Dissolved organic matter originating from the riparian shrub *Salix gracilistyla*

Akiko Sasaki・Shozo Shikenya・Kazuhiko Takeda・Takayuki Nakatsubo

A. Sasaki

Coastal Environment and Monitoring Research Group, Institute of Geology and Geoinformation, National Institute of Advanced Industrial Science and Technology, Chugoku, 2-2-2 Hiro-Suehiro, Kure, Hiroshima 737-0133, Japan

Tel. +81-823-72-1168

Fax +81-823-73-3284

e-mail: a-sasaki@aist.go.jp

S. Shikenya・K. Takeda・T. Nakatsubo

Department of Environmental Dynamics and Management, Graduate School of Biosphere Science, Hiroshima University, Kagamiyama 1-7-1, Higashi-hiroshima, Hiroshima 739-8521, Japan

SHORT COMMUNICATION

Abstract To estimate the importance of leaching of dissolved organic matter (DOM) as a pathway through which organic matter is supplied to stream ecosystems, we examined the amount of leachate over time and chemical properties of DOM leached from leaves in different conditions (i.e., green leaves, yellow senescent leaves, and leaf litter) of *Salix gracilistyla* Miq. the dominant riparian plant species in the middle reaches of rivers in western Japan. We analyzed dissolved organic carbon (DOC), total sugar and polyphenol in the leachate of leaf samples collected from a fluvial bar in the middle reaches of the Ohtagawa River in Hiroshima Prefecture, Japan. A considerable leaching of DOC from senescent leaves (37.3 mg g^{-1} d. w. leaf) and leaf litter (8.1 mg g^{-1} d. w. leaf) occurred within 24 h after the immersion. In contrast, DOC leached from green leaves was negligible until 1 wk after leaf immersion. Carbon loss of leaves by leaching within 24 h after leaf immersion was estimated to be less than 8%, suggesting that leaching of DOC from *S. gracilistyla* leaves is a minor pathway through which organic matter is supplied to stream ecosystems. DOM leached from the leaves included sugar and polyphenol, which were among the major chemical forms of DOM leached from the leaves (based on the molecular mass). In a laboratory experiment in which the difference in the stability of DOM between the chemical forms was examined, sugar decomposed more rapidly than polyphenol.

Key words Dissolved organic matter (DOM) ・ Leaching ・ Leaf litter ・ Riparian vegetation ・ *Salix gracilistyla*

Introduction

Riparian vegetation plays an important role in stream ecosystems as a source of organic matter through its litter fall, especially in headwater streams (Minshall 1967; Fisher and Likens 1973; Cummins et al. 1983; Meyer et al. 1998). Much attention has been focused on the decomposition of leaf litter in aquatic environments (e.g., Anderson and Sedell 1979; Webster and Benfield 1986), and conceptual models describing the fate of leaf litter have been proposed. According to this concept, the process of decomposition of leaves is divided into three phases which are referred to as leaching, conditioning, and fragmentation (Allan 1995). Leaching is a purely abiotic process which occurs within the first 24 h after leaf immersion in water. Previous studies reported that up to 25% of the initial dry mass of leaves is lost due to leaching (Nykvist 1962; Webster and Benfield 1986). Dissolved organic matter (DOM) leaking out the leaves is one of the major forms among the organic matter entering streams (Giller and Malmqvist 1998), and is primarily comprised of soluble carbohydrates and polyphenols (Suberkropp et al. 1976). Evidence suggests that DOM affects metal complexation (McKnight and Bencala 1990) and stream pH (Oliver et al. 1983), and DOM protects organisms from exposure to ultraviolet radiation (Schindler and Curtis 1997).

The relative importance of riparian vegetation as a source of DOM is generally considered to be smaller in middle reaches of rivers than in headwater streams, because the amount of direct leaf litter input into streams is small (e.g., Vannote et al. 1980). However, some riparian vegetation in the middle reaches of rivers has very high productivity supplying a large amount of leaf litter to the riparian zone (Sasaki and Nakatsubo 2003). In addition, in middle reaches of rivers, riparian vegetation is submerged frequently by river flooding. It is possible that DOM is leached from the leaves of canopy and leaf litter accumulated on the forest floor by immersion of the vegetation in riverwater. Although the DOM leaching from leaves of riparian trees might be an important pathway through which organic matter is supplied to stream ecosystems, there is no study on DOM leaching from leaves of riparian trees in middle reaches of rivers.

Salix spp. are among the dominant pioneer tree species in riparian habitats throughout the temperate and subarctic zones in the Northern Hemisphere (Ishikawa 1988; Cooper and van Haveren 1994). Previous studies have indicated that *Salix* spp. have several ecological traits that enable them to be tolerant to disturbance by river flooding (Densmore and Zasada 1978; White 1979; Ishikawa 1994), and that distribution of *Salix* spp. is restricted by the soil texture (Niiyama 1987) and river dynamics (Ishikawa 1991; Yoshikawa and Hukushima 1999). Biomass, production, and the nutrient economy of *Salix* spp. stands have been reported (Tahvabnainen and Rytkönen 1999; Kopp et al. 2001; Rytter 2001; Sasaki and Nakatsubo 2003, in press). There is no report on DOM leaching from leaves of riparian Salicaceous trees in middle reaches of rivers, while DOM leaching kinetics of *Salix* spp. leaves in headwater streams has been studied (Chauvet 1987; Gessnor and Konstanz 1989).

The shrubby willow *Salix gracilistyla* Miq. is one of the dominant plants in the riparian vegetation of the middle reaches of rivers in western Japan (Miyawaki 1983, 1984). In spite of its shrubby form, *S. gracilistyla* stand has high above-ground production comparable to those of the other temperate forests (Sasaki and Nakatsubo 2003). In this study, to estimate the importance of leaching of DOM as a pathway through which organic matter is supplied to stream ecosystems, we examined the amount of leachate over time and chemical properties of DOM leached from *S. gracilistyla* leaves in different conditions (i.e., in conformity with the phenology; green leaves, yellow senescent leaves, and leaf litter). In addition, to compare the stability of the organic matter leached from the leaves, differences in the degradation of DOM between the chemical forms were also assessed in a laboratory experiment.

Materials and methods

Site description

Fig. 1

Leaf samples used for the experiments were collected from a fluvial bar in the middle reaches of the Ohtagawa River in Hiroshima Prefecture (34°30'N, 132°31'E, about 20 m a.s.l.; Fig. 1 a). A gravelly area with sparse vegetation largely covered the bar from its apex to its middle part. Between the distal part and the gravelly area, grassland dominated by *Eragrostis curvula* (Schrad.) Nees was present. *S. gracilistyla* predominated in the wet area along the river, forming a zonal stand (width, 5-10 m; length, 150 m; height; 1-2.5 m; Fig. 1 b). *S. gracilictyla* has high tolerance to sand deposition and a high ability to sprout and to form adventitious roots from stems buried in sand (Ishikawa 1996). As a result of repeated sand burial and subsequent new shoot production, the distinction between individuals is not definite in the zonal stand. The zonal stand was totally covered with riverwater during flood periods in the rainy season or just after heavy rainfall. During the past five years, up to 90% of submergence of the vegetation by river flooding occurs from May to September, when the canopy of the *S. gracilistyl*a stand consists of green leaves (River Bureau, Ministry of Land, Infrastructure and Transport 2000-2005). Each flood lasts only for a few days in an ordinary year (cf. Nakatsubo et al. 1994). Although defoliation is not caused by a usual flooding, from August to October 2004, some leaves were damaged and fallen down by strong flooding owing to major typhoons.

Sample collection

At the study site, in 2004, leaf emergence of *S. gracilistyla* started in the first week of April, and expansion of leaves occurred from May to September. In November, leaves turned yellow and began to shed. In October 2004 green leaves of *S. gracilistyla* were harvested from the branches at 10 randomly selected points in the zonal stand. In each point, three 30 cm branches including about ten leaves were collected at 1 m above from the ground. These points were marked by a tape for the sampling in autumn season. In November 2004 leaf litter of *S. gracilistyla* that had fallen on the ground in the latest senescence period was collected by hands within 1 m^2 at the 10 marked points. At the same time, senescent leaves, which had totally turned yellow, were harvested the same way for green leaves at the 10 points. Visually abnormal or injured leaves were excluded in each sample collection. All samples were stored in a refrigerator at 4 °C until the experiments (within 4 d). Neither leaves nor leaf litter were allowed to dry out nor were sterilized before the experiments.

Leaching experiment

The three types of leaf samples (green leaves, yellow senescent leaves, leaf litter; 500 mg d. w.; n = 3) were each placed in an Erlenmeyer flask containing 100 ml of purified water (Milli-Q water; Milli-RO PLUS 60, Millipore Japan Co., Ltd., Tokyo, Japan). The flasks were sealed with Parafilm (American National Can Company, Chicago, IL, USA) and stored in an incubator at 15 °C, which is average yearly riverwater temperature in the study site provided by River Bureau, Ministry of Land, Infrastructure and Transport (http://www.mlit.go.jp/river/). At intervals of 1, 2, 3, 4, 7, and 14 d for leaf litter and senescent leaves and 1, 7, 14, 21, 28, and 35 d for green leaves, all of the leachate in each flask was removed and analyzed for concentrations of dissolved organic carbon (DOC), total sugar, and polyphenol. After each sampling, 100 ml of purified water was added to the flasks with the leaf samples. Flasks without leaf samples containing 100 ml of purified water were prepared for analysis of each substance (DOC, total sugar, and polyphenol) as controls to reconcile the error induced through the experimental procedure.

Chemical analysis

Each leachate sample was filtered through glassfiber filters (GC-50, pore size 0.45 µm; Advantec, Tokyo, Japan) just before the analysis. To avoid contamination, the filters were previously combusted (at 450 °C for 1 h).

Dissolved organic carbon (DOC), one of the major components of DOM (Allan 1995), in the leachate was determined with a total organic carbon analyzer (TOC-5000A, Shimadzu Corporation, Kyoto, Japan). In addition to DOC, the concentration of total sugar and polyphenol in the leachate were measured because previous studies reported that these are among the most major forms of DOM leached from leaf litter (e.g., Suberkropp et al. 1976; Berg and McClaugherty 2003). The amount of total sugar was determined by the phenol-H_2SO_4 method (Dubois et al. 1956) using D-glucose ($C_6H_{12}O_6$) as the standard. Polyphenol was determined by a modified form of the Folin-Denis method (Folin and Denis 1915), using Folin-Ciocalteu reagent and (+) catechin ($C_{15}H_{14}O_6$) as the standard.

Degradation of DOM in leachate

The availability of leachate DOM to chemical and biological degradation was estimated by measuring the DOM concentration in the laboratory. In the field, senescent leaves rarely submerge because most flooding occurs in growth period. Our leaching experiment showed that the amount of DOC leached from green leaves of *S. gracilistyla* was negligible until 1 wk after leaf immersion (cf. Fig. 2b). Therefore, we examined the degradation of DOM leached from leaf litter only. A leaf litter sample (500 mg d. w.; n = 3) was placed in an Erlenmeyer flask containing 100 ml of purified water (Milli-Q water). The flask was sealed with Parafilm and stored in an incubator at 15 °C. After 24 h, the leaf litter was removed, and the concentrations of DOC, total sugar, and polyphenol in the leachate were determined by the procedures described above. The flask containing the leachate was then stored in an incubator at 15 °C. The concentrations of DOC, total sugar, and polyphenol were determined at intervals of 1, 2, 3, 4, and 7 d after the leaf immersion. The error induced through the experiment was reconciled by using blanks. The differences in DOM concentrations in the leachate between the experimental periods (days) was tested by one-way analysis of variance (ANOVA) and Scheffe's test.

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Results

Leaching experiment

A considerable level of leaching of DOC from leaf litter occurred within 24 h after leaf immersion (Fig. 2 a; 8.1±1.6 mg g^{-1} d. w. leaf; mean ± SD, $n = 3$). The amount of DOC leached within 24 h after leaf immersion was about 65% of the total DOC that had leached after 14 days. The time course of leaching of DOC from yellow senescent leaves was similar to that from leaf litter, showing leaching soon after leaf immersion. However, the total amount of DOC leached from the senescent leaves after 24 h was more than four times higher than the leachate from the leaf litter (Fig. 2 a; 37.3±4.2 mg g^{-1} d. w. leaf; mean ± SD, $n = 3$). The time course of leaching of total sugar and polyphenol from leaf litter and senescent leaves was similar to that of DOC (Figs. 3a, 4a). The amount of total sugar and polyphenol leached within 24 h after leaf immersion was about 40–70% of the total amount of those compounds that had leached after 14 days.

In contrast to leaf litter and senescent leaves, DOC leached from green leaves was negligible until 1 wk after leaf immersion (Fig. 2b). In green leaves, time course of leaching of total sugar and polyphenol was similar to that of DOC (Figs. 3b, 4b). No sugar or polyphenol was detected in the leachate until 2 or 1 wk after leaf immersion, respectively.

Degradation of DOM in leachate

Significant declines in the concentrations of DOC, total sugar, and polyphenol in leaf litter leachate occurred by day 7 of the experiment (Fig. 5; Scheffe's test, $P < 0.01$). At the end of the experimental period (after 7 d), DOC concentration in the leaf litter leachate decreased to 40% of the initial value. The concentration of total sugar in the leachate declined more rapidly than that of polyphenol: after 7 days the concentration of total sugar dropped to 57% of the initial value, whereas the concentration of polyphenol was 78% of the initial value.

Discussion

In this study, the difference between conditions of leaves was determined, which is consistent with a previous study (Gessner and Konstanz 1989). The amount of DOC leached from green leaves was negligible until 1 wk after leaf immersion, although the substance was detected later in the experimental period probably owing to decomposition of the leaves by microorganisms (Sampaio et al. 2001). In contrast, the majority of DOC leaching from leaf litter and senescent leaves occurred within 24 h after immersion. This finding is consistent with results from previous studies that allochthonous litter displays pronounced mass loss within a few days owing to the leaching of water-soluble substances (Nykvist 1962; Petersen and Cummins 1974; Gessner and Konstanz 1989; Benfield 1996). The amount of DOC leached from the senescent leaves was more than four times as high as that from leaf litter.

One possible explanation of the difference in the DOC leaching is an alteration of cells in senescence period, which is a preparation for the abscission of leaves. During growth period, carbohydrates assimilated in green leaves through photosynthesis are locked with cuticles and epicuticular waxes. In senescence period, however, carbohydrates in leaves are broken down into simple sugars such as sucrose, and the biomembranes become permeable to soluble carbohydrates for the retranslocation (Larcher 2001). Therefore, it is likely that the senescent leaves contained a large amount of labile organic carbon, and these compounds could be easily extracted by water. In addition, it is possible that leaf litter might be modified on the ground by leaching owing to rainfall and river flooding, and by soil microorganisms.

Table 1

Previous studies have indicated that the mass or carbon loss of leaves by leaching differs widely among tree species (Table 1). Although mass loss and carbon loss are not equal, it has been indicated that carbon loss ratio of tree leaves shows closely similar value of mass loss ratio of the leaves (Rustad 1994). Assuming that the carbon content in leaves is 47% (Sasaki 2005), carbon loss of green leaves and leaf litter of *S. gracilistyla* by leaching within 24 h after leaf immersion was estimated to be 0.1 and 2%, respectively. These values were similar to carbon loss of coniferous tree leaves by leaching, which produces smaller DOC leachate than those of deciduous tree leaves (Table 1, McArthur and Richardson 2002). The carbon loss of the yellow senescent leaves of *S. gracilistyla* by leaching, estimated to be 8%, was within the range of values reported for the other deciduous tree leaves (Table 1). In comparison, previous study has reported that some riparian deciduous tree leaves (e. g., *Alnus* sp., *Salix* sp.) lose up to 20% of the initial dry mass by leaching within 24 h after leaf immersion (Table 1). Although the amount of DOM leached from leaves of *S. gracilistyla* might vary with temperature, humidity, and microbial activity under field conditions, our results suggest that leaching of DOM from *S. gracilistyla* leaves is a minor pathway through which organic matter is supplied to stream ecosystems regardless of the timing of submergence of the vegetation. In a stream, leaves undergo the conditioning and fragmentation due to microbial and invertebrate activity after leaching of its water-soluble components (Allan 1995). Leaves are converted to particulate organic matter through these processes. Most organic matter provided through leaves of *S. gracilistyla* is likely to become particulate forms in terrestrial and aquatic riparian habitat. In our previous experiment, using a litter bag method, we observed that 40-60% of *S. gracilistyla* leaf litter remained as coarse particulate organic matter in running water and on the forest floor after 1 year (Sasaki 2005).

DOM leached from *S. gracilistyla* leaves includes sugar and polyphenol. The time course of leaching of total sugar and polyphenol from the leaves was nearly the same as that of DOC: a rapid initial leaching from senescent leaves and leaf litter and a very low level of initial leaching from green leaves. Assuming that the average carbon content of total sugar and polyphenol was the same as the glucose (40%) and catechin (62%), the contribution of both substances to the total amount of DOC leached during 24 h was estimated to be more than 50%. Although sugar and polyphenol leached from *S. gracilistyla* leaves should comprise a number of chemical forms, this result suggests that both substances were among the major chemical forms of DOM leached from the leaves.

In the laboratory experiment examining degradation of DOM, significant declines in the DOC, total sugar, and polyphenol concentrations in the leaf litter leachate were observed by 7 days after the beginning of the experiment (Scheffe's test, $P < 0.01$). The observed decline in DOC was likely a net result of mineralization and/or biological uptake during the incubation period. Under field conditions, DOC is removed from water by biotic and abiotic process (i.e., microbial uptake, adsorption, flocculation, photochemical destruction; Allan 1995). The rate of decline of DOM determined in our experiment might be underestimated because, to minimize the background, we used purified water for the experiment instead of riverwater. Therefore, over the course of the experiment the number of decomposers in the water is likely to have been small compared with riverwater. Although the decomposition rate of DOM leached from *S. gracilistyla* leaves in the field is unknown, our results showed that sugar decomposed more rapidly than polyphenol. Under field conditions, sugars are easily utilized by microorganisms, although some of the substances are adsorbed onto clay and chemical complexing with oxides of aluminum and iron (Lock and Hynes 1976; Dham 1981). The role of polyphenols in stream ecosystems is not well known, while many studies reported that polyphenols play various roles in plant biology and terrestrial nutrient cycling including defense against herbivores and contribution to plant colors (Haslam 1981; Scalbert and Haslam 1987). More investigation of the role of water-soluble compounds leached from leaves of riparian trees including *Salix* spp. is necessary.

Acknowledgments This study was partly supported by a grant from the Foundation of River and Watershed Environment Management (Tokyo, Japan).

Literature Cited

Allan JD (1995) Heterotrophic energy sources. In: Stream ecology: structure and function of running waters. Kluwer Academic Publishers, Dordrecht, pp 109-129

Anderson NH, Sedell JR (1979) Detritus processing by macroinvertebrates in stream ecosystems. Ann Rev Entomol 24: 351-77

Benfield EF (1996) Leaf breakdown in stream ecosystems. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology. Academic Press, San Diego, pp 579-589

Berg B, McClaugherty C (2003) Plant litter: decomposition, humus formation, carbon sequestration. Springer-Verlag, Berlin

Chauvet E (1987) Changes in the chemical composition of alder, poplar and willow leaves during decomposition in a river. Hydrobiologia 148: 35-44

Cooper DJ, van Haveren BP (1994) Establishing felt-leaf willow from seed to restore Alaskan, U. S. A., floodplains. Arctic Alpine Res 26: 42-45

Cummins KW, Sedell JR, Swanson FJ, Minshall GW, Fisher SJ, Cushing CE, Petersen RC, Vannote RL (1983) Organic matter budgets for stream ecosystems: problems in their evaluation. In: Barnes JR, Minshall GW (eds) Stream ecology: application and testing of general ecological theory. Plenum Press, New York, pp 299-353

Dahm CN (1981) Pathways and mechanisms for removal of dissolved organic carbon from leaf leachate in streams. Can J Fish Aquat Sci. 38: 68-76

Densmore R, Zasada JC (1978) Rooting potential of Alaskan willow cuttings. Can J Forest Res 8: 477-479

Dubois M, Gilles KA, Hamilton JK, Pebers PA, Smith F (1956) Colorimetric method for determination of sugars and related substances. Anal Chem 28:350-356

Fisher SG, Likens GE (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to ecosystem metabolism. Ecol Monogr 43:421-439

Folin O, Denis W (1915) A colorimetric method for the determination of phenols (and phenol derivatives) in urine. J Biol Chem 22:305-308

Gessner MO, Konstanz JS (1989) Leaching kinetics of fresh leaf-litter with implications for the current concept of leaf-processing in streams. Arch Hydrobiol 115: 81-90

Giller PS, Malmqvist B (1998) Energy and nutrients. In: The biology of streams and rivers. Oxford University Press, Oxford, pp 147-169

Haslam E (1981) Vegetable tannins. In: Conn EE (ed) The biochemistry of plants vol 7, Academic press, New York, pp 527-544

Ishikawa S (1988) floodplain vegetation of the Ibi River in central Japan I. Distribution behavior and habitat conditions of the main species of the river bed vegetation developing on the alluvial

fan. Jpn J Ecol 38: 73-84 (in Japanese with English summary)
Ishikawa S (1991) Floodplain vegetation of the Ibi River in central Japan II. Vegetation dynamics on the bars in the river course of the alluvial fan. Jpn J Eol 41: 31-43 (in Japanese with English summary)
Ishikawa S (1994) Seedling growth traits of three salicaseous species under different conditions of soil and water level. Ecol Rev 23: 1-6
Ishikawa S (1996) The ecological characteristics of riparian plants. In: Okuda S, Sasaki Y (eds) River environment and riparian plants. Soft Science, Inc., Tokyo, pp 116-139
Kopp RF, Abrahamson LP, White EH, Volk TA, Nowark CA, Fillhart RC (2001) Willow biomass production during ten successive annual harvests. Biomass Bioenerg 20: 1-7
Larcher W (2001) Environmental influences on growth and development In: Physiological plant ecology 4th edition. Springer-Verlag, Berlin, pp 297-343
Lock MA, Hynes HBN (1976) The fate of 'dissolved' organic carbon derived from autumn-shed maple leaves (*Acer saccharum*) in a temperate hard water stream. Limnol Oceangr 21: 436-443
McArthur MD, Richardson JS (2002) Microbial utilization of dissolved organic carbon leached from riparian litter fall. Can J Fish Aquat Sci 59: 1668-1676
McKnight DM, Bencala KE (1990) The chemistry of iron, aluminum, and dissolved organic material in three acidic metal-enriched, mountain streams, as controlled by watershed and in-stream processes. Water Resour Res 26:3087-3100
Meyer JL, Wallace JB, Eggert SL (1998) Leaf litter as a source of dissolved organic carbon in streams. Ecosystems 1:240-249
Minshall GW (1967) Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology 48:139-149
Miyawaki A (1983) Vegetation of Japan, vol 4, Chugoku (In Japanese). Shibundo, Tokyo
Miyawaki A (1984) Vegetation of Japan, vol 5, Kinki (In Japanese). Shibundo, Tokyo
Nakatsubo T, Kaniyu M, Nakagoshi N, Horikoshi T (1994) Distribution of vesicular-arbuscular mycorrhizae in plants growing in a river floodplain. Bull Jpn Soc Microb Ecol 9:109-117
Niiyama K (1987) Distribution of salicaceous species and soil texture of habitats along the Ishikari River. Jpn J Ecol 37: 163-174 (in Japanese with English summary)
Nykvist N (1962) Leaching and decomposition of litter V. Experiments on leaf litter of *Alnus glutinosa*, *Fagus silvatica* and *Quercus robur*. Oikos 13: 232-248
Oliver BG, Thurman EM, Malcolm RL (1983) The contribution of humic substances to the acidity of colored natural waters. Geochim Cosmochim Acta 47:2031-2035
Petersen RC, Cummins KW (1974) Leaf processing in a woodland stream. Freshwat Biol 4:343-368
River Bureau, Ministry of Land, Infrastructure and Transport (2000, 2001, 2002, 2003, 2005) River discharges year book of Japan. Japan River Association, Tokyo
Rytter R-M (2001) Biomass production and allocation, including fine-root turnover, and annual N uptake in lysimeter-grown basket willows. Forest Ecol Manag 140: 177-192
Rustad LE (1994) Element dynamics along a decay continuum in a red spruce ecosystem in maine, USA. Ecology 75: 867-879
Sampaio A, Cortes R, Leão C (2001) Invertebrate and microbial colonisation in native and exotic leaf litter species in a mountain stream. Int Rev Hydrobiol 86:527-540
Sasaki A (2005) Estimation of the contribution of riparian vegetation to the matter flow in a river basin ecosystem. Ph. D Thesis, Graduate School of Biosphere Science, Hiroshima University, Hiroshima, Japan (in Japanese)
Sasaki A, Nakatsubo T (2003) Biomass and production of the riparian shrub *Salix gracilistyla*. Ecol Civil Eng 6:35-44
Sasaki A, Nakatsubo T (in press) Nitrogen and phosphorus economy of the riparian shrub *Salix gracilistyla* in western Japan. Wetlands Ecol Manag
Scalbert A and Haslam E (1987) Polyphenols and chemical defence of the leaves of *Quercus robur*. Phytochemistry 26: 3191-3195
Schindler DW, Curtis PJ (1997) The role of DOC in protecting freshwaters subjected to climatic warming and acidification from UV exposure. Biogeochemistry 36:1-8
Suberkropp K, Godshalk GL, Klug MJ (1976) Changes in the chemical composition of leaves during processing in a woodland stream. Ecology 57: 720-727
Tahvabnainen L, Rytkönen V-M (1999) Biomass production of *Salix viminalis* in southern Finland and the effect of soil properties and climate conditions on its production and survival. Biomass Bioenerg 16: 103-117
Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. Can J Fish Aquat Sci 37:130-137
Webster JR, Benfield EF (1986) Vascular plant breakdown in freshwater ecosystems. Ann Rev.

Ecol Syst 17: 567-594
White PS (1979) Pattern, process, and natural disturbance in vegetation. Bot Rev 45: 229-299
Yoshikawa M, Hukusima T (1999) Distribution and developmental patterns of floodplain willow communities along the Kinu River, central Japan. Veg Sci 16: 25-37

Fig. 1. Map showing the location (a) and the over view (b) of the study site. White arrow represents flow direction. The area enclosed by dotted line shows zonal stand of *Salix gracilistyla*.

Fig. 2. Mean cumulative amount of dissolved organic carbon (DOC) leached from leaf litter and senescent leaves (a) and green leaves (b) of *Salix gracilistyla*. Vertical bars represent standard deviations (n = 3).

Fig. 3. Mean cumulative amount of total sugar leached from leaf litter and senescent leaves (a) and green leaves (b) of *Salix gracilistyla*. Vertical bars represent standard deviations (n = 3).

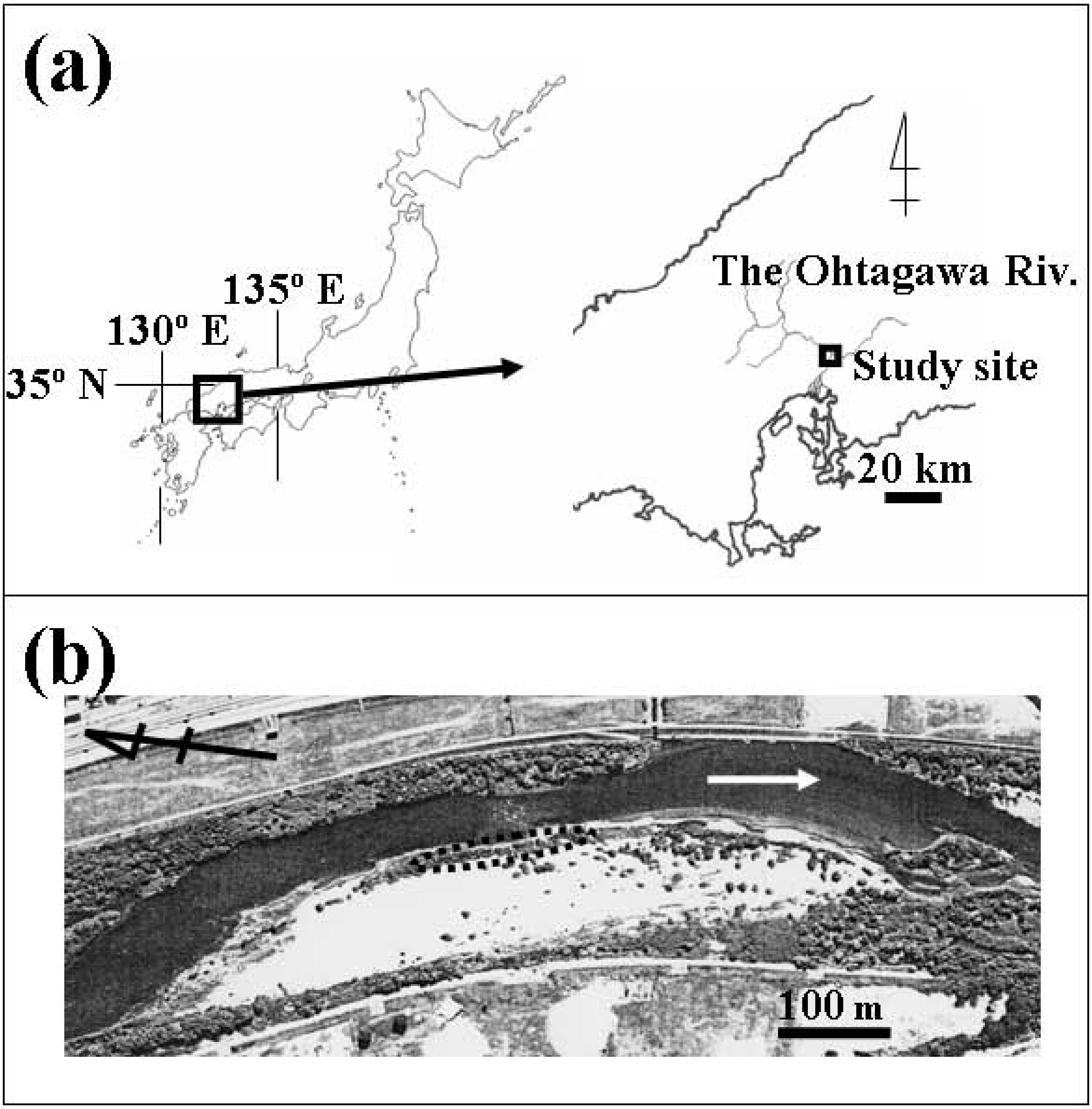
Fig. 4. Mean cumulative amount of polyphenol leached from leaf litter and senescent leaves (a) and green leaves (b) of *Salix gracilistyla*. Vertical bars represent standard deviations (n = 3). The bars are hidden by symbols for leaf litter.

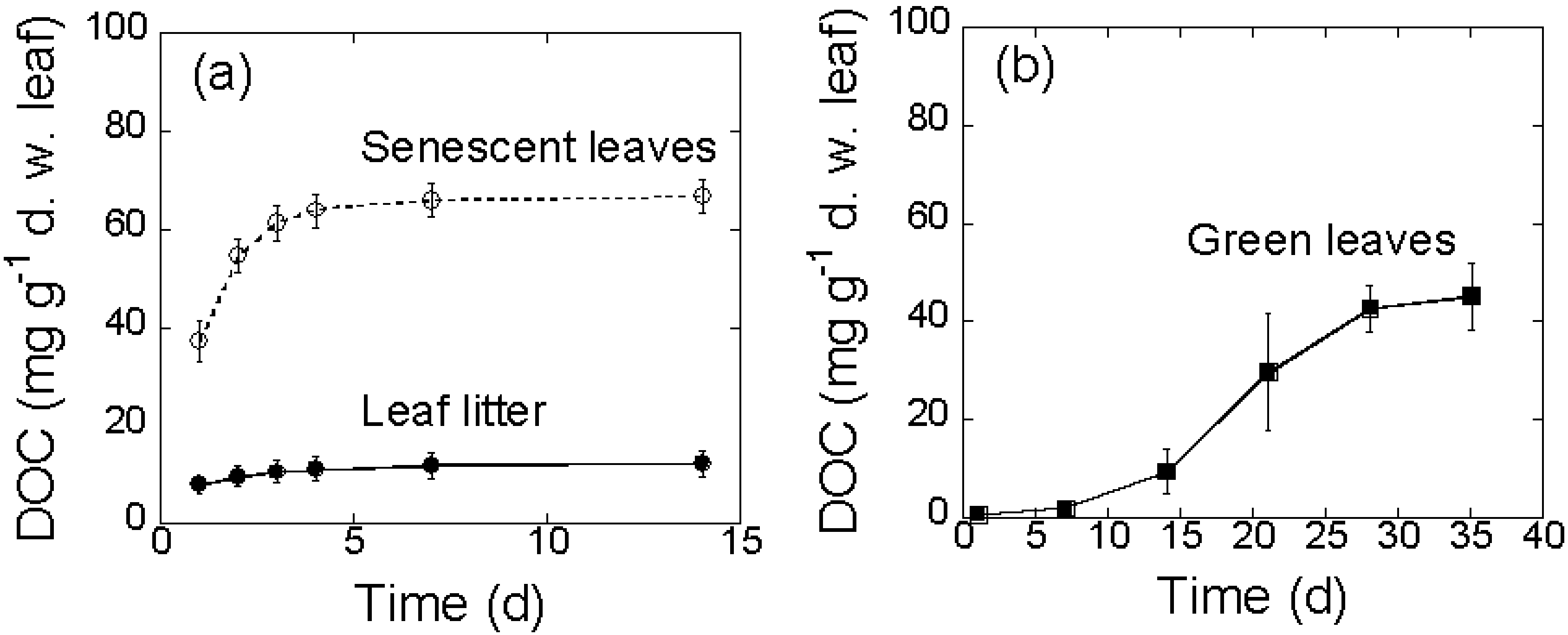
Fig. 5. Time course of degradation of dissolved organic carbon (DOC), total sugar, and polyphenol leached from leaf litter of *Salix gracilistyla*. Vertical bars represent standard deviations (n = 3).

Table 1. Mass or carbon loss (%) of leaves coniferous and deciduous trees by leaching within 24 h after leaf immersion

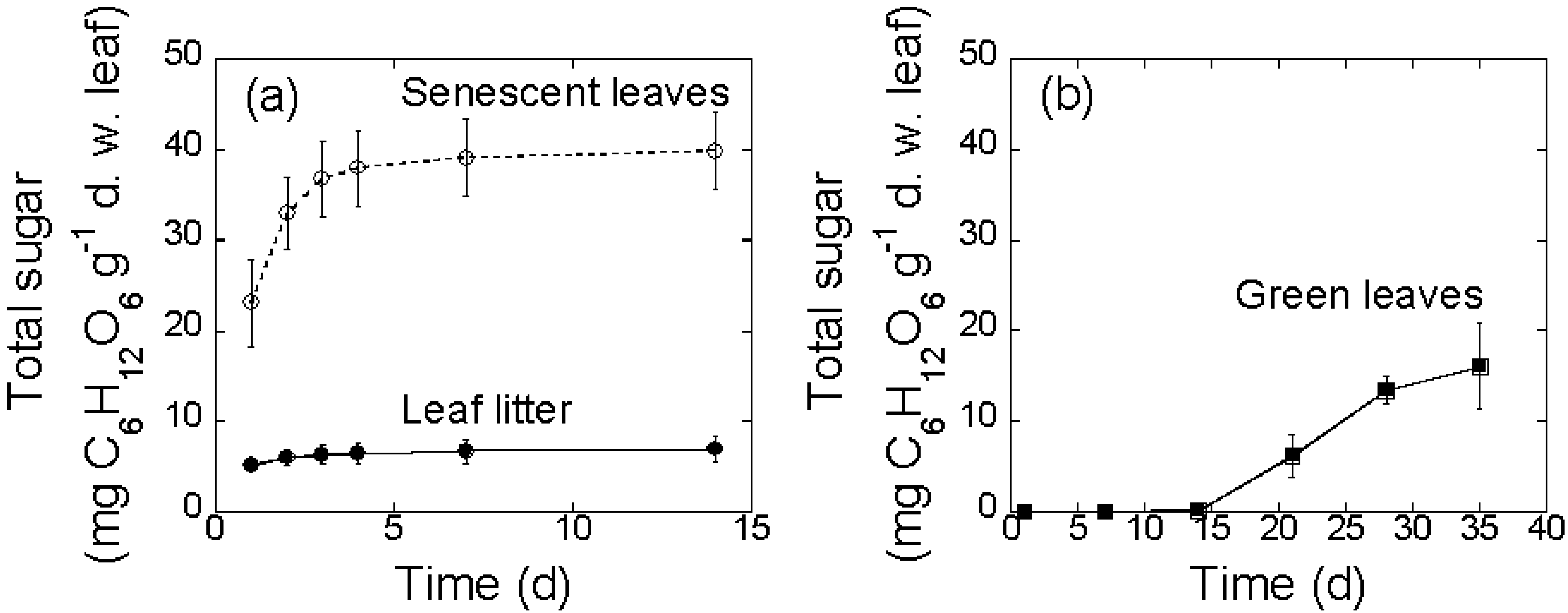
Species	Experimental condition			Mass loss (%)	Carbon loss (%)[1]	Reference
	Leaf condition	Temperature (℃)	Solution			
Coniferous trees						
Pseudotsuga menziesii	Leaf letter[2], air dried	4	Distilled water	-	2	McArthur and Richardson 2002
Thuja plicata	Leaf letter[2], air dried	4	Distilled water	-	1	McArthur and Richardson 2002
Tsuga hetrophylla	Leaf letter[2], air dried	4	Distilled water	-	1	McArthur and Richardson 2002
Deciduous trees						
Acer circinatum	Leaf letter[2], air dried	4	Distilled water	-	5	McArthur and Richardson 2002
Alnus glutinosa	Green[2], air dried	25	Distilled water	12	-	Nykvist 1962
Alnus glutinosa	Green[3], air dried	10	Filtered stream water	20	-	Gessner and Konstanz 1989
Alnus glutinosa	Green[3], fresh	10	Filtered stream water	not detected	-	Gessner and Konstanz 1989
Alnus rubra	Leaf letter[2], air dried	4	Distilled water	-	8	McArthur and Richardson 2002
Fagus silvatica	Brown[2], air dried	25	Distilled water	6	-	Nykvist 1962
Quercus robur	Brown[4], air dried	25	Distilled water	3	-	Nykvist 1962
Salix fragilis	Yellow senescent[3], air dried	10	Filtered stream water	25	-	Gessner and Konstanz 1989
Salix fragilis	Yellow senescent[3], fresh	10	Filtered stream water	not detected	-	Gessner and Konstanz 1989
Salix gracilistyla	Green[4], fresh	15	Purified water	-	0.1	Present study
Salix gracilistyla	Leaf litter[3], air dried	15	Purified water	-	2	Present study
Salix gracilistyla	Yellow senescent[4], fresh	15	Purified water	-	8	Present study

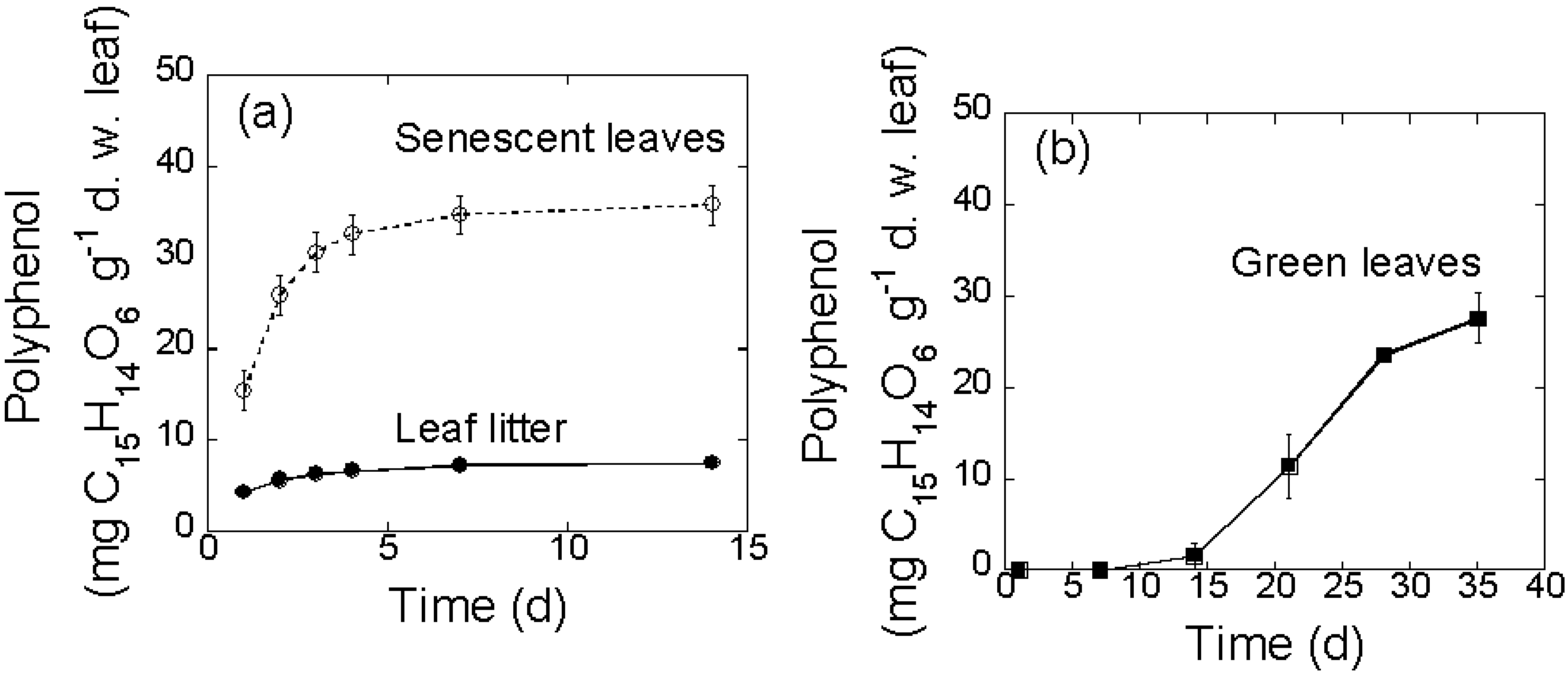
[1] calculated assuming a carbon content in leaf litter of 47%
[2] collected using a litter trap
[3] collected from the ground
[4] collected directly from the tree

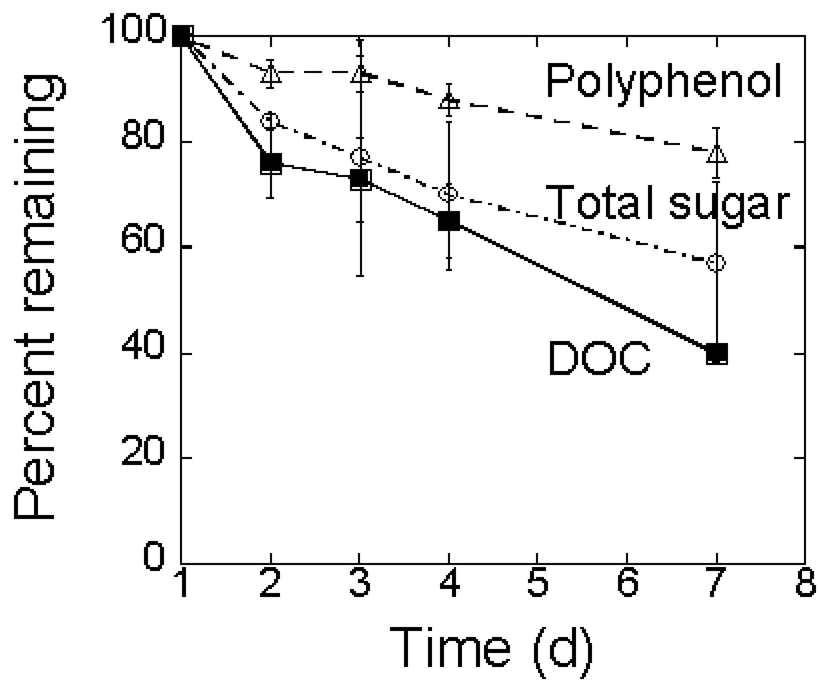

(a)
135° E
130° E
35° N
The Ohtagawa Riv.
Study site
20 km
(b)
100 m



DOC (mg g-1 d. w. leaf)
100
80
60
40
20
0
(a)
Senescent leaves
Leaf litter
0
5
10
15
Time (d)
(b)
Green leaves
0
5
10
15
20
25
30
35
40
Time (d)


Total sugar
(mg $C_6H_{12}O_6$ g^{-1} d. w. leaf)
(a)
Senescent leaves
Leaf litter
Time (d)
0
5
10
15
0
10
20
30
40
50
(b)
Green leaves
Time (d)
0
5
10
15
20
25
30
35
40


(a)
Senescent leaves
Leaf litter
Polyphenol
(mg C15H14O6 g-1 d. w. leaf)
Time (d)
0
10
20
30
40
50
0
5
10
15
(b)
Green leaves
Polyphenol
(mg C15H14O6 g-1 d. w. leaf)
Time (d)
0
10
20
30
40
50
0
5
10
15
20
25
30
35
40



Percent remaining
100
80
60
40
20
0
1
2
3
4
5
6
7
8
Time (d)
Polyphenol
Total sugar
DOC