM (−27.5 to −16.3‰). The C:N ratio was lower for FPOM (6.9–15.6) than for MPOM (6.3–17.4) and CPOM (5.7–27.1). The contribution of periphyton to POM of all size fractions had a tendency to increase downstream, though the trend was less clear and varied seasonally for MPOM and CPOM between sites in middle and downstream reaches. Contrastively, the C:N ratio in all size fractions of POM consistently decreased downstream. The downstream decrease in the C:N ratio of POM can be partly explained by the increase in the contribution of periphyton, which seems to be associated with increased discharge and enhanced periphyton dislodgement, especially in winter. In addition, an increase in bacterial biomass associated with the greater nutrient availability in pool areas is another possible reason for the decrease in the C:N ratio of POM downstream.

Keywords Carbon stable isotope ratio · Carbon-to-nitrogen ratio · Nutrient · Periphyton · Pool-riffle sequence

Handling editor: Judit Padisak

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Introduction

Particulate organic matter (POM) plays an important role as a food source for aquatic consumers and in nutrient dynamics in river ecosystems (Wallace & Merritt, 1980; Triska et al., 1990; Zeug & Winemiller, 2008). POM includes both autochthonous (aquatic products such as periphyton, phytoplankton, and macrophytes) and allochthonous (terrestrial products derived from terrestrial plants) organic materials, which are transported from upstream. The composition of POM varies spatially and temporally according to aquatic primary production (Thorp & Delong, 1994), allochthonous input (Kaiser et al., 2004; Cai et al., 2008), retention and resuspension of these organic materials (Bilby & Likens, 1980), and degradation through use of aquatic consumers including microbes (Wallace & Merritt, 1980; Findlay et al., 1986; Delong & Thorp, 2006). Further, the relative contributions of these sources depend on the river size and flow regimes (Megens et al., 2002; Mills et al., 2003; Atkinson et al., 2009). Thus, the composition of POM is assumed to change downstream in the context of longitudinal changes in the relative importance of these ecosystem processes along the river continuum (Vannote et al., 1980), but little is known about the longitudinal changes in the origin and quality of POM, especially for small-sized fractions (<1 mm in size).

The smaller-sized POM fraction increases downstream, owing to the fragmentation of organic materials by upstream physical and biotic processes (Naiman et al., 1987; Webster & Meyer, 1997). The small-sized POM is decomposed and reduced in size, leaving behind more refractory components such as lignin and cellulose, which are more refractory to microbial action and lower in nutritional value (Peters et al., 1989; Yoshimura et al., 2008). On the other hand, many previous studies have reported that experimental addition of nutrients (NO_3-N, NH_4-N, and PO_4-P) enhances the decomposition rate of terrestrial products such as wood and leaves (Gulis et al., 2004; Greenwood et al., 2007) and increases the nitrogen (N) content of organic matter due to an increase in microbial biomass (Gulis & Suberkropp, 2003). An increase in downstream nutrient input from drainage owing to human activities has the potential to enhance POM derived from bacterial biomass with a low carbon-to-nitrogen (C:N) ratio (wt: wt). Consequently, the C:N ratio of small-sized POM may decrease downstream despite mainly terrestrial components, which usually have a high C:N ratio relative to microbial and aquatic products (Sterner & Elser, 2002).

The C:N ratio indicates the balance between the elemental requirements of organisms and the composition of their food sources (Elser et al., 2000). This approach has been used to integrate energy, available food materials, and trophic linkages in many types of ecosystems and would be helpful for evaluating the quality of POM in aquatic systems (Sterner & Elser, 2002). The stable C isotopic composition ($\delta^{13}C$) is also a powerful tool for evaluating trophic structure and energy flow in ecosystems (Peterson & Fry, 1987). In rivers, $\delta^{13}C$ level is useful for determining the proportion of major sources of organic C, namely, aquatic production from attached algae and phytoplankton, and terrestrial production from terrestrial plants. Aquatic plants such as phytoplankton, periphyton, and macrophytes often have higher $\delta^{13}C$ values than terrestrial C_3 plants (Akamatsu et al., 2004). This is because C isotopic fractionation is relatively small in aquatic environments owing to the low diffusion velocity of CO_2 in water (Yoshioka, 1997), as well as differences in C sources (e.g., dissolved inorganic carbon vs. CO_2).

In this study, to better understand the longitudinal and seasonal changes in the origin and quality of each POM size in relation to physical forces and nutrient dynamics, we investigated 14 sites over four seasons along a gravel-bed river using stoichiometric and stable isotope analyses. In river ecosystems, spatial variation in $\delta^{13}C$ level of aquatic producers and consumers has been used to support the hypothesis that aquatic producers are a more important food source for aquatic consumers from headwater to middle reaches (Doucett et al., 1996), a central prediction of the river continuum concept (Vannote et al., 1980); however, the importance of aquatic producers in downstream reaches is relatively unclear. In particular, the association between hydraulics and geomorphology in longitudinal changes of origin and quality of POM is poorly understood. Our goal was to examine spatiotemporal variations in the origin and quality of POM in pool-riffle sequences, including particle size and nutrient dynamics.

Materials and methods

Study site

The study was conducted at 14 sites along the Toyo River, Aichi Prefecture, central Japan (Fig. 1). The Toyo River originates from Mt. Dando (altitude = 1,172 m above sea level) and flows into Mikawa Bay. The riverbed is mainly composed of cobblestones. The total river length is 77 km, and the

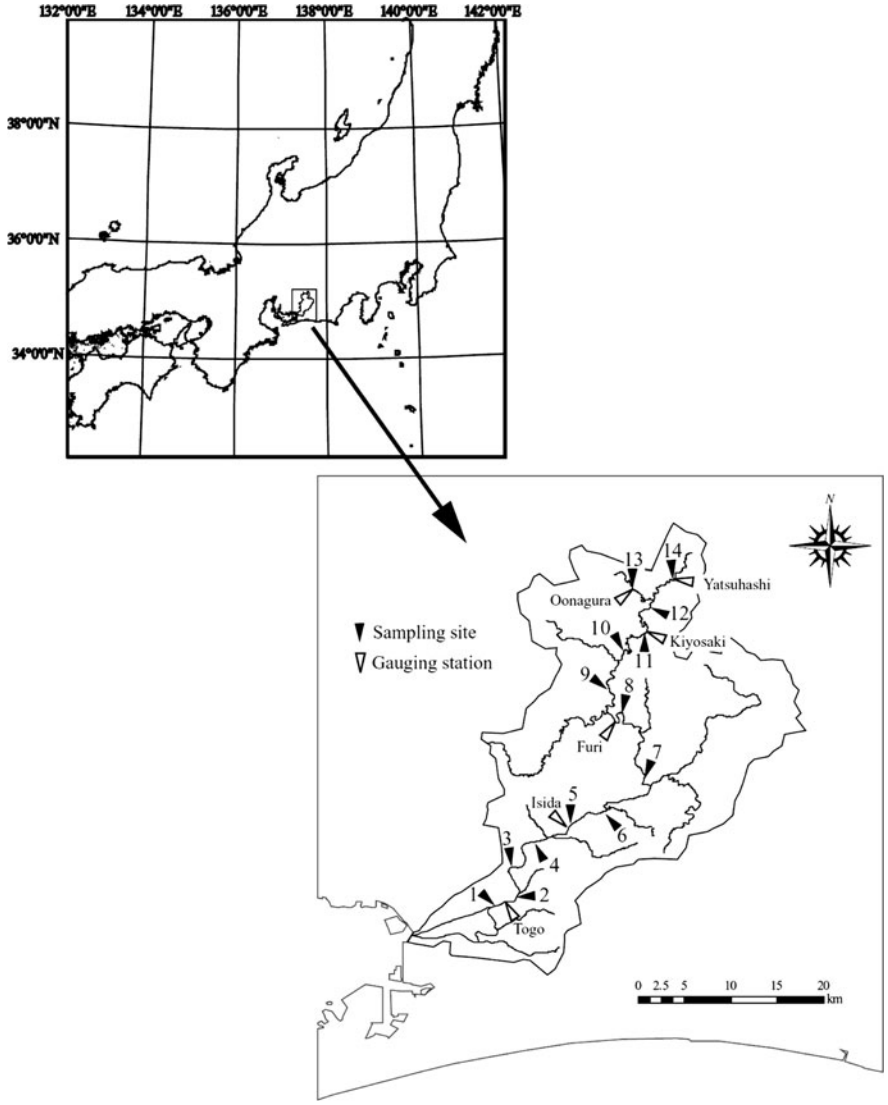

Fig. 1 Map of the study sites along the Toyo River. The *numbers* represent the site numbers

drainage area is 724 km^2. The drainage is divided by the Median Tectonic Line that runs in a northeast–southwest direction, and the geology in the upstream half of the watershed comprises the Ryoke Belt, dominated by granite and metamorphic rocks and Miocene sedimentary rocks, whereas volcanic rocks dominate the downstream half of the watershed.

The 14 sampling sites were classified into three different reaches based on location and physical river characteristics (Fig. 1, Table 1): downstream reach, sites 1–5; middle reach, sites 6–11; and upstream reach, sites 12–14. The downstream reach is located in the lowland region of the watershed and is characterized by a wide and low-gradient channel. The middle reach is located in the mountain region, and is characterized by a moderately steep and wide channel. The upstream reach is characterized by a steep and narrow channel, which is partly covered by tree canopies. There is no large dam along the main river stem, but water is impounded and partially diverted to an agricultural area in the downstream reach (between sites 4 and 5). Site 1 was located 11.8 km from the river mouth and 100–200 m upstream from the brackish zone. At all study sites, the pH ranged from 7.4 to 8.6. The water temperature ranged from 5°C in winter to 30°C in summer at site 1 and from about 0 to 24°C at site 14. The mean annual precipitation was 1,474 mm in 2007 at the

Table 1 Physical characteristics of the Toyo River

Reach	Site number	Drainage area (km^2)	Ordinary discharge ($m^3\ s^{-1}$)	Flow velocity ($m\ s^{-1}$)	Water depth (m)	River width (m)	River slope	Riffle proportion (%)	Water temperature (°C)
Downstream	1	660.0	21.02	0.48	0.55	80.3	0.0005	0.9	15.5 (4.4–27.7)
	2	625.6	20.35	0.68	0.48	62.9	0.0011	2.4	16.6 (3.3–27.9)
	3	622.4	20.29	0.80	0.48	52.6	0.0015	1.8	17.2 (5.1–28.4)
	4	601.2	19.88	0.70	0.35	82.4	0.0018	1.6	29.9 (6.7–29.9)
	5	536.5	18.70	0.59	0.46	68.0	0.0009	10.8	15.5 (5.3–25.7)
Middle	6	487.3	18.17	1.11	0.46	35.9	0.0032	17.1	15.1 (4.1–26.1)
	7	306.2	16.23	1.56	0.43	24.5	0.0068	18.8	13.5 (4.1–22.9)
	8	247.2	15.35	1.12	0.40	34.6	0.0038	19.4	13.8 (4.1–23.5)
	9	156.9	9.75	1.33	0.27	27.1	0.0091	22.8	12.6 (4.2–21.0)
	10	90.5	5.62	1.31	0.21	20.8	0.0127	23.3	11.6 (2.5–20.7)
	11	79.8	4.96	1.13	0.25	17.9	0.0075	23.5	11.9 (2.4–21.6)
Upstream	12	58.9	3.69	1.29	0.21	13.5	0.0118	20.2	11.2 (2.2–21.2)
	13	18.0	1.22	0.96	0.08	15.7	0.0233	36.0	11.0 (1.9–20.1)
	14	22.7	1.50	1.04	0.12	12.0	0.0166	28.6	11.1 (2.6–19.6)

The values represent means and ranges are shown in parentheses

Toyohashi Meteorological Observatory, which is 17 km away from site 1 (Japan Meteorological Agency, 2009). Storm events generally occur most frequently from June to October.

Discharge data from 1997 to 2006 were available at six gauging stations along the main stem of the Toyo River (Ministry of Land, Infrastructure, Transport and Tourism, 2008, Fig. 1). The mean ordinary discharge (i.e., the average over 10 years of 185-day water discharge) at each sampling site was estimated from the drainage area of the site and the discharge data from the nearest two stations. Mean flow velocity was roughly estimated from the ordinary discharge data, the mean river width, and the Manning formula (Gordon et al., 2004).

We defined a riffle as an area with relatively shallow and fast flow and a rough water surface (otherwise the area was considered to be a pool). We estimated the length of riffles per reach according to field measurements of the length of 2–3 consecutive riffles and pools at each site.

Sample collection and chemical analyses

Transported POM, river water, and periphyton were collected at the study sites four times between March 2007 and February 2008 under the base-flow condition (no rain 5 days prior to sampling). We considered three size fractions of POM: fine (FPOM, <100 μm), medium (MPOM, 100–250 μm), and coarse (CPOM, 250–1,000 μm). Coarser fractions of transported POM were collected using a plankton net (mesh size = Ø100 μm, opening diameter = 20 cm) and separated into different size fractions by stainless-steel sieves of 100, 250, and 1,000 μm. The net and sieves were repeatedly cleaned by distilled water for each site. Intact and fragmented leaves of terrestrial plants (transported leaves), which were >10 mm in length, were sorted from the POM samples. The collected samples were kept cool on ice during transportation to the laboratory and were frozen at −30°C before analyses.

River water (1–5 l) was pre-filtered by a 100-μm sieve and then was filtered through a glass fiber filter (Whatman GF/C pre-combusted at 450°C, nominal pore size: 1.2 μm); particles (1.2–100 μm) on the filter were collected as transported POM. The filtered water samples were used to determine nitrate (NO_3-N) concentrations using a continuous flow system (AACS III; Bran & Luebbe, Norderstedt, Germany).

Three to five stones of moderate size (10–20 cm) in each type of river reach were collected from the riffles, and periphyton was scraped from a 5 × 5 cm quadrat with a metallic brush from the upper surface of each stone for chlorophyll *a* and stable isotope analyses. The brush was cleaned by distilled water at each site before sampling. The collected periphyton was filtered through a glass fiber filter, and chlorophyll *a* on the filter was extracted in 99.5% ethanol. After placing the vials in a dark refrigerator at 4°C for 6 h, we measured the extracted pigments using a spectrophotometer (UV-2200A; Shimadzu, Kyoto, Japan). We determined the chlorophyll *a* content from these data according to the UNESCO method (1966) and expressed the abundance of periphyton in micrograms of chlorophyll *a* per square centimeter.

Each POM size fraction, transported leaves, and periphyton samples were dried at 60°C for 48 h and then ground to a powder after removing invertebrates. The carbon isotopic composition was measured using an isotope ratio mass spectrometer equipped with an elemental analyzer (EA/IRMS, Delta Plus XL; Thermo Electron, Bremen, Germany). An aliquot of approximately 1 mg of the sample was placed in a tin capsule and set into the autosampler of the EA/IRMS. Obtained CO_2 gas was separated using a Porapak QS column (3 m long) at 35°C. Results are reported using the δ notation: $\delta^{13}C$ (‰) = $[(^{13}C/^{12}C_{sample})/(^{13}C/^{12}C_{standard}) - 1] \times 1{,}000$, and expressed relative to Pee Dee Belemnite. Working standards of known δ values (glycine, histidine, and leucine) were analyzed every six runs to confirm the reproducibility and accuracy of isotope measurements. The analytical precision was 0.1‰. We determined C:N ratios (wt/wt) in POM fractions, transported leaves, and periphyton from the same bulk samples used for isotope analysis using the elemental analyzer (Flash EA1112; Thermo Electron).

Contribution of periphyton to the POM

We used periphyton and terrestrial transported leaves as aquatic and terrestrial sources, respectively, because they are the main primary producers in each ecosystem, although there were potential alternative sources (e.g., phytoplankton, microbes, and soil that have been re-worked by microbes). We used a two-end member mixing model to determine the contribution of aquatic and terrestrial sources to the transported POM as follows:

$$\delta^{13}C_{POM} = \delta^{13}C_{periphyton} \times f + \delta^{13}C_{transported\ leaves} \times (1 - f),$$

where f is the contribution of periphyton; $\delta^{13}C_{POM}$ is the $\delta^{13}C$ value of each size fraction of POM collected at each site; and $\delta^{13}C_{periphyton}$ and $\delta^{13}C_{transported\ leaves}$ are the average $\delta^{13}C$ values of periphyton and transported leaves, respectively, at each site. When f was <0 or >1, we used 0 or 1, respectively.

Statistical analyses

The proportion, $\delta^{13}C$ values, and C:N ratios of each POM size fraction, the contribution of periphyton to each POM size fraction, the $\delta^{13}C$ values of periphyton and transported leaves, and the chlorophyll *a* concentration were analyzed by split-plot analysis of variance (ANOVA), with season and reach as fixed factors. The pooled variance of the plots nested within the reaches was used as the error term to compare the reaches. Differences in $\delta^{13}C$ values, C:N ratios, and contributions of periphyton among POM size fractions were tested by one-way ANOVA. When ANOVA showed significant differences, the means were separated using Tukey's honestly significant difference test. For insight into the factors that generate the longitudinal trend in the characteristics of transported POM, we also examined correlations of the periphyton contribution and the C:N ratio of POM with each environmental variable (discharge, nitrate concentration, water temperature, flow velocity, depth, slope, stream width, and riffle proportion) by Pearson's product–moment coefficient and compared correlation coefficients between the environmental variables. For all tests, an α value of 0.05 was used to indicate statistical significance. All analyses were conducted using SPSS 15.0J (SPSS, Inc., Tokyo, Japan).

Results

Hydrologic characteristics of the river

The proportion of riffles per reach decreased downstream and was substantially lower in the downstream reach due to an increase in the pool length relative to the riffle length (Table 1). Mean ordinary discharge, water depth, and river width increased downstream, while river slope became shelving downstream. Mean flow velocity tended to be greater at sites in the middle reaches than in the other reaches.

Quantitative features of nutrients, POM, and benthic periphyton

The NO_3-N concentration ranged from 0.2 to 1.2 mg N l^{-1} and was significantly higher in the downstream reach than in the middle and upstream reaches, with little variation between the seasons (Table 2). The concentration of each size POM fraction varied temporally, and there was no significant difference among reaches. The concentration of FPOM and MPOM increased in the summer. FPOM and MPOM constituted on average 90% of the total transported POM in the Toyo River (Table 3). The average proportion of FPOM in the transported POM was higher in the downstream reach than in the other reaches (Table 2). Chlorophyll *a* on stone surfaces tended to be greater in the upstream reach than the other reaches, though the difference was not significant, partly due to the variation between sites within each reach. Chlorophyll *a* content was greater in winter than in other seasons.

δ^{13}C value of periphyton, transported leaves, and POM

The δ^{13}C value was higher for periphyton than transported leaves and POM throughout the reaches. The periphyton δ^{13}C value was significantly lower in the downstream reach than in the upstream and middle reaches, and had a tendency to increase from the upstream to middle reaches (Table 2). There was no significant difference in the periphyton δ^{13}C value among seasons. The δ^{13}C value of terrestrial transported leaves was lower than that for periphyton and transported POM throughout the reaches and varied little between reaches or seasons (Table 2).

The δ^{13}C value of all POM size fractions fell between that of periphyton and transported leaves in all reaches (Table 2). The average δ^{13}C value of FPOM was significantly lower than that of CPOM and MPOM (Table 3). For all size fractions, the δ^{13}C value was higher in the middle reach than in the upstream and downstream reaches (Table 2). The effect of reach × season was significant for the δ^{13}C values of all size POM fractions; these δ^{13}C values were higher in winter than in other seasons, and this seasonal difference was most pronounced in the middle reaches.

The contribution of periphyton calculated by the two-source mixing model was lower for FPOM than CPOM and MPOM (Table 3). The contribution of periphyton to FPOM and MPOM was significantly higher in the downstream reach than in the upstream reach. CPOM also showed a similar trend, but the effect of reach was not significant (Table 2). A longitudinal trend was also evident by plotting the annual mean contribution of periphyton against the base-flow discharge at each site (Fig. 2a). Although the contribution of periphyton to each size fraction of POM tended to increase with discharge (Fig. 2a, Table 4), the tendency was less clear for CPOM and MPOM between the middle and downstream reaches, especially in winter (Fig. 2b). In addition to discharge, there were correlations between the contribution of periphyton and other environmental factors, especially the contribution of periphyton to each size fraction of POM, which showed a strongly positive correlation with water temperature and a strongly negative correlation with riffle proportion (Table 4).

C:N ratios of periphyton, transported leaves, and POM

The C:N ratio was lowest for periphyton (6.3 ± 0.6) and highest for transported leaves (23.0 ± 10.1) in all reaches. For both periphyton and leaves, the C:N ratio did not differ significantly between reaches (Table 2).

For all POM size fractions, the C:N ratio fell between the C:N ratio of periphyton and transported leaves throughout the river (Table 2). The average C:N ratio of FPOM was lower than that of CPOM and MPOM (Table 3). The C:N ratios of CPOM and MPOM were lower in winter than in the other seasons, but the C:N ratio of FPOM showed less seasonal variation (Table 2). For all POM size fractions, the C:N ratios were significantly lower in the downstream reach than in the upstream and middle reaches (Table 2). The C:N ratio of MPOM was also significantly lower in the middle reach than in the upstream reach. This longitudinal trend was also evident when plotting C:N ratios against the base-flow discharge (Fig. 3a). The longitudinal trend was most clear in winter for all POM size fractions (Fig. 3b, Table 4). In addition, there were correlations between the C:N ratio of each POM size fraction and other environmental factors, with the C:N ratios of all POM size fractions showing a strongly significant positive correlation with riffle proportion and a negative correlation with nitrate concentration, water temperature, and river width (Table 4).

Table 2 Characteristics of each size of particulate organic matter (POM), periphyton, transported leaves, and nitrate in the Toyo River

	Reach			Reach		Season		Site		Reach × season	
	Downstream	Middle	Upstream	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
NO_3-N (mgN l^{-1})											
River water											
Annual mean	0.9 ± 0.3 a	0.3 ± 0.1 b	0.3 ± 0.1 b	23.13	<0.001	2.60	0.069	8.14	<0.001	2.20	0.068
Spring	0.7 ± 0.1	0.3 ± 0.1	0.2 ± 0.0								
Summer	0.9 ± 0.4	0.3 ± 0.1	0.3 ± 0.3								
Autumn	0.9 ± 0.2	0.3 ± 0.1	0.3 ± 0.1								
Winter	1.0 ± 0.2	0.3 ± 0.1	0.2 ± 0.0								
Concentration(μg l^{-1})											
CPOM											
Annual mean	1.1 ± 0.2	1.2 ± 0.2	2.5 ± 3.6	3.08	0.087	2.38	0.087	0.88	0.566	1.48	0.215
Spring	1.8 ± 0.4	1.7 ± 0.1	2.4 ± 1.8								
Summer	1.2 ± 0.5	1.0 ± 0.4	5.4 ± 3.7								
Autumn	0.6 ± 0.5	0.9 ± 1.0	1.6 ± 0.9								
Winter	0.9 ± 0.6	1.1 ± 0.6	0.7 ± 0.4								
MPOM											
Annual mean	8.8 ± 6.3	9.7 ± 6.5	5.7 ± 2.8	3.5	0.067	10.16	<0.001	0.99	0.472	1.74	0.142
Spring	13.4 ± 6.3	8.8 ± 3.8	5.9 ± 3.2								
Summer	12.0 ± 6.9	17.8 ± 7.4	8.8 ± 2.1								
Autumn	5.1 ± 2.2	7.6 ± 0.9	5.2 ± 1.2								
Winter	4.8 ± 4.1	4.6 ± 1.9	2.7 ± 1.2								
FPOM											
Annual mean	21.7 ± 18.7	13.6 ± 13.4	5.9 ± 3.6	3.88	0.053	4.8	0.007	2.22	0.038	3.23	0.013
Spring	22.7 ± 20.0	7.1 ± 2.8	6.0 ± 2.0								
Summer	22.8 ± 8.6	33.8 ± 10.0	10.6 ± 5.6								
Autumn	10.1 ± 8.5	6.8 ± 3.0	3.5 ± 0.7								
Winter	31.2 ± 28.8	6.8 ± 8.2	3.2 ± 2.0								
Chlorophyll *a* (μg cm^{-2})											
Periphyton											
Annual mean	158.9 ± 175.8	194.2 ± 169.2	378.7 ± 299.4	3.17	0.082	6.80	0.001	2.97	0.008	3.71	0.006
Spring	37.4 ± 33.3	120.9 ± 77.2	546.8 ± 441.2								
Summer	141.6 ± 158.3	123.5 ± 108.8	73.1 ± 89.0								

Table 2 continued

	Reach			Reach		Season		Site		Reach × season	
	Downstream	Middle	Upstream	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Autumn	79.8 ± 74.7	259.3 ± 206.6	439.3 ± 265.4								
Winter	376.8 ± 170.4	273.0 ± 214.8	455.7 ± 172.7								
Proportion (%)											
CPOM											
Annual mean	4.2 ± 2.7 b	7.7 ± 8.1 b	15.4 ± 12.3 a	8.90	0.005	0.80	0.501	0.82	0.619	0.95	0.475
Spring	6.5 ± 3.9	9.8 ± 6.9	19.5 ± 18.1								
Summer	3.4 ± 1.0	2.2 ± 1.4	17.1 ± 10.5								
Autumn	3.3 ± 1.6	5.7 ± 5.9	14.4 ± 6.4								
Winter	3.6 ± 2.5	13.1 ± 11.7	10.5 ± 2.2								
MPOM											
Annual mean	30.7 ± 13.4 b	44.7 ± 14.8 a	43.1 ± 12.0 a	8.21	0.007	3.05	0.042	0.91	0.539	1 65	0.166
Spring	38.3 ± 8.5	50.1 ± 10.2	39.0 ± 13.4								
Summer	31.9 ± 5.1	33.4 ± 7.8	39.9 ± 13.5								
Autumn	38.3 ± 16.1	50.8 ± 9.1	50.8 ± 1.2								
Winter	14.5 ± 3.9	44.5 ± 22.0	42.6 ± 13.4								
FPOM											
Annual mean	65.1 ± 14.0 a	47.6 ± 18.5 b	41.5 ± 8.6 b	11.38	0.002	3.63	0.023	1.43	0.207	2.60	0.036
Spring	55.2 ± 10.2	40.1 ± 4.8	41.5 ± 4.8								
Summer	64.8 ± 4.8	64.4 ± 7.9	42.9 ± 13.2								
Autumn	58.5 ± 15.4	43.5 ± 12.7	34.8 ± 5.2								
Winter	82.0 ± 6.2	42.3 ± 29.4	46.9 ± 12.7								
$\delta^{13}C$ (‰)											
CPOM											
Annual mean	−25.0 ± 1.8 b	−22.0 ± 2.4 a	−24.0 ± 1.5 b	8.55	<0.001	18.51	0.006	7.16	<0.001	11.17	<0.001
Spring	−25.9 ± 0.9	−22.5 ± 0.8	−24.9 ± 1.4								
Summer	−25.3 ± 1.4	−24.1 ± 1.1	−24.1 ± 1.7								
Autumn	−24.4 ± 2.5	−23.1 ± 0.6	−23.4 ± 2.0								
Winter	−24.4 ± 2.3	−18.3 ± 1.3	−23.6 ± 1.7								
MPOM											
Annual mean	−24.5 ± 2.0 b	−21.9 ± 2.1 a	−24.5 ± 1.0 b	8.60	0.006	8.73	<0.001	4.08	0.001	4.40	0.002
Spring	−26.1 ± 0.5	−23.5 ± 0.7	−24.8 ± 1.1								

Table 2 continued

	Reach			Reach		Season		Site		Reach × season	
	Downstream	Middle	Upstream	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Summer	−24.3 ± 2.6	−23.3 ± 2.1	−24.4 ± 2.0								
Autumn	−23.4 ± 2.5	−21.5 ± 1.1	−24.5 ± 1.2								
Winter	−24.4 ± 1.2	−19.3 ± 1.1	−24.2 ± 1.4								
FPOM											
Annual mean	−25.4 ± 1.0 b	−24.0 ± 1.6 a	−26.2 ± 1.4 b	14.56	0.001	23.35	<0.001	2.35	0.029	2.94	0.021
Spring	−24.4 ± 0.3	−23.0 ± 1.3	24.5 ± 0.5								
Summer	−26.5 ± 1.1	−24.3 ± 0.9	−26.8 ± 1.0								
Autumn	−25.7 ± 0.6	−25.8 ± 1.2	−27.5 ± 1.4								
Winter	−25.1 ± 0.6	−22.9 ± 0.7	−26.0 ± 1.2								
Periphyton											
Annual mean	−18.6 ± 3.4 b	−12.6 ± 2.8 a	−13.1 ± 3.5 a	9.85	0.004	2.63	0.066	3.94	0.001	1.26	0.302
Spring	−17.7 ± 2.6	−14.6 ± 4.2	−12.6 ± 4.0								
Slimmer	−20.5 ± 3.3	−12.5 ± 1.1	−14.5 ± 4.3								
Autumn	−19.4 ± 4.2	−12.0 ± 2.5	−13.6 ± 5.01								
Winter	−16.9 ± 2.9	−11.4 ± 2.0	−11.5 ± 3.9								
Transported leaves											
Annual mean	−28.6 ± 1.5	−27.1 ± 2.8	−27.8 ± 2.2	3.30	0.076	1.20	0.326	0.61	0.81	0.56	0.762
Spring	−29.1 ± 1.4	−28.4 ± 4.6	−29.1 ± 1.8								
Summer	−28.4 ± 0.9	−27.2 ± 1.2	−27.0 ± 1.9								
Autumn	−28.1 ± 1.5	−26.2 ± 2.3	−29.1 **± 2**.5								
Winter	−28.7 ± 2.3	−26.7 ± 2.0	−26.1 ± 1.6								
Contribution of periphyton (%)											
CPOM											
Annual mean	38.1 ± 21.9	34.5 ± 20.3	25.1 ± 11.8	2.79	0.105	0.42	0.739	0.74	0.695	3.61	0.007
Spring	28.1 ± 7.4	41.2 ± 22.4	26.4 ± 8.4								
Summer	40.9 ± 15.5	20.7 ± 13.3	22.9 ± 26.2								
Autumn	51.1 ± 33.1	20.6 ± 11.2	35.3 ± 12.8								
Winter	31.7 ± 22.5	55.3 ± 6.6	15.7 ± 6.4								
MPOM											
Annual mean	46.3 ± 32.9 a	34.4 ± 17.3 ab	22.0 ± 10.7 b	5.40	0.023	1.10	0.369	0.88	0.57	2.36	0.053
Spring	26.1 ± 5.8	33.6 ± 23.2	27.1 ± 10.0								

Table 2 continued

	Reach			Reach		Season		Site		Reach × season	
	Downstream	Middle	Upstream	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Summer	54.4 ± 23.9	24.8 ± 14.3	20.8 ± 25.3								
Autumn	58.4 ± 29.0	31.0 ± 13.1	28.7 ± 9.3								
Winter	33.9 ± 16.4	48.4 ± 9.8	11.3 ± 7.0								
FPOM											
Annual mean	34.8 ± 23.7 a	22.1 ± 17.3 ab	13.3 ± 14.0 b	5.60	0.021	2.70	0.06	0.96	0.501	0.73	0.628
Spring	42.8 ± 9.7	36.4 ± 23.7	29.4 ± 16.1								
Summer	27.2 ± 13.9	19.2 ± 11.0	6,1 ± 27.1								
Autumn	36.6 ± 37.5	8.0 ± 9.1	12.9 ± 12.3								
Winter	29.6 ± 13.7	24.5 ± 10.3	5.3 ± 9.2								
C:N ratio											
CPOM											
Annual mean	10.2 ± 3.4 b	12.8 ± 4.3 ab	13.2 ± 1.5 a	5.77	0.019	1370	<0.001	1.44	0.201	1.80	0.131
Spring	10.2 ± 0.8	10.5 ± 1.0	12.7 ± 0.8								
Summer	13.1 ± 4.3	17.5 ± 4.8	14.8 ± 2.9								
Autumn	10.8 ± 3.2	14.5 ± 2.0	13.1 ± 0.5								
Winter	6.7 ± 0.7	8.9 ± 1.6	12.2 ± 1.6								
MPOM											
Annual mean	10.4 ± 2.3 b	11.6 ± 1.8 b	14.6 ± 1.6 a	22.80	<0.001	29.19	<0.001	3.35	0.003	8.12	<0.001
Spring	13.3 ± 1.2	13.1 ± 0.7	16.2 ± 1.3								
Summer	10.3 ± 1.4	12.9 ± 1.6	13.5 ± 1.6								
Autumn	10.1 ± 1.0	10.7 ± 0.8	13.3 ± 1.0								
Winter	7.7 ± 1.3	9.9 ± 1.2	15.4 ± 1.7								
FPOM											
Annual mean	7.8 ± 0.6 b	9.2 ± 1.7 a	9.3 ± 2.0 a	11.20	0.002	3.70	0.021	0.82	0.624	4.23	0.003
Spring	8.0 ± 0.2	8.1 ± 0.9	7.8 ± 0.7								
Summer	8 0 ± 0.9	9.6 ± 0.5	9.5 ± 1.3								
Autumn	7.3 ± 0.5	10.2 ± 2.9	8.0 ± 0.4								
Winter	7.6 ± 0.6	8.9 ± 0.7	12.0 ± 1.7								
Periphyton											
Annual mean	6.4 ± 0.4	6.2 ± 0.4	6.4 ± 0.7	0.57	0.580	7.40	0.001	4.57	<0.001	2.99	0.019
Spring	7.0 ± 0.8	6.2 ± 0.2	6.5 ± 0.8								

Table 2 continued

	Reach			Reach		Season		Site		Reach × season	
	Downstream	Middle	Upstream	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Summer	7.0 ± 0.3	6.5 ± 0.6	6.4 ± 0.5								
Autumn	5.9 ± 0.3	60 ± 0.2	6.3 ± 0.8								
Winter	5.8 ± 04	6.1 ± 0.4	6.4 ± 0.7								
Transported leaves											
Annual mean	20.3 ± 9.4	23.5 ± 10.3	26.4 ± 10.3	1.02	0.455	0.65	0.589	1.02	0.455	2.05	0.086
Spring	14.4 ± 4.0	20.7 ± 7.2	25.6 ± 6.0								
Summer	21.7 ± 9.9	19.1 ± 3.8	32.8 ± 12.7								
Autumn	21.0 ± 7.9	33.6 ± 12.2	19.0 ± 5.7								
Winter	24.0 ± 13.4	20.6 ± 10.3	28.1 ± 11.3								

Split-plot ANOVA was performed using reach and season as between subject factors and site as a within subject factor. Values represent means and standard deviations. a and b are significantly different, while ab are not significantly different from either a or b (Turkey's test, $P < 0.05$)

Discussion

This study revealed that FPOM included more terrestrial-derived organic matter compared to MPOM and CPOM at all study sites along the river (Table 2). This finding is probably due to the fact that periphyton detached from the riverbed first constitutes coarse particulates and includes fewer refractory substances that concentrate in fine particulates after decomposition. On the other hand, the fine-sized fraction of POM, such as FPOM in this study, has been reported to include more lignin and cellulose, which are derived from terrestrial leaves and woods, and resemble organic matter in soil (Kaiser et al., 2004; Yoshimura et al., 2008). Periphyton in MPOM and CPOM may be assimilated disproportionately more by aquatic consumers due to its low C:N ratio and palatability (Sterner & Elser, 2002; Delong & Thorp, 2006). As a consequence, FPOM may include more refractory materials that remain after feeding by consumers.

Although MPOM and CPOM are considered to be better food sources for aquatic consumers than FPOM based on the periphyton content, the C:N ratio was consistently lower for FPOM compared with CPOM and MPOM (Table 3). The low C:N ratio of fine-sized fractions despite their refractory nature have also been observed in other studies (Edwards, 1987; Kaiser et al., 2004; Yoshimura et al., 2008). The greater N content in the fine-sized fractions is probably due to the greater surface area to volume ratio, which enables more nutrients to be absorbed chemically and/or to be incorporated by microbes colonized on the surface (Findlay et al., 1986; Jones & Lock, 1993).

We revealed that the contribution of periphyton to POM increased from the upstream reach to the downstream reach, and this longitudinal trend appeared to be roughly associated with discharge. The amount of detached periphyton in gravel-bed rivers is known to increase with increased discharge due to enhancement of shear stress, physical abrasion by suspended solids, and moving substrata (Biggs & Thomsen, 1995; Uehlinger et al., 1996). In the river, the increase in periphyton content in the POM pool from the upstream reach to the middle reach likely occurs as a result of the increased river flow breaking off more periphyton from the substrate. From the upstream reach to the middle reach, a decrease in tree canopies over the river potentially increases the

Table 3 Results of one-way ANOVA for differences in the proportion, δ^{13} C, contribution of periphyton, and C:N ratio among size fractions of particulate organic matter (POM) in the Toyo River

	FPOM	MPOM	CPOM	Size	
	$n = 56$	$n = 56$	$n = 56$	F	P
Proportion (%)	52.5 ± 17.9 a	39.4 ± 15.0 b	8.1 ± 8.8 c	140.63	<0.001
δ^{13} C (‰)	−25.0 ± 1.6 b	−23.4 ± 2.3 a	−23.5 ± 2.5 a	9.52	<0.001
Contribution of periphyton (%)	24.5 ± 19.4 b	34.9 ± 20.2 a	33.7 ± 19.7 a	4.69	0.010
C:N ratio	8.7 ± 1.6 b	11.8 ± 2.5 a	12.0 ± 3.7 a	24.93	<0.001

One-way ANOVA was performed using size as a fix factor. Values represent means and standard deviations. Different letters indicate a significant difference among size fractions (Tukey's test, $P < 0.05$)

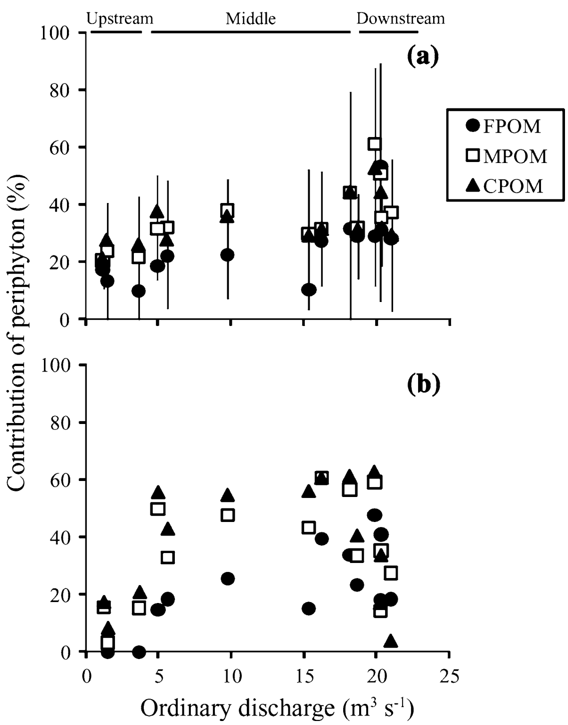

Fig. 2 Relationship between ordinary discharge and (**a**) annual mean and (**b**) winter-time contributions of periphyton to each size fraction of particulate organic matter (POM) in the Toyo River. For fine size fraction (FPOM), $n = 14$; for medium size fraction (MPOM), $n = 14$; for coarse size fraction (CPOM), $n = 14$. Each *symbol* and *bar* represents the mean and standard deviation, respectively

production of periphyton (Finlay, 2001; Walters et al., 2007). A relative decrease in the input of terrestrial organic matter from the surroundings may also contribute to the downstream increase in periphyton content, because the portion of riverbank covered by tree canopies or linked to riparian vegetation decreases as the channel widens downstream.

Despite this overall longitudinal trend in the periphyton content of transported POM, the trend was unclear for different POM size fractions and varied seasonally between middle and downstream reaches. For instance, the contribution of periphyton in MPOM and CPOM tended to be higher in the middle reach than the downstream reach in winter (Table 2). The relatively high periphyton content of each POM size in winter may be attributable to the increased biomass of periphyton in winter, related to the relatively stable flow conditions and low feeding activities by aquatic consumers under low water temperatures (Kawaguchi & Nakano, 2001; Miyasaka & Genkai-Kato, 2009). In fact, the average chlorophyll *a* concentration on the riverbed was 1.5–3.0-fold higher in winter than in the other seasons. In addition, the production of periphyton is potentially greater in the middle reach than the downstream reach, considering that the middle reach has a large area of riffles that enhances periphyton production.

The C:N ratio of POM in all size fractions also decreased downward along the river (Table 2). The increase in the periphyton content would partly contribute to this decrease in C:N ratio. However, the C:N ratio decreased from the middle reach to the downstream reach despite no clear increase in periphyton content (Table 2). This observation was especially clear in winter, when the periphyton content of MPOM and CPOM was greater in the middle reach, whereas the C:N ratio was greater in the downstream reach (Fig. 3b). Phytoplankton have the potential to depress the C:N ratio of transported POM, but their contribution would be small in our case, because the main stem of the river has no lakes or large dams where phytoplankton can thrive. One of the factors that can lower the C:N ratio of POM in the

Table 4 Coefficients of correlations ($n = 14$) between the contribution of periphyton and C:N ratio in each size fraction of particulate organic matter (POM) and environmental factors in the Toyo River

Size fraction	Ordinary discharge	Flow velocity	Water depth	River width	River slope	Riffle proportion	Water temperature	NO_3-N
Contribution of periphyton								
FPOM	0.694**	−0.407	0.642*	0.565*	−0.572*	−0.683**	0.745**	0.64*
MPOM	0.701**	−0.36	0.532	0.678**	−0.66*	−0.719**	0.84**	0.51
CPOM	0.555*	−0.202	0.411	0.482	−0.59*	−0.56*	0.712**	0.294
C:N ratio								
FPOM	−0.524	0.55*	−0.427	−0.698**	0.475	0.749**	−0.651*	−0.755**
MPOM	−0.881**	0.352	−0.826**	−0.750**	0.892**	0.852**	−0.836**	−0.697**
CPOM	−0.636*	0.51	−0.576*	−0.709**	0.567*	0.806**	−0.704**	−0.797**

Asterisks (* and **) indicate a statistically significant difference at the $P < 0.05$ and $P < 0.01$ level, respectively

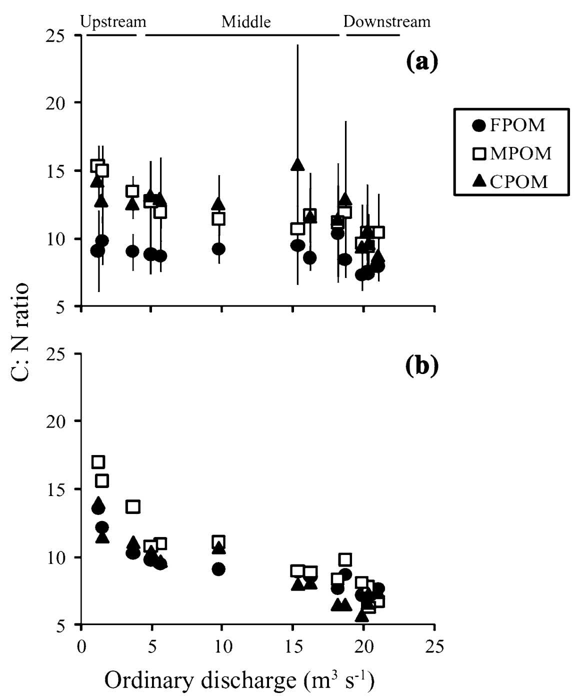

Fig. 3 Relationship between ordinary discharge and (**a**) annual mean and (**b**) winter-time carbon-to-nitrogen (C:N) ratio of each size fraction of POM in the Toyo River. For fine size fraction (FPOM), $n = 14$; for medium size fraction (MPOM), $n = 14$; for coarse size fraction (CPOM), $n = 14$. Each *symbol* and *bar* represents the mean and standard deviation, respectively

downstream reach is the nutrient input from watersheds. Since NO_3-N concentrations increased downward (Table 2), the nutrients could be more readily absorbed in POM. Moreover, bacterial biomass is known to increase with high nutrient concentrations, including NO_3-N and PO_4-P (Gulis et al., 2004; Greenwood et al., 2007), and bacterial activities on POM can also be greater in the lower reaches, because of the higher water temperatures, greater number of pools that retain detritus, and higher nutrient concentrations. Although we did not find any studies that show downstream increases in microbial biomass, the importance of bacterial production has been increasingly recognized in lowland rivers (Edwards & Meyer, 1990; Fischer & Pusch, 2001; Castillo et al., 2003). The increase in bacterial production in the downstream reaches may depress the C:N ratio of POM. Bacterial colonization and growth can improve the quality of POM even for terrestrial-derived detritus (Edwards, 1987). Some studies have indicated that aquatic insects such as filterers assimilate more terrestrial-derived materials in FPOM downstream (Akamatsu et al., 2010, Kobayashi et al., 2011). Filterers are considered to assimilate disproportionately more high-quality and palatable materials such as diatoms, microbes, and animal tissues in FPOM (Wallace & Merritt, 1980, Hall et al., 1996). The implication of this observation is that an improved quality of terrestrial-derived materials in FPOM by bacterial colonization has the potential to enhance terrestrial-derived material transfer in aquatic food webs (e.g., Zeug & Winemiller, 2008). The depressed C:N ratio of FPOM may impact on nutrient dynamics not only in riverine systems, but also estuary and marine systems.

This study showed some longitudinal trends in the characteristics of transported POM along a gravel-bed river and assessed the effects of potential factors such as discharge, riffle proportion, and nutrient concentration. The effects of these potential factors require further validation in other rivers with different longitudinal patterns in pool-riffle structure and nutrient inputs. In particular, the pool-riffle structure is one of the fundamental conditions governing flow environments in rivers and may be substituted for discharge data, which are difficult to obtain for small- and medium-sized rivers due to the lack of gauging stations. However, our understanding of the relationship between pool-riffle structure and POM dynamics is still limited, and we need to validate further results in other rivers. Studies focusing more on POM dynamics in individual riffles and pools, as well as comparisons of longitudinal patterns in POM characteristics in rivers with different geomorphologies, would help further understanding of nutrient dynamics in rivers at the catchment scale.

Acknowledgments We thank the Toyohashi Office of River and the Shitara Dam Construction Office of the Ministry of Land, Infrastructure, Transport, and Tourism for their cooperation and research support. We also thank K. Nakata, M. Fujiwara, and Y. Yajima for help with the fieldwork. We are grateful to two anonymous reviewers for their valuable suggestions and critical comments. This study was funded by the Ise Bay Eco-compatible River Basin Research Project of the Council of Science and Technology Policy, Ministry of Education, Culture, Sports, Science, and Technology, Japan.

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