

# Hydrology and carbon pool characteristics regulate dissolved carbon export in a subtropical forest headwater stream

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**Abstract:** Headwater streams are key pathways for carbon (C) transfer from terrestrial to aquatic ecosystems. Sediments and plant litter constitute major C pools in streams, yet their roles in regulating dissolved carbon (DC) exports remain poorly understood. Here, we investigated dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) concentrations and export through monthly sampling over one year in a subtropical forest headwater stream. DOC export peaked during the wet season ( $98.9 \pm 171.8 \text{ kg}\cdot\text{h}^{-1}$ ), whereas DIC export showed no significant seasonal variation. During the wet season, C pool characteristics were more strongly related to DOC dynamics, whereas during the dry season they were more closely associated with DIC dynamics. DOC concentrations in sediments and plant litter were positively related to stream DOC concentrations, while higher total carbon (TC) storage showed weak relationships with DC exports. These results indicate that C pool characteristics influence stream C dynamics mainly through C quality rather than pool size, and that different C pools exert different effects on DOC and DIC dynamics. However, hydrological variables – especially stream discharge – exerted the strongest control on DC export. Together, these findings indicate that hydrology controls C export, whereas C pools regulate the composition of DC in headwater streams.

Keywords: carbon storage; decay classes; dynamic; litter; sediment

Headwater streams play a critical role in the global carbon (C) cycle by linking terrestrial and aquatic ecosystems and transporting C from surrounding landscapes to downstream waters (Cole et al. 2007; Battin et al. 2023; Tiegs et al. 2024). Due to their close connectivity with adjacent terrestrial environ-

ments, headwater streams receive substantial inputs of organic matter (OM) and dissolved carbon (DC) from surrounding soils and vegetation. Once introduced into the stream environment, C undergoes a series of biogeochemical processes, including microbial metabolism, physicochemical transfor-

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mation, temporary storage, and downstream export (Polis et al. 1997; Casas-Ruiz et al. 2016). DC, including dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC), represents the dominant fraction of C transported in stream water. Although individual headwater streams are small, their vast abundance collectively accounts for over 70% of the total length of the river network, making them a significant component of the global C balance (Boyero et al. 2011; Downing et al. 2012; Marx et al. 2017). Understanding the dynamics and driving mechanisms of DC in headwater streams is therefore essential for quantifying C export at the terrestrial–aquatic interface and improving predictions of regional and global C cycling.

DC export in headwater streams is driven not only by the continuous input of terrestrial OM, but also by characteristics and biogeochemical behaviour of C pools within the stream channel (Gregory et al. 1991; Vachon et al. 2021). Stream sediments represent relatively stable C reservoirs with slow turnover rates. Interactions at the sediment–water interface, including adsorption–desorption processes and microbial metabolism, can regulate DC concentrations in the water column (Babakhani et al. 2025). These processes are closely governed by the physicochemical properties of the sediments and the aquatic environment (Gao et al. 2021). Specific ultraviolet absorbance (*SUVA*), for example, provides important information about the aromaticity, composition and bioavailability of dissolved OM, thereby linking C source characteristics to C cycling processes in aquatic systems (Weishaar et al. 2003). In contrast, plant litter represents a more dynamic and reactive C pool. The types of plant litter differ markedly in chemical composition, nutrient content and decomposition rates, which in turn influence their contributions to C transport and transformation within streams (Stelzer et al. 2014; Wymore et al. 2018). Leaves, which have higher concentrations of water-soluble OM and lower lignin content than woody debris, decompose more rapidly and are more readily transported by streamflow, thereby contributing to short-term fluctuations in local C export (Yue et al. 2016; Zhang et al. 2019). In addition, plant litter undergoes sequential decomposition upon entering stream environments (Battin et al. 2008). The extent of litter decay not only reflects its nutrient release potential but also modulates microbial respiration rates, alters dissolved OM composition

and contributes to fluctuations in stream biogeochemistry (Robbins et al. 2023). Despite these insights, most previous studies have focused primarily on terrestrial C inputs, while the regulatory roles of sediment and plant litter C pools within streams remain insufficiently understood. As a result, the mechanisms by which these C pools influence DC export in headwater streams remain poorly constrained (Wei et al. 2024; Wang et al. 2025).

In addition to C pool characteristics, hydrological and physicochemical characteristics play key roles in regulating C transport and transformation in streams. Hydrological factors such as discharge and flow velocity directly influence C mobilisation, dilution and downstream transport, while physicochemical conditions including pH, dissolved oxygen (DO) and temperature affect C transformation processes (Schulte et al. 2011; Salimon et al. 2013; Kopáček et al. 2018). For instance, DOC tends to remain in a dissolved state under low pH conditions, thereby facilitating its downstream transport (Laudon et al. 2011). Flow rate not only influences the diffusion and dilution of C but also affects the frequency and intensity of interactions between DC and in-stream C pools (Gao et al. 2024). These interactions form a multifactorial, coupling-driven regulatory network that shapes DC behaviour. Seasonal rainfall can further enhance terrestrial OM inputs and alters stream physicochemical properties, leading to pronounced seasonal variability in DOC and DIC export (Raymond, Saiers 2010; Song et al. 2020). Consequently, DC dynamics in headwater streams are shaped by complex interactions between hydrological processes and C pool characteristics.

To better understand these interactions, we investigated DC dynamics in a subtropical forest headwater stream based on monthly sampling over one year. We quantified C characteristics of sediments and plant litter, including C concentrations, storage and litter decomposition stages, and integrated these measurements with hydrological and physicochemical parameters to identify the key drivers of DC export. Specifically, this study addresses the following questions: (i) Do DOC and DIC exhibit distinct seasonal dynamics in headwater streams? (ii) How do C characteristics of sediments and plant litter influence DC concentrations and export? (iii) What is the relative importance of in-stream C pools and hydrological conditions in regulating DC export?

## MATERIAL AND METHODS

**Study site.** The study was conducted in a subtropical forest catchment in Sanming City, Fujian Province (26°19'N, 117°36'E), characterised by a mean annual temperature of 19.3 °C and the mean annual precipitation of 1 610 mm. The closed headwater catchment contains a single perennial stream (length: 4 859 m; flow direction: southwest to northeast) with a narrow channel draining a 5.64 km<sup>2</sup> watershed. Located in a remote forested area with minimal anthropogenic disturbance, this stream provides an ideal natural experimental system. Its primary hydrological input is rainfall

recharge without glacial influence, exhibiting discharge patterns reflective of the subtropical monsoon climate, with distinct wet (March–August) and dry seasons. Riparian vegetation is dominated by broad-leaved evergreen forest, primarily *Castanopsis carlesii*, with associated species including *Cunninghamia lanceolata* and *Pinus massoniana* (Figure 1) (Zhao et al. 2023).

Sampling reaches ( $n = 17$ ), defined as stream sections between sampling points, were established from stream source to mouth based on integrated assessment of: (i) tributary confluences, (ii) transitions in riparian forest composition, (iii) spatial distance along the channel, and (iv) field accessibil-

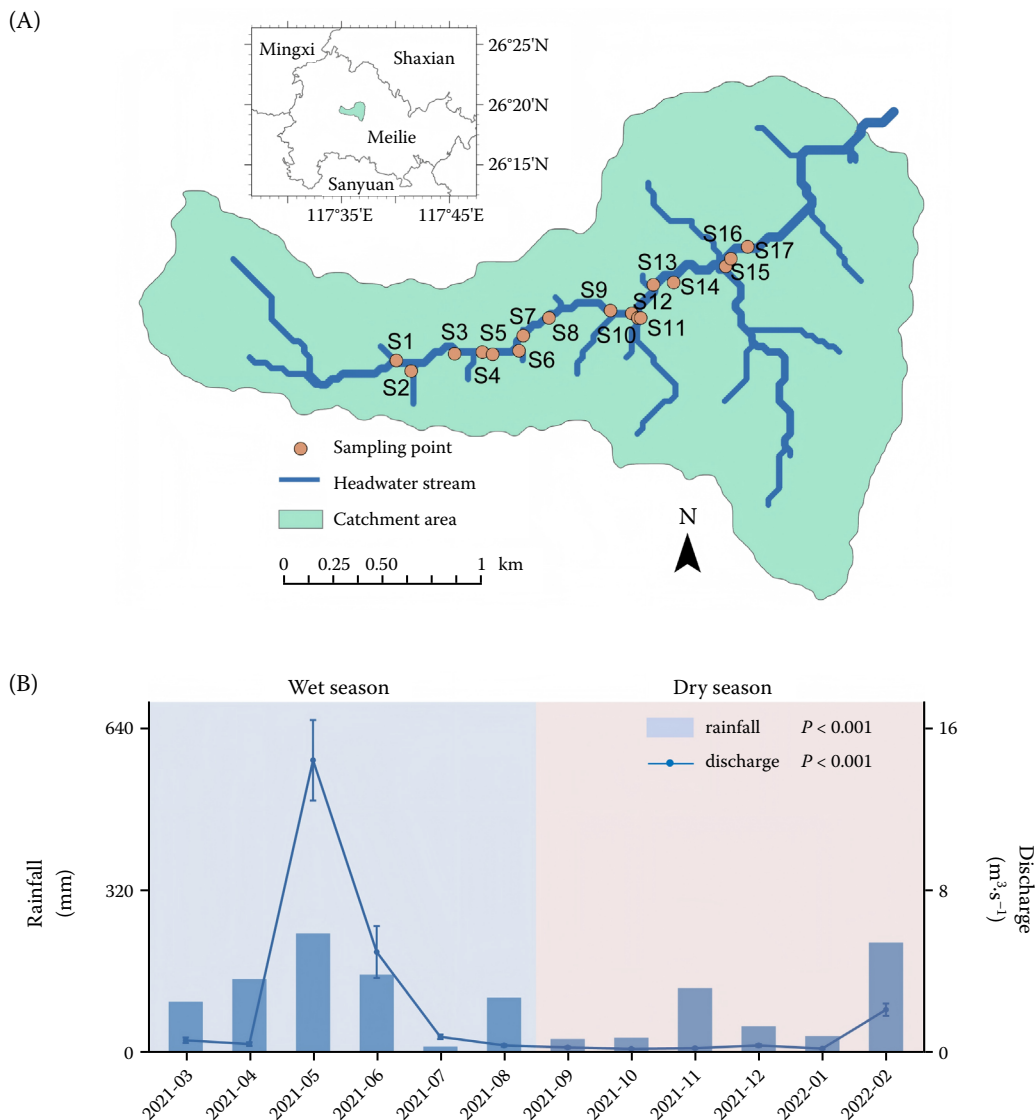


Figure 1. Study area and hydrological conditions during the study period: (A) Location of the study area and sampling points in the headwater stream in Sanming, Fujian Province, China; (B) temporal variation in rainfall and stream discharge during the study period

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ity. Subdivision of reaches was designed to maintain internal physical consistency. All reaches were georeferenced using a GPS device (GPS-A8, ZL, China) and visibly marked in the field [Table S1 in the Electronic Supplementary Material (ESM)].

**Sample collection.** Monthly sampling campaigns were conducted across all 17 reaches from March 2021 to February 2022 ( $n = 12$  sampling events). Water, sediment, and plant litter samples were collected at each reach. Water samples were taken from mid-channel using 50 mL centrifuge tubes, with care taken to minimise sediment resuspension. Samples were immediately preserved in a portable refrigerator (temperature maintained at approximately 4 °C) and transported to the laboratory for analysis.

To account for spatial heterogeneity in sediment distribution, three replicate quadrats (1 m × channel width) were established per reach, delineated by sediment depth profiles extending to parent bedrock. Sediment samples were collected following a standardised five-point sampling protocol using plastic spatulas, then transferred to 250 mL polyethylene bottles pre-rinsed with deionised water. Three random depth measurements were recorded per quadrat (total  $n = 9$  measurements per reach).

In each stream reach, three quadrats (1 m × channel width) were randomly established to collect plant litter. To avoid repeated sampling at the same location, the centre point of each quadrat was marked and recorded along the stream bank. Within each quadrat, plant litter was collected manually or using a 2 mm mesh net (Figure S1 in the ESM). The collected material included leaves, twigs (< 1 cm diameter), and fine woody debris (FWD, 1–10 cm diameter). Coarse woody debris was excluded due to its slow decomposition rate and limited nutrient release. To ensure complete sampling, litter collection was conducted down to the bedrock surface, where the channel substrate consisted of exposed bedrock, or to the base of the sediment layer, where sediments were silty (Hu et al. 2023). All plant litter samples were placed in polyethylene bags and transported to the laboratory for drying. To track changes in plant litter storage, a quadrat-based repeated sampling approach was used across multiple quadrats with monthly sampling throughout the year.

During each sampling campaign, pH, DO, and electrical conductivity (EC) were measured in-stream using a portable multiparameter analyser

(YSI ProPlus, Xylem, USA) at all 17. Flow rate was measured with a streamflow meter, while water depth and channel width were recorded per reach (Table S1 in the ESM). In addition, three tipping-bucket rain gauges (SL3-1, Shanghai Meteorological Instrument Factory Co., China) were installed in an open area 15 m from reach 8 (midstream position) to collect monthly precipitation data.

**Sample analysis.** Stream water samples were filtered through a 0.45 µm membrane filters. The TC and DOC concentrations were quantified via combustion-catalytic oxidation at 680 °C using a Total Organic Carbon analyser (TOC-L CPH, Shimadzu, Japan). DIC concentrations were calculated as the difference between TC and DOC. Sediment samples were transferred to polythene containers and thoroughly mixed. Fresh samples were divided, with a portion used for moisture content determination, while the rest were air-dried in a well-ventilated area. After drying, macroscopic impurities (e.g. weeds, root detritus) were manually removed prior to gravimetric measurement. The dried sediments were pulverised with an agate mill and sieved through a 100-mesh sieve for subsequent analysis.

Plant litter samples were classified by type (leaves, twigs, and FWD) and decay class, then oven-dried at 65 °C until a constant weight was achieved. Dry weights were recorded, followed by chopping, pulverisation (using a stainless-steel mill), and sieving through a 60-mesh sieve. FWD decay classes were defined as: Decay class 1: Structurally intact wood; bark firmly attached; no visible decomposition. Decay class 2: Initial decomposition; partial bark loss; texture remains hard. Decay class 3: Extensive bark loss; wood softening; fungal/moss colonisation evident. Decay class 4: Easily punctured; residual hard zones; no bark; abundant epiphytes. Decay class 5: Complete structural loss; friable to powder; no residual hardness (Burrows et al. 2012).

Sediment TC was analysed via dry combustion using an elemental analyser (vario EL III, Elementar, Germany). Plant litter TC was determined with the same instrument model, following solid sample combustion protocols. For sediment DOC: 10 g homogenised sample was mixed with 50 mL deionised water, shaken (25 °C, 30 min), settled, and filtered through 0.45 µm membranes. For plant litter DOC: milled samples were mixed at a 1:80 solid-to-liquid ratio, shaken (30 min), centrifuged (30 min), and supernatant membrane-filtered (0.45 µm).

DOC absorbance was measured at 254 nm, 260 nm, 360 nm, and 365 nm (UV-2450 spectrophotometer, Shimadzu, Japan).  $SUVA_\lambda$  was calculated according to Equation (1):

$$SUVA_\lambda = \frac{UV_\lambda}{DOC} \times 100\% \quad (1)$$

where:

$SUVA_\lambda$  – spectral indicator reflecting the chemical nature of DOC ( $L \cdot mg^{-1} \cdot m^{-1}$ );

$UV_\lambda$  – absorbance of DOC at wavelength  $\lambda$  nm;

DOC – dissolved organic carbon concentration ( $mg \cdot L^{-1}$ ).

**Statistics and analysis of data.** To quantify sediment storage in the stream channel, the channel was approximated as a rectangular prism to estimate sediment volume based on measurements of stream length, width, and sediment depth. Additional parameters, including sediment moisture content and sediment density, were also calculated. Plant litter storage was estimated separately using quadrat sampling.

Moisture content ( $M$ ; %) was calculated according to Equation (2):

$$M = \frac{m - (m_2 - m_1)}{m} \times 100\% \quad (2)$$

where:

$m$  – fresh sample mass (g);

$m_1$  – mass of ceramic crucible (g);

$m_2$  – combined mass of the crucible and dried sample (g).

Sediment volume ( $V$ ;  $m^3$ ) was calculated according to Equation (3):

$$V = L \times W \times D \quad (3)$$

where:

$L$  – stream length (m);

$W$  – stream width (m);

$D$  – sediment depth (m).

Sediment density ( $\rho$ ;  $g \cdot cm^{-3}$ ) was calculated according to Equation (4):

$$\rho = \frac{m_3}{(1 - M)V_3} \quad (4)$$

where:

$m_3$  – dry sediment mass (g);

$M$  – moisture content (%);

$V_3$  – sediment volume ( $m^3$ ).

Sediment storage ( $R_1$ ;  $kg \cdot m^{-2}$ ) was calculated according to Equation (5):

$$R_1 = \frac{V \times \rho}{S} \times 0.001 \quad (5)$$

where:

$V$  – sediment volume ( $m^3$ );

$\rho$  – sediment density ( $g \cdot cm^{-3}$ );

$S$  – stream surface area ( $m^2$ ).

Plant litter storage ( $R_2$ ;  $g \cdot m^{-2}$ ) was calculated according to Equation (6):

$$R_2 = \frac{X}{Y} \quad (6)$$

where:

$X$  – total dry mass in the quadrat (g);

$Y$  – quadrat surface ( $m^2$ ).

Before statistical analysis, raw data were tested for normality and homoscedasticity. Variables that did not meet these assumptions were log-transformed. Linear models were fitted to examine how C in sediments and plant litter influences stream C dynamics, with stream DOC and DIC concentrations and export as response variables. Explanatory variables included C concentrations and storage in sediments and plant litter,  $SUVA$  values, FWD storage across different decay classes, and hydrological and physicochemical parameters of stream water (Table S2 in the ESM). To evaluate the influence of hydrological conditions on stream C dynamics, two-sample  $t$ -tests were used to compare C-related variables between the 'wet' and 'dry' groups. Here, 'wet' and 'dry' groups represent sampling periods characterised by higher and lower rainfall and stream discharge, respectively. Differences in FWD storage among decay classes were tested using Tukey's HSD test to determine whether C storage differed among decomposition stages, which could subsequently influence stream C concentrations and export. To further identify key predictors influencing stream DOC and DIC export, SHAP (Shapley Additive Explanations) analysis was conducted

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based on models implemented in the 'CatBoost' package. All statistical analyses were conducted in R (Version 4.4.2., 2024).

## RESULTS

**Seasonal dynamics of stream DOC and DIC.** Stream DC exhibited clear seasonal patterns. DOC concentrations and export exhibited pronounced seasonal variability, with significantly higher DOC concentrations and export observed during the wet season ( $16.2 \pm 25.6 \text{ mg}\cdot\text{L}^{-1}$  and  $98.9 \pm 171.8 \text{ kg}\cdot\text{h}^{-1}$ ) compared to the dry season ( $1.9 \pm 0.7 \text{ mg}\cdot\text{L}^{-1}$  and  $3.9 \pm 8.1 \text{ kg}\cdot\text{h}^{-1}$ ; Figure 2A, C). DOC dynamics displayed considerable heterogeneity throughout the wet season (Figure 2C). In contrast, DIC dynamics showed weaker seasonal variability. Mean DIC concentration was  $2.9 \pm 1.9 \text{ mg}\cdot\text{L}^{-1}$  and export averaged  $6.7 \pm 13.4 \text{ kg}\cdot\text{h}^{-1}$ . However, DIC concentrations were significantly higher during the dry season ( $4.0 \pm 1.4 \text{ mg}\cdot\text{L}^{-1}$ ) than during the wet season ( $1.5 \pm 1.5 \text{ mg}\cdot\text{L}^{-1}$ ; Figure 2B). These results indicate contrasting seasonal dynamics between DOC and DIC, with DOC more strongly influenced by wet-season hydrological processes.

**Effects of sediment C characteristics on stream C dynamics.** Sediment C concentrations and storage exhibited significant seasonal variation. Sediment DOC concentrations were positively correlated with stream DOC concentrations (Figure S2A in the ESM) but negatively related to stream DOC export (Figure 3A). In contrast, sediment DIC concentrations were negatively associated with both stream DIC concentration and export (Figure S2B in the ESM; Figure 3B). Sediment TC concentration exhibited negative relationships with both DOC and DIC concentrations and export (Figure S2C, D in the ESM; Figure 3C, D), indicating that higher sediment C content may limit the mobilisation of DC forms in the stream. By comparison, sediment TC storage showed relatively weak relationships with stream C variables (Figure S2E, F in the ESM; Figure 3E, F). In addition, stream DOC concentrations increased with increasing  $SUVA_{254}$  and  $SUVA_{260}$  values in sediments (Table 1). Overall, these results suggest that sediment C characteristics contribute to regulating stream C dynamics, although their effects differ among C forms.

**Effects of plant litter C characteristics on stream C dynamics.** Plant litter contained substantially higher DOC, DIC, and TC concentra-

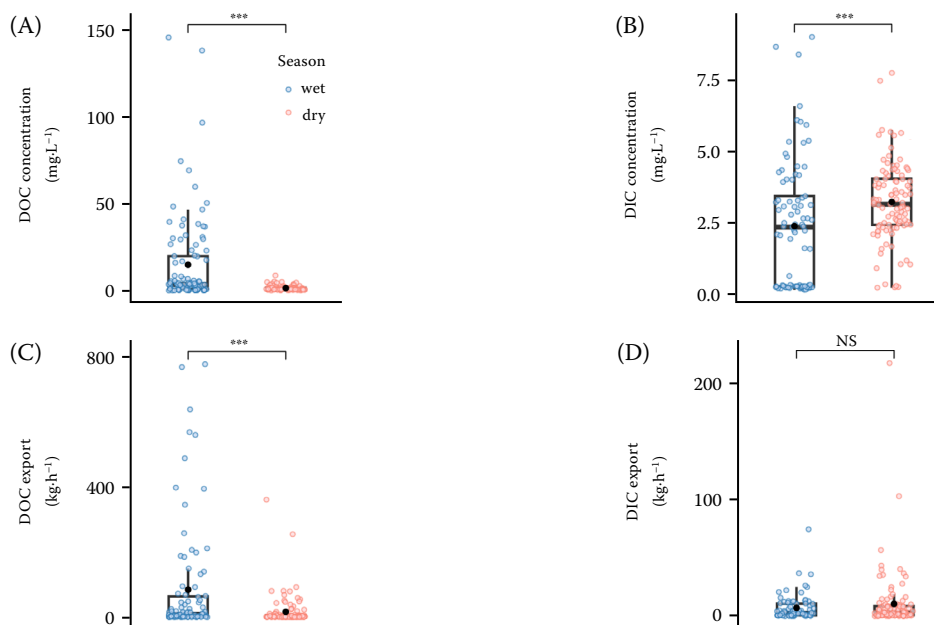


Figure 2. Seasonal variations in concentration and export of dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) in the headwater stream: (A) Stream DOC concentration; (B) stream DIC concentration; (C) stream DOC export; (D) stream DIC export

Asterisks – significant differences between seasons: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , NS – non-significant difference; box-plots – the median and interquartile range; solid dots – mean values (coloured by season)

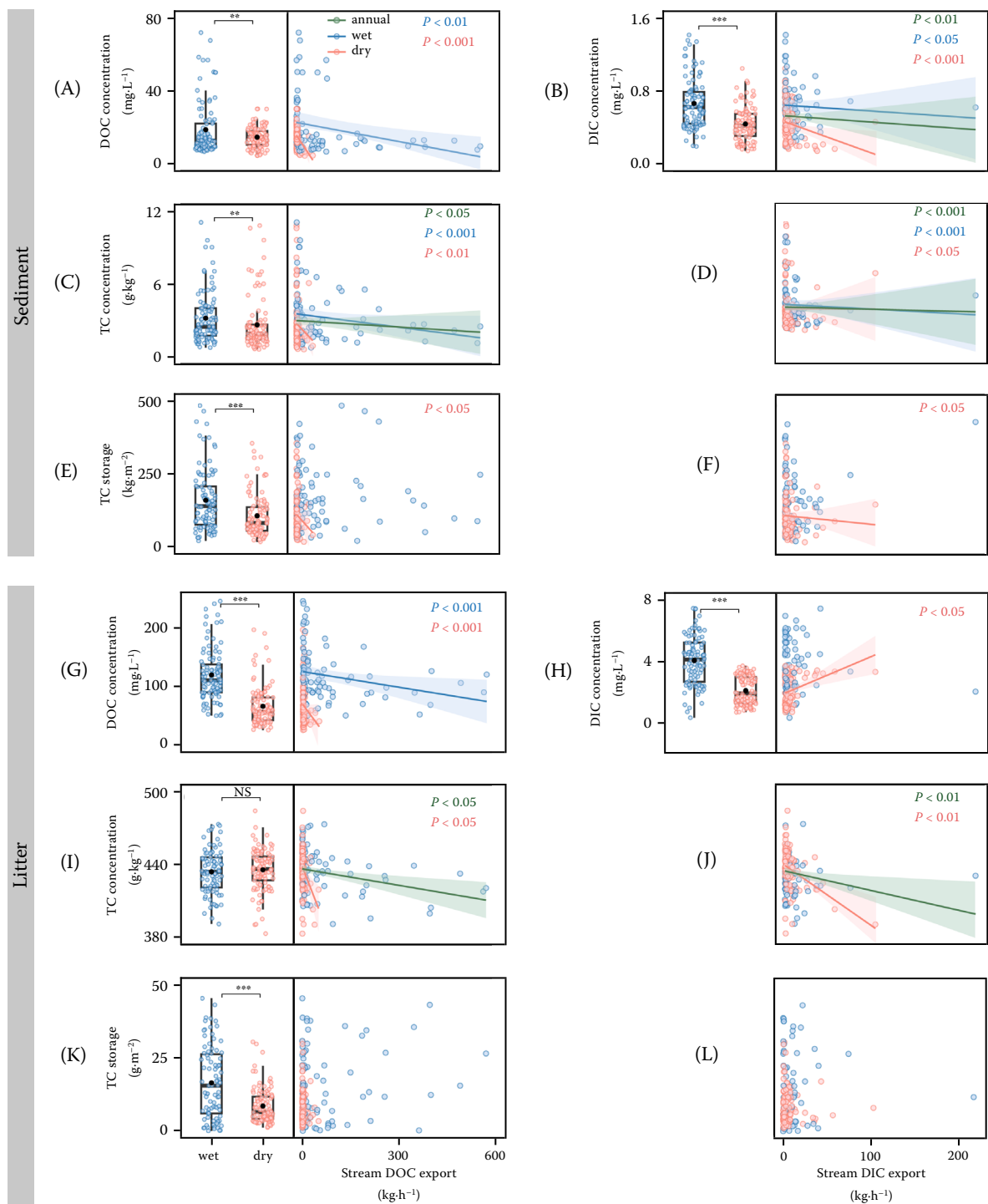
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Figure 3. Seasonal variations in concentrations and storage in sediments and plant litter, and their relationships with stream carbon (C) export: (A, B) Dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) concentrations in sediments; (C, D) total carbon (TC) concentration in sediments; (E, F) TC storage in sediments; (G, H) DOC and DIC concentrations in plant litter; (I, J) TC concentration in plant litter; (K, L) TC storage in plant litter

Asterisks – significant differences between wet and dry seasons: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , NS – non-significant difference; blue and red points – measurements from the wet and dry seasons, respectively; green lines – relationships based on the annual dataset; boxplots – the median and interquartile range; black dots – mean values; for each row, the left panels show seasonal comparisons between wet and dry periods, and the right panels show relationships between C variables and stream C export; linear regression lines and shaded areas represent fitted relationships and 95% confidence intervals

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Table 1. Effects of specific UV absorbance (*SUVA*) of sediment and plant litter [leaves, twigs, and fine woody debris (FWD)] on stream dissolved organic carbon concentrations – estimates (i.e. model slopes) and significant effects are reported

Sample type	<i>SUVA</i> <sub>254</sub>		<i>SUVA</i> <sub>260</sub>		<i>SUVA</i> <sub>360</sub>		<i>SUVA</i> <sub>365</sub>	
	estimate	<i>P</i>	estimate	<i>P</i>	estimate	<i>P</i>	estimate	<i>P</i>
Sediment	15.3	< 0.001	7.7	< 0.001	−0.1	1.0	−0.1	1.0
Leaves	−1.3	0.3	3.9	< 0.001	0.4	< 0.001	0.4	< 0.001
Twigs	1.8	0.1	3.6	< 0.001	0.3	< 0.001	0.3	< 0.001
FWD	0.4	0.5	0.8	< 0.01	0.3	< 0.001	0.5	< 0.001

tions than sediments, although sediments exhibited greater TC storage. Most litter C variables showed clear seasonal variation, with higher DOC and DIC concentrations and TC storage during the wet season, while TC concentration varied less strongly (Figure 3G–I, K). In the wet season, leaves had significantly higher DOC and DIC concentrations than twigs and FWD (Figure S4A, B in the ESM), whereas FWD exhibited lower TC concentration and storage than leaves and twigs (Figure S4A, D in the ESM).

These differences likely reflect contrasts in chemical composition among litter components.

Regression analyses revealed significant relationships between litter C characteristics and stream C dynamics. Higher DOC concentrations in litter were associated with increased stream DOC concentrations (Figure S3A in the ESM). In contrast, higher TC concentrations in leaves corresponded to reduced stream DOC export (Figure 4F), whereas higher TC concentrations in twigs were linked

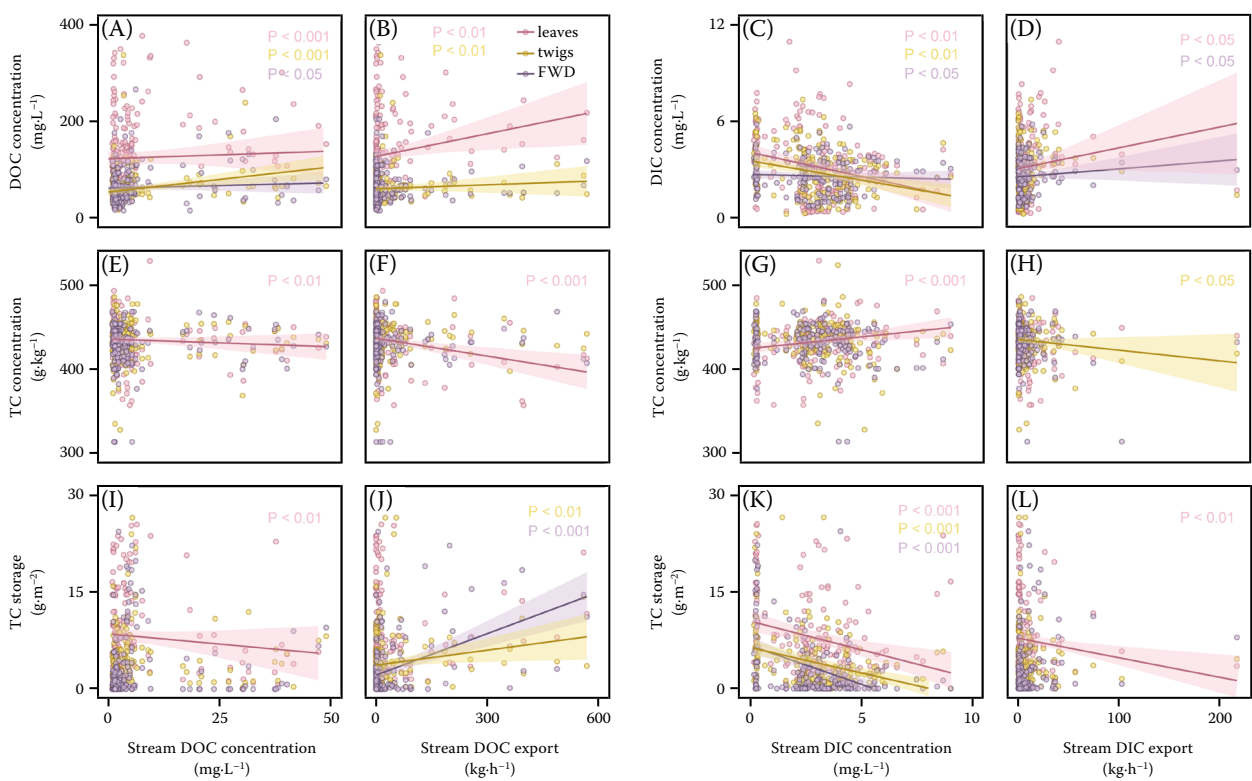


Figure 4. Relationships between carbon (C) characteristics of different plant litter types and stream C dynamics: (A, B, E, F, I, J) show relationships between plant litter C characteristics [dissolved organic carbon (DOC) concentration, total carbon (TC) concentration, and TC storage] and stream DOC concentration and export, respectively; (C, D, G, H, K, L) show relationships between plant litter C characteristics [dissolved inorganic carbon (DIC) concentration, TC concentration, and TC storage] and stream DIC concentration and export, respectively

Points represent measurements from different plant litter types: red – leaves, yellow – twigs, purple – fine woody debris (FWD); linear regression lines and shaded areas represent fitted relationships and 95% confidence intervals

to lower stream DIC export (Figure 4H). Several litter C variables were also negatively correlated with stream DIC concentrations (Figure 4C, K). Higher  $SUVA_{260}$ ,  $SUVA_{360}$ , and  $SUVA_{365}$  values in litter were positively associated with stream DOC concentrations (Table 1).

FWD storage varied among decay classes and between seasons (Figure 5A). Storage was generally higher in the wet season than in the dry season across all decay classes. During the wet season, storage in decay class 1 was significantly higher than in classes 2, 3, and 5, whereas during the dry season storage in decay class 2 exceeded that in classes 4 and 5. Storage in several decay classes was positively associated with stream DOC concentration and

export (Figure 5B, D). Similarly, storage in decay classes 1 and 2 was positively related to stream DIC exports but negatively related to DIC concentration (Figure 5C, E). These results suggest that both the quantity and decomposition stage of FWD may influence stream C dynamics.

**Effects of hydrological and physicochemical variables.** Hydrological and physicochemical variables were strongly associated with variations in stream C dynamics. Rainfall was negatively related to both DOC and DIC concentrations (Figure 6A, C), whereas stream discharge and flow rate were positively associated with DOC and DIC export (Figure 6B, D). These patterns indicate that increased water flow enhances the transport of DC

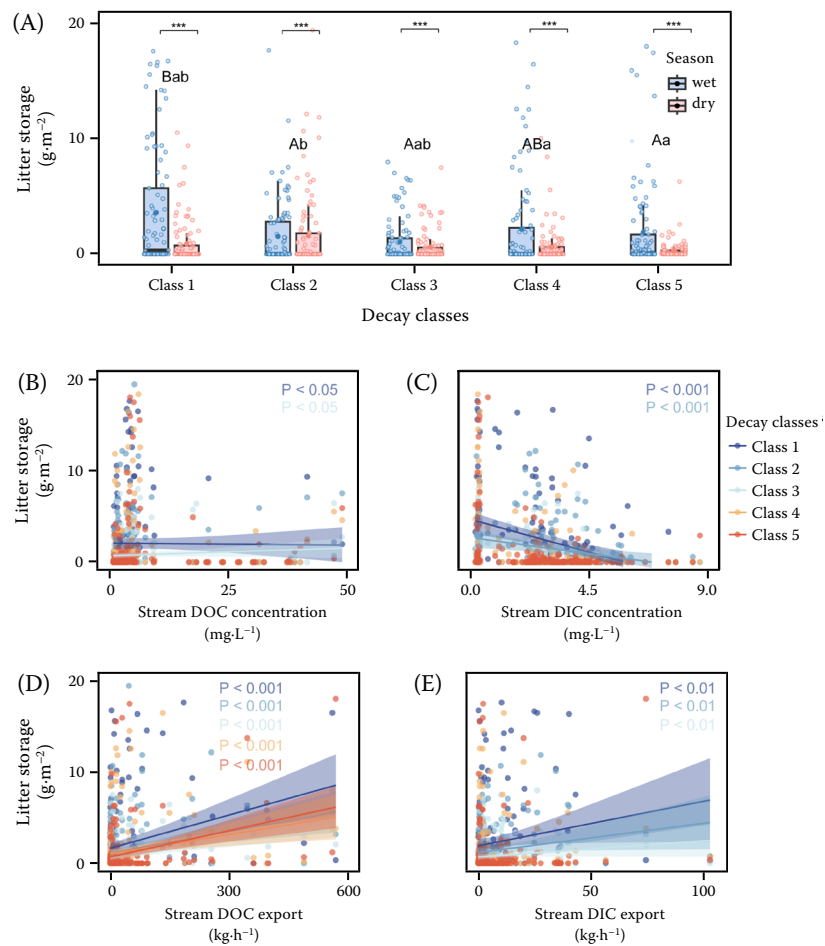


Figure 5. Seasonal variations in fine woody debris (FWD) storage across decay classes and its relationships with stream carbon dynamics: (A) Seasonal differences in FWD storage among five decay classes; (B, C) relationships between FWD storage and stream dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) concentrations; (D, E) relationships between FWD storage and stream DOC and DIC export

Asterisks – significant differences between seasons: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ; boxplots – median and interquartile range; solid dots – mean values (coloured by season); uppercase letters – significant differences among decay classes in the wet season; lowercase letters – differences in the dry season ( $\alpha = 0.05$ ); lines and shaded areas represent linear fits and 95% confidence intervals

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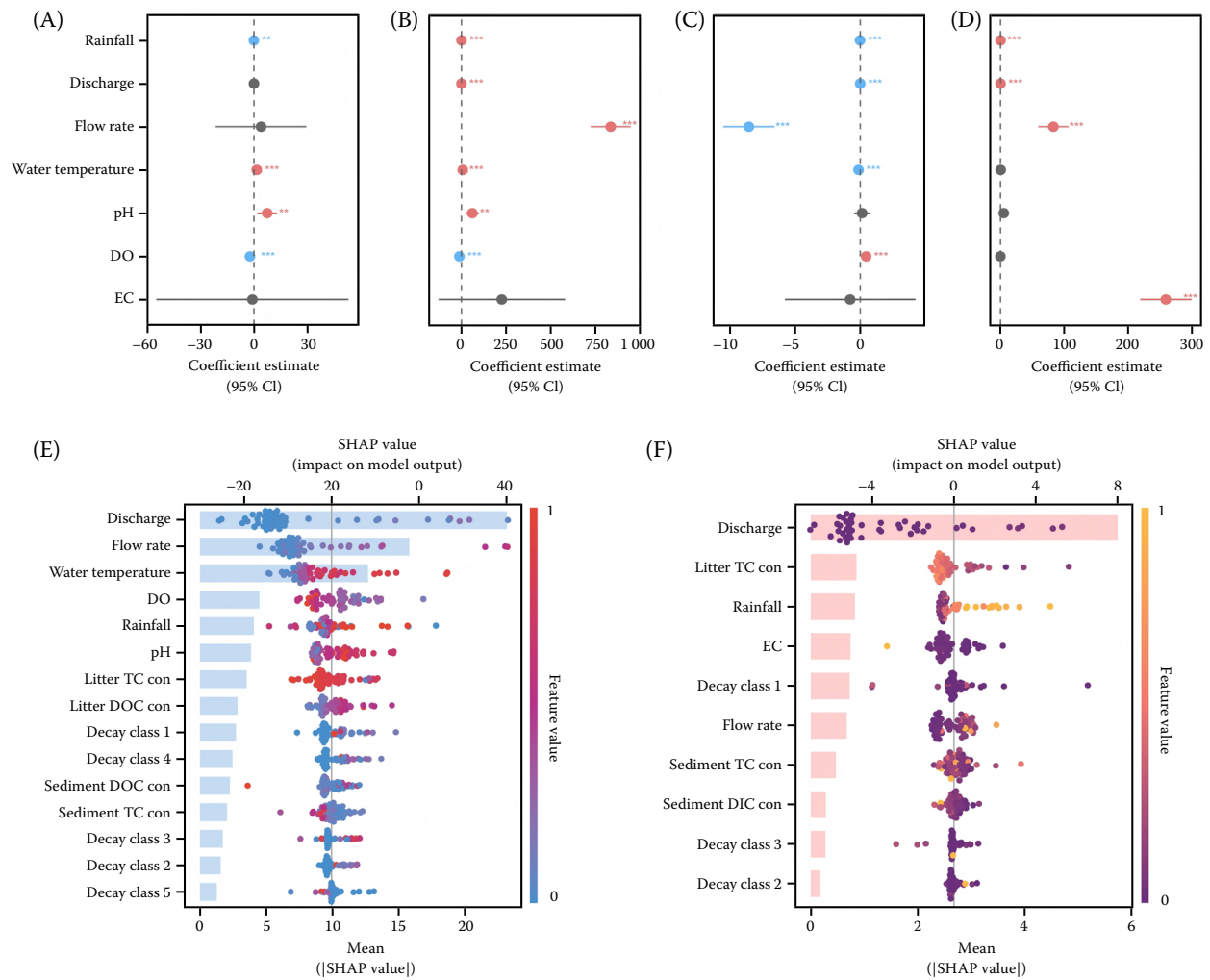


Figure 6. Effects of environmental variables on stream dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) dynamics: (A–D) Estimated effects of environmental variables on stream DOC and DIC concentrations and export derived from linear models – panels (A) and (C) show effects on DOC and DIC concentrations, respectively, whereas panels (B) and (D) show effects on DOC and DIC export

Points – coefficient estimates; horizontal bars – 95% confidence intervals; red, blue, and grey colours – positive, negative, and non-significant effects, respectively (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ); (E, F) SHAP (Shapley Additive Explanations) summary plots showing the relative importance of predictors influencing DOC export (E) and DIC export (F); features are ranked by their mean absolute SHAP values, indicating their contribution to model output; point colours represent feature values (low to high); con – concentration

from the catchment to the stream. Water temperature and pH were positively correlated with DOC concentration, whereas DO showed negative relationships with DOC (Figure 6A). In contrast, DIC concentrations decreased with increasing water temperature but increased with higher DO levels (Figure 6C). Together, these contrasting responses suggest that DOC and DIC are governed by different environmental drivers in the stream.

SHAP analysis further quantified the relative importance of variables influencing DOC and DIC

export (Figure 6E, F). Hydrological variables, particularly stream discharge, exhibited the strongest contribution to DOC export, followed by flow rate and water temperature. For DIC export, discharge and litter TC concentration emerged as the most influential predictors. Overall, hydrological variables explained a larger share of variability in stream C export than C characteristics of sediments and plant litter, underscoring the dominant role of hydrological processes in regulating C transport in headwater streams.

## DISCUSSION

**Seasonal controls on DC dynamics.** Seasonal hydrological variability strongly influenced the mobilisation of C from in-stream pools. Increased rainfall during the wet season enhanced terrestrial OM inputs and intensified soil erosion, thereby increasing the delivery of OM to headwater streams (Coulson et al. 2022). Simultaneously, greater litter inputs combined with rainfall-driven leaching enhanced the release of DOC from plant litter into the aquatic system. This effect was particularly pronounced for leaf litter, owing to its higher content of low-molecular-weight, readily soluble compounds and its less lignified, more permeable structure, which together promote water infiltration and DOC mobilisation (Yoshimura et al. 2010). Despite strong seasonal inputs, TC concentration in plant litter remained relatively stable, likely reflecting a dynamic balance between high C inputs and accelerated decomposition during the wet season, and reduced inputs and decomposition rates during the dry season (Hao et al. 2022).

DOC derived from sediments and plant litter constituted a primary source of stream DOC, with leaching from these C pools elevating stream DOC concentrations (Meyer et al. 1998). However, DOC export was predominantly regulated by water discharge.

Although stream margins and low-velocity zones rich in plant litter and sediment often exhibited elevated DOC concentrations (Wohl et al. 2017), reduced flow rates and prolonged water residence times constrained mass transfer, resulting in lower DOC export. In contrast to DOC, DIC dynamics appeared to be more closely associated with in-stream mineralisation processes under low-flow conditions. Reduced rainfall during the dry season likely limited vertical mixing and promoted the accumulation of respiration-derived CO<sub>2</sub> produced during OM degradation in sediments and benthic zones (Argerich et al. 2016; Coulson et al. 2022). Consequently, higher DIC concentration under low discharge in the dry season, contrasted with low concentration but higher discharge in wet season, maintained a dynamic balance in annual DIC export (Rehn et al. 2023).

**C pool characteristics regulate DOC and DIC dynamics.** Beyond seasonal inputs, the chemical composition of C pools played a key role in regulating DC dynamics. Elevated *SUVA*<sub>254</sub> and *SUVA*<sub>260</sub>

values in sediment DOC suggest a higher proportion of aromatic and humic substances derived from terrestrial inputs (Chen, Hur 2015; McKnight et al. 2001). These compounds are typically more refractory and less bioavailable, yet they may accumulate in sediments and contribute to DOC concentrations in overlying stream water through gradual leaching or episodic resuspension (Burrows et al. 2012). In contrast, dissolved OM derived from plant litter often exhibits higher aromaticity and structural complexity, as reflected by elevated *SUVA* values (Lau 2021; Wymore et al. 2015). This structural stability enables prolonged persistence in stream environments, particularly under low-flow conditions, thereby contributing to sustained DOC accumulation. Differences in *SUVA* profiles between sediment- and litter-derived DOC therefore highlight the importance of source-specific chemical traits in regulating DOC reactivity and transport.

The contrasting behaviour of sediment and litter C pools also reflects differences in C stabilisation mechanisms. Sediment C is commonly associated with mineral surfaces or protected within soil aggregates, which can physically stabilise OM and limit its transformation into dissolved forms (Gao et al. 2021; Repasch et al. 2021). By contrast, plant litter contains a greater proportion of labile organic compounds that are rapidly utilised by microorganisms. When litter has relatively low C content or low C:N ratios, microbial activity can convert C into DOC and its subsequent transformation into DIC via respiration (Marks 2019).

Once introduced into the stream environment, litter undergoes continuous decomposition accompanied by gradual mass loss. Our results indicate that FWD in early decay stages plays a disproportionate role in regulating DC dynamics (Don, Kalbitz 2005). In the initial phase, fresh FWD contains readily hydrolysable compounds that are solubilised, generating early DOC inputs (Strauss, Lamberti 2002). Rapid colonisation by bacteria and primary fungi accelerates breakdown and releases substantial reactive DOC (Abelho, Descals 2019). Under oxygen-rich and high-flow conditions, this process may enhance downstream transport of DC (De Almeida Assunção et al. 2018). In contrast, the structural complexity and lignin content of FWD render it resistant to microbial degradation in later stages, thereby reducing C conversion efficiency (Chakrawal et al. 2024; Hall et al. 2020). Consequently, early-stage FWD represents an im-

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portant source of DC in headwater streams. These findings suggest that the influence of in-stream C pools on DC dynamics depends less on the absolute size of C reservoirs and more on the chemical characteristics and bioavailability of C. In other words, C quality rather than C pool size appears to be a primary determinant of DOC and DIC dynamics in headwater streams.

**Dominance of stream hydrological and physicochemical parameters.** Hydrological processes exerted the strongest control on DC export in the studied headwater stream. Although C pool characteristics influenced the composition and chemical properties of DC, stream discharge and flow velocity primarily determined the magnitude of C export. Higher discharge during the wet season likely enhanced downstream transport by increasing water movement through the stream network and reducing water residence time. In contrast, low-flow conditions can promote in-stream processing of OM, allowing microbial mineralisation and other biogeochemical transformations to occur before C is transported downstream (Berggren et al. 2022; Carey et al. 2022). Overall, stream hydrological and physicochemical conditions regulate not only DC export but also C transformation and redistribution among in-stream C pools (McKnight et al. 2001).

## CONCLUSION

This study highlights the distinct roles of C pools and hydrological processes in regulating DC dynamics in a subtropical forest headwater stream. C characteristics of sediments and plant litter influenced stream C dynamics mainly through C quality rather than C pool size, and their effects varied seasonally. Different C pools exerted contrasting influences on DOC and DIC dynamics, reflecting differences in C composition and decomposition status within stream ecosystems. However, hydrological processes – particularly stream discharge – remained the primary driver of DC export. Hydrological variables explained a greater proportion of variability in C export than sediment and litter C characteristics, emphasising the dominant role of hydrological dynamics in controlling C transport from headwater streams. Together, these findings suggest a consistent pattern in headwater streams: hydrology primarily controls C export, whereas C pools regulate the composition of DC.

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## REFERENCES

- Abelho M., Descals E. (2019): Litter movement pathways across terrestrial–aquatic ecosystem boundaries affect litter colonization and decomposition in streams. *Functional Ecology*, 33: 1785–1797.
- Argerich A., Haggerty R., Johnson S.L., Wondzell S.M., Dosch N., Corson-Rikert H., Ashkenas L.R., Pennington R., Thomas C.K. (2016): Comprehensive multiyear carbon budget of a temperate headwater stream. *Journal of Geophysical Research: Biogeosciences*, 121: 1306–1315.
- Babakhani P., Dale A.W., Woulds C., Moore O.W., Xiao K.Q., Curti L., Peacock C.L. (2025): Preservation of organic carbon in marine sediments sustained by sorption and transformation processes. *Nature Geoscience*, 18: 78–83.
- Battin T.J., Kaplan L.A., Findlay S., Hopkinson C.S., Marti E., Packman A.I., Newbold J.D., Sabater F. (2008): Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geoscience*, 1: 95–100.
- Battin T.J., Lauerwald R., Bernhardt E.S., Bertuzzo E., Gener L.G., Hall Jr R.O., Hotchkiss E.R., Maavara T., Pavelsky T.M., Ran L., Raymond P., Rosentreter J.A., Regnier P. (2023): River ecosystem metabolism and carbon biogeochemistry in a changing world. *Nature*, 613: 449–459.
- Berggren M., Guillemette F., Bierzoza M., Buffam I., Deininger A., Hawkes J.A., Kothawala D.N., LaBrie R., Lapierre J.F., Murphy K.R., Al-Kharusi E.S., Rulli M.P.D., Hensgens G., Younes H., Wünsch U.J. (2022): Unified understanding of intrinsic and extrinsic controls of dissolved organic carbon reactivity in aquatic ecosystems. *Ecology*, 103: e3763.
- Boyero L., Pearson R.G., Dudgeon D., Graça M.A.S., Gessner M.O., Albariño R.J., Ferreira V., Yule C.M., Boulton A.J., Arunachalam M., et al. (2011): Global distribution of a key trophic guild contrasts with common latitudinal diversity patterns. *Ecology*, 92: 1839–1848.
- Burrows R.M., Magierowski R.H., Fellman J.B., Barmuta L.A. (2012): Woody debris input and function in old-growth and clear-felled headwater streams. *Forest Ecology and Management*, 286: 73–80.
- Carey C.C., Hanson P.C., Thomas R.Q., Gerling A.B., Hounshell A.G., Lewis A.S., Lofton M.E., McClure R.P., Wander H.L., Woelmer W.M., Niederlehner B.R., Schreiber M.E. (2022): Anoxia decreases the magnitude of the carbon, nitrogen, and phosphorus sink in freshwaters. *Global Change Biology*, 28: 4861–4881.

<https://doi.org/10.17221/68/2025-JFS>

- Casas-Ruiz J.P., Tittel J., von Schiller D., Catalán N., Obrador B., Gómez-Gener L., Zwirnmann E., Sabater S., Marcé R. (2016): Drought-induced discontinuities in the source and degradation of dissolved organic matter in a Mediterranean river. *Biogeochemistry*, 127: 125–139.
- Chakrawal A., Lindahl B.D., Manzoni S. (2024): Modelling optimal ligninolytic activity during plant litter decomposition. *New Phytologist*, 243: 866–880.
- Chen M., Hur J. (2015): Pre-treatments, characteristics, and biogeochemical dynamics of dissolved organic matter in sediments: A review. *Water Research*, 79: 10–25.
- Cole J.J., Prairie Y.T., Caraco N.F., McDowell W.H., Tranvik L.J., Striegl R.G., Duarte C.M., Kortelainen P., Downing J.A., Middelburg J.J., Melack J. (2007): Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems*, 10: 172–185.
- Coulson L.E., Weigelhofer G., Gill S., Hein T., Griebler C., Schelker J. (2022): Small rain events during drought alter sediment dissolved organic carbon leaching and respiration in intermittent stream sediments. *Biogeochemistry*, 159: 159–178.
- De Almeida Assunção A.W., Souza B.P., da Cunha-Santino M.B., Bianchini Jr I. (2018): Formation and mineralization kinetics of dissolved humic substances from aquatic macrophytes decomposition. *Journal of Soils and Sediments*, 18: 1252–1264.
- Don A., Kalbitz K. (2005): Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. *Soil Biology and Biochemistry*, 37: 2171–2179.
- Downing J.A., Cole J.J., Duarte C., Middelburg J.J., Melack J.M., Prairie Y.T., Kortelainen P., Striegl R.G., McDowell W.H., Tranvik L.J. (2012): Global abundance and size distribution of streams and rivers. *Inland Waters*, 2: 229–236.
- Gao Y., Jia J., Lu Y., Sun K., Wang J., Wang S. (2024): Carbon transportation, transformation, and sedimentation processes at the land-river-estuary continuum. *Fundamental Research*, 4: 1594–1602.
- Gao Y., Jia J., Lu Y., Yang T., Lyu S., Shi K., Zhou F., Yu G. (2021): Determining dominating control mechanisms of inland water carbon cycling processes and associated gross primary productivity on regional and global scales. *Earth-Science Reviews*, 213: 103497.
- Gregory S.V., Swanson F.J., McKee W.A., Cummins K.W. (1991): An ecosystem perspective of riparian zones. *BioScience*, 41: 540–551.
- Hall S.J., Huang W., Timokhin V.I., Hammel K.E. (2020): Lignin lags, leads, or limits the decomposition of litter and soil organic carbon. *Ecology*, 101: e03113.
- Hao X., Ouyang W., Zhang K., Wan X., Cui X., Zhu W. (2022): Enhanced release, export, and transport of diffuse nutrients from litter in forested watersheds with climate warming. *Science of the Total Environment*, 837: 155897.
- Hu W., Wu F., Ni X., Peng Y., Wang Z., Zhao Z., Wang Y., Yue K. (2023): Dynamics of plant litter storage in a subtropical forest headwater stream during the rainy season. *Polish Journal of Ecology*, 70: 129–141.
- Kopáček J., Evans C.D., Hejzlar J., Kaňa J., Porcal P., Šantrůčková H. (2018): Factors affecting the leaching of dissolved organic carbon after tree dieback in an unmanaged European mountain forest. *Environmental Science & Technology*, 52: 6291–6299.
- Lau M.P. (2021): Linking the dissolved and particulate domain of organic carbon in inland waters. *Journal of Geophysical Research: Biogeosciences*, 126: e2021JG006266.
- Laudon H., Berggren M., Ågren A., Buffam I., Bishop K., Grabs T., Jansson M., Köhler S. (2011): Patterns and dynamics of dissolved organic carbon (DOC) in boreal streams: The role of processes, connectivity, and scaling. *Ecosystems*, 14: 880–893.
- Marks J.C. (2019): Revisiting the fates of dead leaves that fall into streams. *Annual Review of Ecology, Evolution, and Systematics*, 50: 547–568.
- Marx A., Dusek J., Jankovec J., Sanda M., Vogel T., van Geldern R., Hartmann J., Barth J. (2017): A review of CO<sub>2</sub> and associated carbon dynamics in headwater streams: A global perspective. *Reviews of Geophysics*, 55: 560–585.
- McKnight D.M., Boyer E.W., Westerhoff P.K., Doran P.T., Kulbe T., Andersen D.T. (2001): Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. *Limnology and Oceanography*, 46: 38–48.
- Meyer J.L., Wallace J.B., Eggert S.L. (1998): Leaf litter as a source of dissolved organic carbon in streams. *Ecosystems*, 1: 240–249.
- Polis G.A., Anderson W.B., Holt R.D. (1997): Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 28: 289–316.
- Raymond P.A., Saiers J.E. (2010): Event controlled DOC export from forested watersheds. *Biogeochemistry*, 100: 197–209.
- Rehn L., Sponseller R.A., Laudon H., Wallin M.B. (2023): Long-term changes in dissolved inorganic carbon across boreal streams caused by altered hydrology. *Limnology and Oceanography*, 68: 409–423.
- Repasch M., Scheingross J.S., Hovius N., Lupker M., Wittmann H., Haghypour N., Gröcke D.R., Orfeo O., Eglinton T.I., Sachse D. (2021): Fluvial organic carbon cycling regulated by sediment transit time and mineral protection. *Nature Geoscience*, 14: 842–848.

<https://doi.org/10.17221/68/2025-JFS>

- Robbins C.J., Manning D.W., Halvorson H.M., Norman B.C., Eckert R.A., Pastor A., Dodd A.K., Jabiol J., Bastias E., Gossiaux A., Mehring A.S. (2023): Nutrient and stoichiometry dynamics of decomposing litter in stream ecosystems: A global synthesis. *Ecology*, 104: e4060.
- Salimon C., Santos Sousa E., Alin S.R., Krusche A.V., Ballester M.V. (2013): Seasonal variation in dissolved carbon concentrations and fluxes in the upper Purus River, southwestern Amazon. *Biogeochemistry*, 114: 245–254.
- Schulte P., van Geldern R., Freitag H., Karim A., Négrel P., Petelet-Giraud E., Probst A., Probst J.L., Telmer K., Veizer J., Barth J.A.C. (2011): Applications of stable water and carbon isotopes in watershed research: Weathering, carbon cycling, and water balances. *Earth-Science Reviews*, 109: 20–31.
- Song C., Wang G., Mao T., Huang K., Sun X., Hu Z., Chang R., Chen X., Raymond P.A. (2020): Spatiotemporal variability and sources of DIC in permafrost catchments of the Yangtze River source region. *Water Resources Research*, 56: e2019WR025343.
- Stelzer R.S., Scott J.T., Bartsch L.A., Parr T.B. (2014): Particulate organic matter quality influences nitrate retention and denitrification in stream sediments. *Biogeochemistry*, 119: 387–402.
- Strauss E.A., Lamberti G.A. (2002): Effect of dissolved organic carbon quality on microbial decomposition and nitrification rates in stream sediments. *Freshwater Biology*, 47: 65–74.
- Tiegs S.D., Capps K.A., Costello D.M., Schmidt J.P., Patrick C.J., Follstad Shah J.J., Leroy C.J. (2024): Human activities shape global patterns of decomposition rates in rivers. *Science*, 384: 1191–1195.
- Vachon D., Sponseller R.A., Karlsson J. (2021): Integrating carbon emission, accumulation and transport in inland waters to understand their role in the global carbon cycle. *Global Change Biology*, 27: 719–727.
- Wang S., Benoit G., Raymond P.A., Yu G., Zhou F., Liu S., Miao C., Sun K., Li Z., Jia J., Gao Y. (2025): Dissolved carbon storage and flux dynamics in China's inland waters over the past 30 years. *National Science Review*, 12: nwaf229.
- Wei X., Hayes D.J., Butman D.E., Qi J., Ricciuto D.M., Yang X. (2024): Modeling exports of dissolved organic carbon from landscapes: A review of challenges and opportunities. *Environmental Research Letters*, 19: 053001.
- Weishaar J.L., Aiken G.R., Bergamaschi B.A., Fram M.S., Fujii R., Mopper K. (2003): Evaluation of specific ultraviolet absorbance as an indicator of the chemical composition and reactivity of dissolved organic carbon. *Environmental Science & Technology*, 37: 4702–4708.
- Wohl E., Hall Jr R.O., Lininger K.B., Sutfin N.A., Walters D.M. (2017): Carbon dynamics of river corridors and the effects of human alterations. *Ecological Monographs*, 87: 379–409.
- Wymore A.S., Compson Z.G., McDowell W.H., Potter J.D., Hungate B.A., Whitham T.G., Marks J.C. (2015): Leaf-litter leachate is distinct in optical properties and bioavailability to stream heterotrophs. *Freshwater Science*, 34: 857–866.
- Wymore A.S., Salpas E., Casaburi G., Liu C.M., Price L.B., Hungate B.A., McDowell W.H., Marks J.C. (2018): Effects of plant species on stream bacterial communities via leachate from leaf litter. *Hydrobiologia*, 807: 131–144.
- Yoshimura C., Fujii M., Omura T., Tockner K. (2010): In-stream release of dissolved organic matter from coarse and fine particulate organic matter of different origins. *Biogeochemistry*, 100: 151–165.
- Yue K., Peng C., Yang W., Peng Y., Zhang C., Huang C., Wu F. (2016): Degradation of lignin and cellulose during foliar litter decomposition in an alpine forest river. *Ecosphere*, 7: e01523.
- Zhang M., Cheng X., Geng Q., Shi Z., Luo Y., Xu X. (2019): Leaf litter traits predominantly control litter decomposition in streams worldwide. *Global Ecology and Biogeography*, 28: 1469–1486.
- Zhao Z., Wu F., Peng Y., Hedéne P., Wang Y., Hu W., Ni X., Yue K. (2023): Dynamics of heavy metals in the fine sediments from a subtropical forest headwater stream during a rainy season. *Inland Waters*, 13: 131–141.

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