Received: 1 March 2022 | Revised: 1 December 2022 | Accepted: 8 February 2023

DOI: 10.1002/eco.2531

RESEARCH ARTICLE

WILEY

Woody debris dominates the exports of carbon and nitrogen from headwater streams in an alpine forest

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Funding information

Fok Ying-Tong Education Foundation for Young Teachers, Grant/Award Number: 161101; Key Technologies R&D Program of Sichuan, Grant/Award Number: 18ZDYF0307; National Key Technologies R&D Program of China, Grant/Award Number: 2017YFC0505003; National Natural Science Foundation of China, Grant/Award Numbers: 31670526, 31800373; the Natural Science Foundation of Sichuan Province, Grant/Award Number: 2022NSFSC0997

Abstract

The exports of carbon and nitrogen with water flowing in the headwater streams could be important components of material mitigation in forest ecosystems. Plant debris is a major source of dissolved organic matter for headwater streams, but few studies have investigated the differences between the impacts of woody debris and non-woody debris inputs on headwater streams in terms of carbon and nitrogen exports. Here, we assessed the effects of plant debris (i.e., woody debris, non-woody debris and mixed debris) on the concentrations and exports of dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) in the headwater streams of an alpine forest on the eastern Tibetan Plateau. Woody and non-woody debris only weakly affected the DOC and TDN concentrations in the headwater streams. Compared with those in the reference stream excluding plant debris, woody debris increased the exports of DOC and TDN by 19% and 13%, whereas non-woody debris decreased the exports of DOC and TDN by 22% and 25%, respectively. However, when fall approached, the role of non-woody debris reversed to enhance the stream-water exports of DOC and TDN. The effect of non-woody debris during the fall season differed from that during the overall growing season, indicating that restricting non-woody debris inputs might improve the ability of the stream to retain forest carbon and nitrogen. Notwithstanding the relatively limited experimental period, this work revealed the critical importance of plant debris for carbon and nutrients within water conservation regions like alpine forests.

KEYWORDS

alpine forest, dissolved organic carbon, headwater stream, non-woody debris, total dissolved nitrogen, woody debris

1 | INTRODUCTION

Streams and rivers significantly contribute to global carbon and nitrogen migration. Numerous studies on the carbon and nitrogen cycles have emphasized the importance of river networks in the storage and export of terrestrial carbon and nitrogen in recent years (Allan & Castillo, 2007; Aufdenkampe et al., 2011; Sutfin et al., 2016; Wohl et al., 2012; Xia et al., 2018). Headwater streams are an essential part of the river network, which account for 75% of the global sum of stream lengths and continuously exchange water with sediments and stream banks (Battin et al., 2008; Downing et al., 2012; Wondzell, 2011). Their close relationship with adjacent uplands allows headwater streams to play a critical role in terrestrial carbon and nitrogen migration. The bulk of terrestrial organic matter from dense riparian vegetation and canopies enters headwater streams through litterfall, throughfall and surface runoff. These plant debris in the headwater stream are the primary sources of organic matter (Allan & Castillo, 2007; Vannote et al., 1980) and have the potential to influence the export of carbon and nitrogen from the stream-water not only by releasing the carbon and nitrogen stored in them during the decomposition but also by converting and storing carbon and nitrogen in the stream through the adsorption/absorption processes (Cole & Caraco, 2001; Corson-Rikert et al., 2016; Webster et al., 2000).

Because the heavy canopies of riparian vegetation block considerable amounts of light from reaching forest floors, autotrophic production accounts for only a small part of the food web in forest headwater streams; in contrast, high inputs of riparian organic matter are the main energy supply (Hill, 1995; Webster, 2007). Plant debris supplied from forests to streams consists mainly of woody and non-woody debris, with fallen wood, root stumps and large dead branches being the main woody debris components; leaves, barks, flowers, fruit, seeds and twigs less than 1 cm in diameter are the main non-woody debris components (Harmon & Sexton, 1996). These plant debris are broken down, decomposed and leached as dissolved organic matter in the channel (Bunte et al., 2016; França et al., 2009; Meyer et al., 1998; Wallace, Cuffney, et al., 1997). Woody debris is an important link between forest and aquatic ecosystems and not only provides the main biological pathway for energy and nutrient transfer (Chen et al., 2005; Richardson & Danehy, 2007) but also increases habitat diversity for stream biota (Burrows et al., 2012; Rinella et al., 2009). In addition, some large woody debris, such as deadwood and small logs, can alter the morphology and biological functioning of streams (Gomi et al., 2001), and many studies have shown that large woody debris is critical for the physical retention of sediments and organic matter (Eggert et al., 2012; Nakamura & Swanson, 1993; Thompson, 1995; Wohl & Scott, 2017). Non-woody debris can decay more rapidly in running water than in forests (Graça et al., 2015), and its decomposition rate increases with increasing temperature (Taylor & Chauvet, 2014), introducing more dissolved carbon and nitrogen into streams. As non-woody debris enters a stream, it is often retained locally or is transported over a short distance until it is trapped around obstacles (Muto et al., 2009; Osei et al., 2015; Webster et al., 1999), such as root masses, instream wood or other woody debris. Hence, non-woody debris is drawn into the water by flow and then submerged and accumulated around woody debris (Turowski et al., 2016) or buried within the streambed by sediment movement and flooding (Cornut et al., 2012), thus extending the residence time of the non-woody debris and promoting the transformation of dissolved organic matter.

Most studies have focused on the biological functions of riparian matter and its influence on channel morphology (Foucreau et al., 2013; Merten et al., 2013), emphasizing the role of organic matter in contributing and storing carbon and nitrogen for stream ecosystems (Elosegi et al., 2007). However, few studies have reported the relative contributions of plant debris inputs to stream carbon and nitrogen concentrations and exports. In addition, woody debris can regulate the width and gradient of streams and provide more habitats for instream communities (Gomi et al., 2001; Hall et al., 2000; Tank et al., 2010). On the other hand, non-woody debris decomposes rapidly in aquatic systems (Yue et al., 2018). These differences suggest that woody and non-woody debris have different effects on stream-water dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) concentrations and exports, but few studies have distinguished them through comparison experiments. Here, we examine how woody and non-woody debris influence the waters in headwater streams in alpine forests. This study focused on the stream-water DOC and TDN concentrations and exports, which generally depend on the climatic, geologic, geomorphic and hydrological characteristics of the ecosystem and the physical complexity of the channel (Beckman & Wohl, 2014; Sutfin et al., 2016). To highlight the inputs of plant debris, we used artificially excavated streams as the representative systems in an alpine forest located on the eastern Tibetan Plateau because relatively smooth and straight channels can reduce bank erosion, physical complexity and the lateral impact of surface runoff. We compared the concentrations and exports of DOC and TDN among the streams with different plant debris inputs to examine the effect of plant debris. We hypothesized that (1) non-woody debris would increase the concentrations and exports of DOC and TDN and (2) woody debris could reduce the exports of DOC and TDN.

2 | MATERIALS AND METHODS

2.1 | Site description

The experiment was conducted at the Long-term Research Station of Alpine Forest Ecosystem in the Miyaluo Nature Reserve (31°14′–31°19′ N, 102°53′–102°57′ E, 2458–4169 m a.s.l.), which is located in Li county, Sichuan, China (Figure 1). This region is in the eastern Tibetan Plateau and the upper Yangtze River. The annual mean air temperature is 2.7°C, and the maximum and minimum temperatures are 23 and −18°C, respectively. The annual precipitation is approximately 850 mm, with heavy rainfall in summer and smaller in winter. The growing season is short, and snow is accumulated from late October to late April of the following year. The study streams are located in an alpine coniferous forest, and the dominant tree species

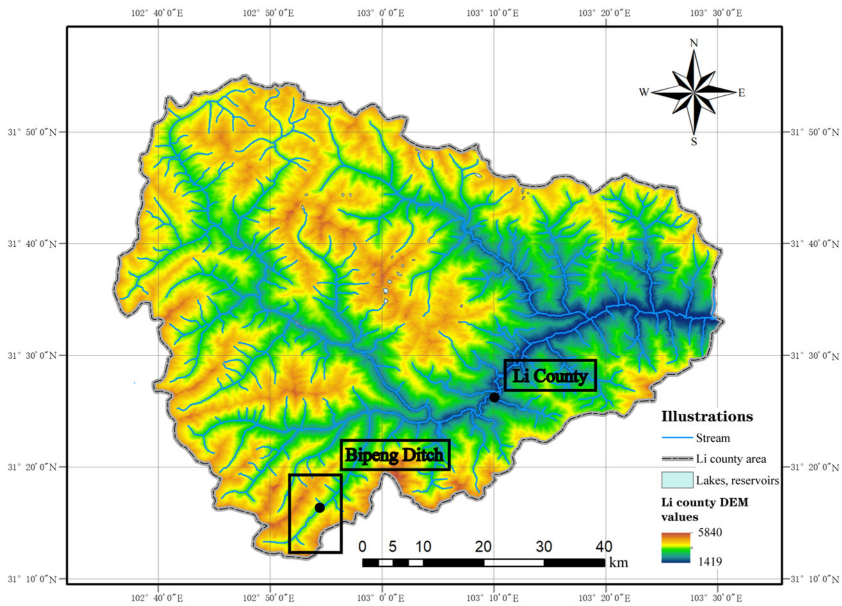

FIGURE 1 Geographical coordinates of the study area.

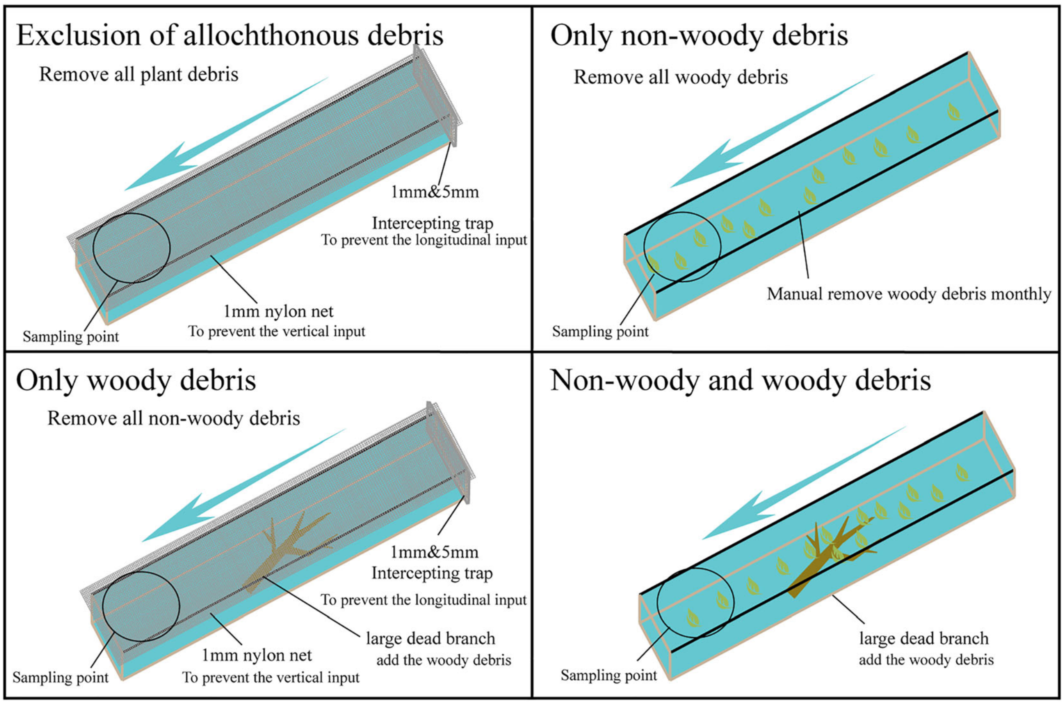

FIGURE 2 Schematic diagram of experimental design.

are *Abies faxoniana*, *Picea asperata* and associated *Cerasus duclouxii* and *Sabina saltuaria*. The main understory shrubs include *Salix paraplesia*, *Rosa omeiensis* and *Rhododendron lapponicum*.

2.2 | Experimental design

To highlight the effects of plant inputs, the role of geological, geomorphological, climatical and hydrological features on streamflow needed to be eliminated or reduced. Therefore, we used artificially excavated channels as the study streams and used nylon nets to intercept and control the entry of plant debris into the streams in order to reduce lateral, longitudinal and vertical carbon and nitrogen transport.

Every channel shared the similar substrate, slope, length (25 m), width (0.5 m) and depth (0.15 m) to avoid influencing the travel time and retention of water; moreover, smooth channels can reduce the effects of streambank erosion and promote the control of lateral inputs from riparian vegetation. We divided the streams into three types of plant debris inputs: only non-woody debris, only woody debris and mixed debris. Moreover, a stream that did not include plant debris was served as the reference.

This experiment included four kinds of plant debris inputs (Figure 2), each with three replicates. The settings were as follows:

1. a stream with exclusion of plant debris as a reference: all plant debris were removed from the channel, and then, two kinds of intercepting traps with diameters of 1 and 5 mm were installed at the inlet of the stream to prevent longitudinal inputs of litter. A nylon net with an aperture of 1 mm was placed above the stream to prevent vertical inputs of litter. Intercepted debris was cleared during each sampling to prevent its decomposition and influence on water flow.
2. a stream with non-woody debris input only: all woody debris were removed from the stream during each sampling.
3. a stream with woody debris input only: intercepting traps and nylon nets identical to those installed in (1) were employed to prevent longitudinal and vertical inputs of plant debris. A large dead branch from the surrounding riparian vegetation was added to the stream as the woody debris input, and any intercepted non-woody debris was removed from the stream during each sampling.
4. a stream with mixed non-woody and woody debris input: woody debris identical to that in was added to the stream at the beginning of the experiment, but additional non-woody debris was not added; instead, the plant debris input originated mainly from natural litterfall from riparian vegetation.

Non-woody debris included leaves, fruit, small bark fragments, twigs and flowers. Woody debris included wood, branches and roots. The stream parameter indices (water temperature, dissolved oxygen, conductivity, etc.) were measured by a YSI Professional Plus multiparameter meter (Pro Plus, YSI, Yellow Springs, OH, USA). The water samples were collected once a month from May to October 2017, because the field sample was difficult with cruel frozen condition in winter. For each stream, three replicate 0.5 L water samples were collected at random points at approximately one-half of the water depth using precleaned polyethylene bottles. The water samples were taken back to the laboratory within 24 h and stored at 4°C for chemical analyses.

2.3 | Chemical analyses

All water samples were passed through a 0.45 μm polyether sulfone (PES) filter membranes prior to the chemical analyses (State Environmental Protection Administration of China, 2002). The DOC content was determined using a total organic carbon analyser (multi N/C 2100, Analytik Jena, Thüringen, Germany). To determine the TDN concentration, potassium persulfate was first used as the oxidant under alkaline conditions at 120–124°C to oxidize ammonia nitrogen, nitrate nitrogen and most of the organic nitrogen compounds in the water samples into nitrate. Then, an ultraviolet-visible spectrophotometer (TU-1901, Puxi, Beijing, China) was used to determine the absorbances at 220 and 275 nm to calculate the TDN concentration.

2.4 | Calculations and statistical analyses

DOC and TDN exports were calculated as follows: $E = c \times Q$, where c is either the DOC or the TDN concentration (mg/L) and Q is the discharge at the outlet of the stream (L/s).

Repeated-measures analysis of variance (ANOVA) was performed to test the effects of litter inputs and time on environmental factors, DOC and TDN concentrations, and DOC and TDN exports. One-way ANOVA was employed to test for significant ($p < 0.05$) differences in the environmental factors, DOC and TDN concentrations, and DOC and TDN exports among the monthly samples and litter inputs. Spearman's correlation was selected to test the correlation coefficients between the environmental factors and DOC and TDN concentrations and exports. These statistical analyses were performed using SPSS 22.0 (IBM SPSS Statistics Inc., Chicago, IL, USA).

3 | RESULTS

3.1 | Effects of plant debris inputs on water environmental characteristics

During the growth season, different plant debris inputs have few effects on the dynamics of the water temperature, dissolved oxygen, conductivity or pH but had significant effects on the flow velocity and discharge (Table S1). Compared with the reference stream, woody debris input substantially increased the flow velocity; in contrast, non-woody debris input significantly decreased the flow velocity. In the woody debris and mixed debris streams, the monthly dynamic changes in the flow velocity and discharge were more stable than those in the non-woody debris stream (Figure S2).

3.2 | Effects of plant debris inputs on DOC

The inputs of plant debris to the headwater streams slightly increased the average DOC concentration (Table 1), but the effects were insignificant ($p = 0.111$, Table S2). In addition, the monthly dynamics of the DOC concentrations in the streams were not affected by the various debris inputs, and the peaks all occurred in October (Figure S3). However, plant debris inputs had a significant impact on the DOC export in the headwater streams ($p < 0.001$, Table S2). Compared with the reference stream, non-woody debris input significantly reduced DOC export by 22%, whereas woody debris input significantly increased DOC export, with the DOC in the woody debris only stream increasing by 19%, and that in the mixed debris stream increased by 23%. Furthermore, the plant debris input changed the monthly dynamics of DOC export, with woody debris input increasing DOC export and causing it to peak in October (Figure 3c,d). Non-woody debris input initially decreased DOC export before increasing to a peak in October (Figure 3b).

In the reference stream, the key factor influencing the DOC concentration was the flow velocity, which had a significant negative

TABLE 1 Effects of different plant debris inputs on DOC and TDN concentrations and export.

Variations	DOC concentration (mg/L)	DOC export (kg/d)	TDN concentration (mg/L)	TDN export (kg/d)
EAD	7.21 ± 1.24 a	5.06 ± 0.96 b	0.88 ± 0.08 a	0.63 ± 0.15 a
NWD	7.26 ± 1.22 a	3.93 ± 1.17 c	0.87 ± 0.09 a	0.47 ± 0.13 b
WD	7.35 ± 1.10 a	6.01 ± 1.49 ab	0.87 ± 0.06 a	0.71 ± 0.16 a
NWD + WD	7.71 ± 1.05 a	6.22 ± 1.40 a	0.86 ± 0.06 a	0.69 ± 0.13 a

Note: Mean ± SD ($n = 36$), different lowercase letters in the same column denote significant ($p < 0.05$) differences among different plant debris inputs based on repeated-measure ANOVA followed by multiple comparisons.
Abbreviations: DOC, dissolved organic carbon; TDN, total dissolved nitrogen; EAD, exclusion of allochthonous debris; NWD, non-woody debris; WD, woody debris.

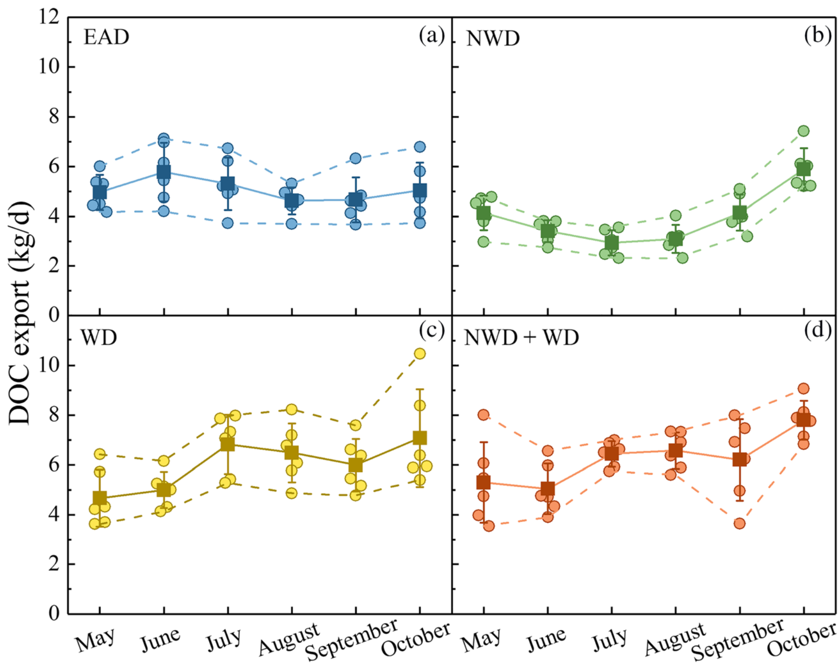

FIGURE 3 Dynamics of dissolved organic carbon (DOC) export under different plant debris inputs. The solid line represents means and the dotted lines are 5% and 95% connecting lines.

TABLE 2 Correlation coefficients (*r*) between the environmental factors and DOC in the streams.

Factor		EAD		NWD		WD		NWD + WD	
		DOC conc.	DOC export	DOC conc.	DOC export	DOC conc.	DOC export	DOC conc.	DOC export
Temperature	F	0.232	−0.277	0.412	−0.119	0.090	0.417	0.253	0.380
	p	0.174	0.102	0.013	0.489	0.603	0.011	0.137	0.022
Dissolved oxygen	F	−0.286	0.264	−0.180	−0.659	−0.310	0.034	−0.414	−0.117
	p	0.091	0.120	0.294	<0.001	0.065	0.845	0.012	0.496
Conductivity	F	−0.009	−0.111	−0.027	−0.045	−0.151	−0.020	0.214	0.123
	p	0.961	0.518	0.878	0.793	0380	0.910	0.210	0.476
pH	F	−0.072	−0.310	−0.242	0.051	−0.120	−0.269	0.132	−0.117
	p	0.678	0.065	0.155	0.767	0.487	0.112	0.441	0.497
Flow velocity	F	−0.596	0.676	−0.187	0.478	−0.223	0.596	−0.302	0.298
	p	<0.001	<0.001	0.276	0.003	0.191	<0.001	0.073	0.077

Abbreviations: DOC, dissolved organic carbon; EAD, exclusion of allochthonous debris; NWD, non-woody debris; WD, woody debris.

correlation with the DOC concentration ($p < 0.001$) and a significant positive correlation with DOC export ($p < 0.001$). After non-woody and woody debris were input to the streams, the effect of the flow velocity on the DOC concentration was weakened. However, the correlation between the flow velocity and DOC export was not significant only in the mixed debris stream (Table 2).

3.3 | Effects of plant debris input on TDN

There were few differences in TDN concentration or export over the growing season in the reference stream, whereas TDN export tended to decrease in the reference stream (Figure 4a). The inputs of plant debris had no effects on the TDN concentrations during the growth season (Figure S3), but non-woody debris significantly influenced TDN export in the headwater streams. Non-woody debris input reduced TDN export by 160 g/d, a 25% reduction over the reference stream; TDN export first declined and then increased, reaching a minimum in August and a peak in October (Figure 4b). Although woody debris input increased TDN export, the difference was not significant (Table 1): woody debris increased TDN export by only 80 g/d, while mixed debris increased TDN export by only 60 g/d, constituting 13% and 10% increases over the reference stream, respectively. In contrast with the non-woody debris only stream, the TDN export of the woody debris only stream first increased and then decreased after peaking in August (Figure 4c). The seasonal variation in TDN export was diminished in the mixed stream (Figure 4d). In the streams with plant debris inputs, the TDN concentration was negatively correlated with dissolved oxygen ($p < 0.01$). For TDN export, flow velocity was the main parameter affecting all streams (Table 3).

4 | DISCUSSION

As mentioned previously, several reports have noted the importance of leaf and wood inputs to forested headwater streams (Tank &

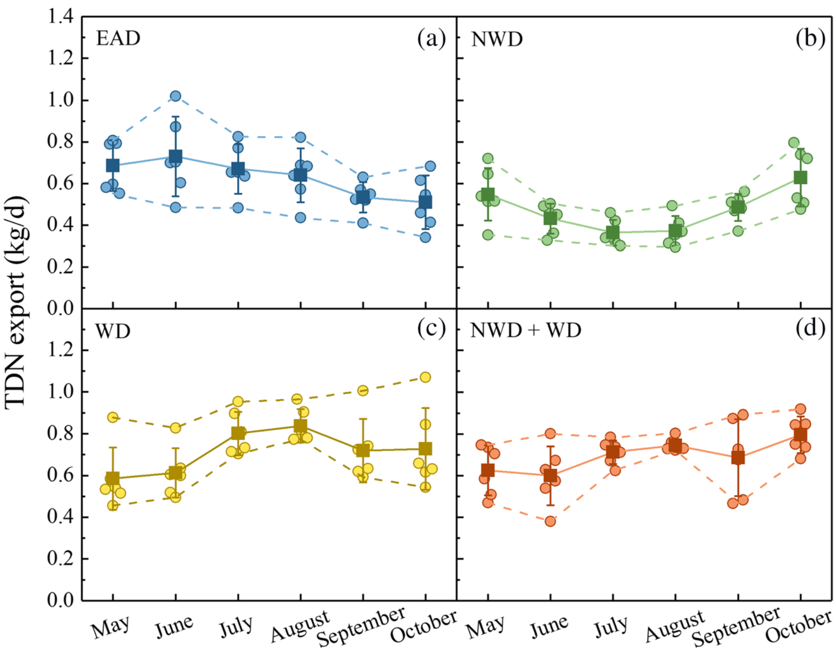

FIGURE 4 Dynamics of total dissolved nitrogen (TDN) export under different plant debris inputs. The solid line represents means and the dotted lines are 5% and 95% connecting lines.

TABLE 3 Correlation coefficients (*r*) between the environmental factors and TDN in the streams.

Factor		EAD		NWD		WD		NWD + WD	
		TDN conc.	TDN export	TDN conc.	TDN export	TDN conc.	TDN export	TDN conc.	TDN export
Temperature	F	0.092	−0.248	0.267	−0.255	0.191	0.524	0.186	0.403
	p	0.592	0.144	0.115	0.134	0.264	0.001	0.277	0.015
Dissolved oxygen	F	−0.313	0.301	−0.478	−0.758	−0.607	0.128	−0.600	0.018
	p	0.063	0.075	0.003	<0.001	<0.001	0.458	<0.001	0.917
Conductivity	F	0.235	0.046	0.153	−0.043	0.125	0.117	0.291	0.065
	p	0.167	0.791	0.374	0.802	0.467	0.498	0.085	0.707
pH	F	0.060	−0.091	−0.025	0.194	−0.125	−0.205	0.204	−0.237
	p	0.729	0.596	0.884	0.258	0.467	0.230	0.232	0.164
Flow velocity	F	−0.309	0.826	0.012	0.592	−0.132	0.824	−0.267	0.553
	p	0.067	<0.001	0.943	<0.001	0.444	<0.001	0.115	<0.001

Abbreviations: NWD, non-woody debris; TDN, total dissolved nitrogen; WD, woody debris; EAD, exclusion of allochthonous debris.

Webster, 1998; Wallace, Eggert, et al., 1997). However, none of them distinguish between the effects of these non-woody and woody debris input into stream on water DOC and TDN. Prior studies have noted that non-woody debris decomposes faster, is important in supporting the activities of microbes, algae and fungi (Eggert & Wallace, 2007; Wallace, Cuffney, et al., 1997; Gulis et al., 2008), and is the main source of carbon and nitrogen (Bantle et al., 2014; Meyer et al., 1998). Therefore, our first hypothesis is that non-woody debris can increase the concentration and export of DOC and TDN. Unfortunately, in our study, we found that the inputs of non-woody debris did not have much impact on the concentrations of DOC and TDN in the headwater stream. Some studies have found that non-woody debris can rapidly decompose in streams due to the strong effects of leaching and the mechanical forces of running water (Yue et al., 2016), and the decomposition of non-woody debris releases up to 50% of its initial nitrogen concentration into the dissolved nitrogen pool (Triska et al., 1984). However, this result was not observed in this study, which may be attributed to the rapid removal of dissolved nitrogen from the water by a series of biological processes, such as uptake, sorption, assimilation, deposition and immobilization (Peterson et al., 2001; Swank & Caskey, 1982).

Furthermore, some studies have reported that the flow velocity has significant influences not only on the retention and redistribution of non-woody debris inputs in the channel but also on the decomposition rate of non-woody debris (Bastias et al., 2020). An interesting finding in our study was that non-woody debris significantly reduced the flow velocity, but this effect disappeared during the fall season (October). This suggests that the effect of flow velocity on the distribution of non-woody debris in streams may not be a purely linear relationship. The results from comparative analysis suggest that non-woody debris plays a role in immobilizing the exports of DOC and TDN when it first enters the stream. The density of directly falling non-woody debris is generally lower than that of water, and a large portion of non-woody debris flows downstream until it becomes entangled in the water column or trapped by obstacles (Quinn et al., 2007). Because types of non-woody debris have larger surface areas and more irregular boundaries than woody debris, they provide more opportunities for the retention of carbon and nitrogen (Beckman & Wohl, 2014). Therefore, the adsorption and storage capacity of non-woody debris after initially entering a stream might predominantly explain the reduced DOC and TDN exports in headwater streams.

Many studies have shown the critical effects of woody debris on the physical storage of carbon in headwater streams (Guyette et al., 2002; Nakamura & Swanson, 1993; Thompson, 1995), and woody debris also serves as a carbon sink (Tank et al., 2010; Wohl et al., 2012). However, our results are contrary to the second hypothesis, that woody debris increased the export of DOC and TDN. Variations in absorption, mineralization, nitrification and denitrification, as well as changes in the carbon and nitrogen concentrations in the streams, may be attributed to the concentrations, available types and relative abundances of substrates (Kemp & Dodds, 2002; Webster et al., 2000). Considering that the decomposition rate of woody debris is relatively slow, its low impact on the concentrations of DOC and TDN is not surprising. Our results showed that the increase in DOC and TDN export from woody debris is related to its effect on stream flow and discharge. Yochum et al. (2012) showed that woody debris may reduce the flow velocity by increasing hydraulic resistance within channels. Our findings suggest a different outcome; a possible explanation for this might be that woody debris input could alter (narrow) the channel morphology (Jackson et al., 2001), by obstructing the flow space and thus accelerating the flow velocity. This effect was first observed 3 months after woody debris was introduced into the headwater streams, and the promoting effects of woody debris on DOC and TDN exports arose simultaneously.

In addition, the abundances and distributions of non-woody and woody debris in headwater streams determine the species richness of decomposers (Riedl et al., 2013). Although plant debris supports more instream habitats (Wilkins & Peterson, 2000), aquatic biodiversity (Floyd et al., 2009) and invertebrate densities (Eggert & Wallace, 2007), too few 'new residents' colonized this environment, thus affecting the release of carbon and nitrogen. The comparative results found that non-woody debris need to be submerged and accumulated before they can affect stream DOC concentrations; this implies that the abundance and distribution of non-woody debris in a stream may be the key to affecting the DOC concentration. After more non-woody debris is intercepted and gradually accumulated by woody debris, the non-woody debris may experience physical abrasion due to sediment transport in the running water (Graça et al., 2015), undergo microbial colonization (such as forming new habitats for denitrifying bacteria) (Swank & Caskey, 1982; Webster et al., 2000) and/or be subjected to shredding by invertebrates (Merten et al., 2013); as a result, non-woody debris may release nitrogen from the stream sediments to the water (Peterson et al., 2001) or it may leach more carbon into the water (Foucreau et al., 2013). Hence, increasing amounts of DOC and TDN can enter the water column and be exported with the flow downstream. Overall, non-woody and woody debris did not affect the concentrations of DOC and TDN in the initial period after being introduced to the headwater streams, and the effect of flow on the DOC concentration was reduced with the increasing input of plant debris. These results clearly reflect the potential influences of non-woody and woody debris inputs on the concentrations of carbon and nitrogen in headwater streams.

5 | CONCLUSION

Throughout the growing season, non-woody and woody debris inputs had different effects on the exports of carbon and nitrogen in the artificially excavated alpine forested headwater streams investigated herein. Woody debris dominates stream DOC and TDN export, and non-woody debris reduced the exports of DOC and TDN. Compared with the reference stream, woody debris increased the exports of DOC and TDN by 19% and 13%, non-woody debris significantly reduced the exports of DOC and TDN by 22% and 25%, respectively.

However, the reduction of non-woody debris gradually weakened with the arrival of fall; that is, the role non-woody debris played in diminishing the exports of DOC and TDN disappeared with the accumulation of non-woody debris in the stream. In contrast, woody debris input enhanced the exports of DOC and TDN throughout the growing season. A comparison between the results in the woody debris only and mixed debris streams also showed that non-woody debris can reduce the exports of carbon and nitrogen with the flow of water before it becomes submerged and sinks to the bottom. Therefore, notwithstanding the relatively limited experimental period, these results contribute to further understanding of DOC and TDN migration processes in the forest-stream continuum, and provide a basis for the management and protection of headwater stream forests.

ACKNOWLEDGEMENTS

We would like to thank Junyi Hu, Junwei Wu, Zhuang Wang, Jiao Zhou and Fei Duan for their assistance with sampling, and we are very grateful to Wanqin Yang, Zhenfeng Xu, Bo Tan and Li Zhang for their advice in study design. This work was partially supported by the National Natural Science Foundation of China (31800373, 31670526 and 31901295), the National Key Technologies R&D Program of China (2017YFC0505003), the Key Technologies R&D Program of Sichuan (18ZDYF0307) and Fok Ying-Tong Education Foundation for Young Teachers (161101). Open Access funding enabled and organized by Projekt DEAL.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Allan, J., & Castillo, M. (2007). *Stream ecology* (second ed.). Springer. https://doi.org/10.1007/978-1-4020-5583-6

Aufdenkampe, A. K., Mayorga, E., Raymond, P., Melack, J. M., Doney, S. C., Alin, S. R., Aalto, R. E., & Yoo, K. (2011). Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere. *Frontiers in Ecology and the Environment*, *9*(1), 53–60. https://doi.org/10.1890/100014

Bantle, A., Borken, W., & Matzner, E. (2014). Dissolved nitrogen release from coarse woody debris of different tree species in the early phase of decomposition. *Forest Ecology and Management*, *344*, 277–283. https://doi.org/10.1016/j.foreco.2014.09.015

Bastias, E., Bolivar, M., Ribot, M., Peipoch, M., Thomas, S. A., Sabater, F., & Martí, E. (2020). Spatial heterogeneity in water velocity drives leaf litter dynamics in streams. *Freshwater Biology*, *65*(3), 435–445. https://doi.org/10.1111/fwb.13436

Battin, T., Kaplan, L., 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. https://doi.org/10.1038/ngeo101

Beckman, N., & Wohl, E. (2014). Carbon storage in mountainous headwater streams: The role of old-growth forest and logjams. *Water Resources Research*, *50*, 2376–2393. https://doi.org/10.1002/2013WR014167

Bunte, K., Swingle, K., Turowski, J., Abt, S. R., & Cenderelli, D. A. (2016). Measurements of coarse particulate organic matter transport in steep mountain streams and estimates of decadal CPOM exports. *Journal of Hydrology*, *539*, 162–176. https://doi.org/10.1016/j.jhydrol.2016.05.022

Burrows, R., Magierowski, R., Fellman, J., & Barmuta, L. A. (2012). Woody debris input and function in old-growth and clear-felled headwater streams. *Forest Ecology and Management*, *286*, 73–80. https://doi.org/10.1016/j.foreco.2012.08.038

Chen, X., Wei, X., & Scherer, R. (2005). Influence of wildfire and harvest on biomass, carbon pool, and decomposition of large woody debris in forested streams of southern interior British Columbia. *Forest Ecology and Management*, *208*(1–3), 101–114. https://doi.org/10.1016/j.foreco.2004.11.018

Cole, J., & Caraco, N. (2001). Carbon in catchments: Connecting terrestrial carbon losses with aquatic metabolism. *Marine and Freshwater Research*, *52*, 101–110. https://doi.org/10.1071/MF00084

Cornut, J., Elger, A., Greugny, A., Bonnet, M., & Chauvet, E. (2012). Coarse particulate organic matter in the interstitial zone of three french headwater streams. *Annales de Limnologie - International Journal of Limnology*, *48*(3), 303–313. https://doi.org/10.1051/limn/2012019

Corson-Rikert, H., Wondzell, S., Haggerty, R., & Santelmann, M. V. (2016). Carbon dynamics in the hyporheic zone of a headwater mountain stream in the cascade mountains, Oregon. *Water Resources Research*, *52*, 7556–7576. https://doi.org/10.1002/2016WR019303

Downing, J., Cole, 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. https://doi.org/10.5268/IW-2.4.502

Eggert, S., & Wallace, J. (2007). Wood biofilm as a food resource for stream detritivores. *Limnology and Oceanography*, *52*(3), 1239–1245. https://doi.org/10.4319/lo.2007.52.3.1239

Eggert, S., Wallace, J., Meyer, J., & Webster, J. R. (2012). Storage and export of organic matter in a headwater stream: Responses to long-term detrital manipulations. *Ecosphere*, *3*(9), 1–25. https://doi.org/10.1890/ES12-00061.1

Elosegi, A., Díez, J., & Pozo, J. (2007). Contribution of dead wood to the carbon flux in forested streams. *Earth Surface Processes and Landforms*, *32*(8), 1219–1228. https://doi.org/10.1002/esp.1549

Floyd, T., MacInnis, C., & Taylor, B. (2009). Effects of artificial woody structures on Atlantic salmon habitat and populations in a Nova Scotia stream. *River Research and Applications*, *25*(3), 272–282. https://doi.org/10.1002/rra.1154

Foucreau, N., Puijalon, S., Hervant, F., & Piscart, C. (2013). Effect of leaf litter characteristics on leaf conditioning and on consumption by *Gammarus pulex*. *Freshwater Biology*, *58*(8), 1672–1681. https://doi.org/10.1111/fwb.12158

França, J., Gregório, R., D'Arc de Paula, J., Gonçalves Júnior, J. F., Ferreira, F. A., & Callisto, M. (2009). Composition and dynamics of allochthonous organic matter inputs and benthic stock in a Brazilian stream. *Marine and Freshwater Research*, *60*(10), 990–998. https://doi.org/10.1071/MF08247

Gomi, T., Sidle, R., Bryant, M., & Woodsmith, R. D. (2001). The characteristics of woody debris and sediment distribution in headwater streams, southeastern Alaska. *Canadian Journal of Forest Research*, *31*(8), 1386–1399. https://doi.org/10.1139/x01-070

Graça, M., Ferreira, V., Canhoto, C., Encalada, A. C., Guerrero-Bolaño, F., Wantzen, K. M., & Boyero, L. (2015). A conceptual model of litter breakdown in low order streams. *International Review of Hydrobiology*, *100*(1), 1–12. https://doi.org/10.1002/iroh.201401757

Gulis, V., Suberkropp, K., & Rosemond, A. (2008). Comparison of fungal activities on wood and leaf litter in unaltered and nutrient-enriched headwater streams. *Applied and Environmental Microbiology*, *74*(4), 1094–1101. https://doi.org/10.1128/AEM.01903-07

Guyette, R., Cole, W., Dey, D., & Muzika, R. M. (2002). Perspectives on the age and distribution of large wood in riparian carbon pools. *Canadian*

Journal of Fisheries and Aquatic Sciences, 59(3), 578–585. https://doi.org/10.1139/f02-026

Hall, R. Jr., Wallace, J., & Eggert, S. (2000). Organic matter flow in stream food webs with reduced detrital resource base. *Ecology*, *81*(12), 3445–3463. https://doi.org/10.2307/177506

Harmon, M., & Sexton, J. (1996). *Guidelines for measurements of woody detritus in forest ecosystems*. U.S. LTER Network Office: University of Washington.

Hill, W. (1995). Light limitation in a stream ecosystem: Responses by primary producers and consumers. *Ecology*, *76*(4), 1297–1309. https://doi.org/10.2307/1940936

Jackson, C., Sturm, C., & Ward, J. (2001). Timber harvest impacts on small headwater stream channels in the coast ranges of Washington. *Journal of the American Water Resources Association*, *37*(6), 1533–1549. https://doi.org/10.1111/j.1752-1688.2001.tb03658.x

Kemp, M., & Dodds, W. (2002). The influence of ammonium, nitrate, and dissolved oxygen concentrations on uptake nitrification, and denitrification rates associated with prairie stream substrata. *Limnology and Oceanography*, *47*(5), 1380–1393. https://doi.org/10.4319/lo.2002.47.5.1380

Merten, E., Vaz, P., Decker-Fritz, J., Finlay, J. C., & Stefan, H. G. (2013). Relative importance of breakage and decay as processes depleting large wood from streams. *Geomorphology*, *190*, 40–47. https://doi.org/10.1016/j.geomorph.2013.02.006

Meyer, J., Wallace, J., & Eggert, S. (1998). Leaf litter as a source of dissolved organic carbon in streams. *Ecosystems*, *1*(3), 240–249. https://doi.org/10.1007/s100219900019

Muto, E., Kreutzweiser, D., & Sibley, P. (2009). The influence of riparian vegetation on leaf litter inputs to boreal shield streams: Implications for partial-harvest logging in riparian reserves. *Canadian Journal of Forest Research*, *39*(5), 917–927. https://doi.org/10.1139/X09-017

Nakamura, F., & Swanson, F. (1993). Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. *Earth Surface Processes and Landforms*, *18*(1), 43–61. https://doi.org/10.1002/esp.3290180104

Osei, N., Gurnell, A., & Harvey, G. (2015). The role of large wood in retaining fine sediment, organic matter and plant propagules in a small, single-thread forest river. *Geomorphology*, *235*, 77–87. https://doi.org/10.1016/j.geomorph.2015.01.031

Peterson, B., Wollheim, W., Mulholland, P., Webster, J. R., Meyer, J. L., Tank, J. L., Martí, E:., Bowden, W. B., Valett, H. M., Hershey, A. E., McDowell, W. H., Dodds, W. K., Hamilton, S. K., Gregory, S., & Morrall, D. D. (2001). Control of nitrogen export from watersheds by headwater streams. *Science*, *292*(5514), 86–90. https://doi.org/10.1126/science.1056874

Quinn, J., Phillips, N., & Parkyn, S. (2007). Factors influencing retention of coarse particulate organic matter in streams. *Earth Surface Processes and Landforms*, *32*(8), 1186–1203. https://doi.org/10.1002/esp.1547

Richardson, J., & Danehy, R. (2007). A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. *Forest Science*, *53*(2), 131–147. https://doi.org/10.1093/forestscience/53.2.131

Riedl, H., Marczak, L., McLenaghan, N., & Hoover, T. M. (2013). The role of stranding and inundation on leaf litter decomposition in headwater streams. *Riparian Ecology and Conservation*, *1*(2013), 3–10. https://doi.org/10.2478/remc-2013-0002

Rinella, D., Booz, M., Bogan, D., Boggs, K., Sturdy, M., & Rinella, M. J. (2009). Large woody debris and salmonid habitat in the Anchor River basin, Alaska, following an extensive spruce beetle (*Dendroctonus rufipennis*) outbreak. *Northwest Science*, *83*(1), 57–69. https://doi.org/10.3955/046.083.0106

State Environmental Protection Administration of China. (2002). *Analytical methods for water and wastewater monitoring*. China Environmental Science Press.

Sutfin, N., Wohl, E., & Dwire, K. (2016). Banking carbon: A review of organic carbon storage and physical factors influencing retention in floodplains and riparian ecosystems. *Earth Surface Processes and Landforms*, *41*, 38–60. https://doi.org/10.1002/esp.3857

Swank, W., & Caskey, W. (1982). Nitrate depletion in a second-order mountain stream. *Journal of Environmental Quality*, *11*(4), 581–584. https://doi.org/10.2134/jeq1982.00472425001100040006x

Tank, J., Rosi-Marshall, E., Griffiths, N., Entrekin, S. A., & Stephen, M. L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society*, *29*(1), 118–146. https://doi.org/10.1899/08-170.1

Tank, J., & Webster, J. (1998). Interaction of substrate and nutrient availability on wood biofilm processes in streams. *Ecology*, *79*(6), 2168–2179. https://doi.org/10.1890/0012-9658(1998)079[2168:IOSANA]2.0.CO;2

Taylor, B., & Chauvet, E. (2014). Relative influence of shredders and fungi on leaf litter decomposition along a river altitudinal gradient. *Hydrobiologia*, *721*(1), 239–250. https://doi.org/10.1007/s10750-013-1666-7

Thompson, D. (1995). The effects of large organic debris on sediment processes and stream morphology in Vermont. *Geomorphology*, *11*(3), 235–244. https://doi.org/10.1016/0169-555X(94)00064-X

Triska, F., Sedell, J., Cromack, K., Gregory, S. V., & McCorison, F. M. (1984). Nitrogen budget for a small coniferous forest stream. *Ecological Monographs*, *54*, 119–140. https://doi.org/10.2307/1942458

Turowski, J., Hilton, R., & Sparkes, R. (2016). Decadal carbon discharge by a mountain stream is dominated by coarse organic matter. *Geology*, *44*(11), 27–30. https://doi.org/10.1130/G37192.1

Vannote, R., Minshall, G., Cummins, K., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Wallace, J., Cuffney, T., Eggert, S., & Whiles, M. R. (1997). Stream organic matter inputs, storage, and export for satellite branch at coweeta hydrologic laboratory, North Carolina, USA. *Journal of the North American Benthological Society*, *16*(1), 67–74. https://doi.org/10.2307/1468236

Wallace, J., Eggert, S., Meyer, J., & Webster, J. R. (1997). Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, *277*(5322), 102–104. https://doi.org/10.1126/science.277.5322.102

Webster, J. (2007). Spiraling down the river continuum: Stream ecology and the U-shaped curve. *Journal of the North American Benthological Society*, *26*(3), 375–389. https://doi.org/10.1899/06-095.1

Webster, J., Benfield, E., Ehrman, T., Schaeffer, M. A., Tank, J. L., Hutchens, J. J., & D'Angelo, D. J. (1999). What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology*, *41*(4), 687–705. https://doi.org/10.1046/j.1365-2427.1999.00409.x

Webster, J., Tank, J., Wallace, J., Meyer, J. L., Eggert, S. L., Ehrman, T. P., Ward, B. R., Bennett, B. L., Wagner, P. F., & McTammany, M. E. (2000). Effects of litter exclusion and wood removal on phosphorus and nitrogen retention in a forest stream. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *27*, 1337–1340. https://doi.org/10.1080/03680770.1998.11901453

Wilkins, R., & Peterson, N. (2000). Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. *Forest Ecology and Management*, *139*(1–3), 79–91. https://doi.org/10.1016/S0378-1127(99)00336-9

Wohl, E., Dwire, K., Sutfin, N., Polvi, L., & Bazan, R. (2012). Mechanisms of carbon storage in mountainous headwater rivers. *Nature Communications*, *3*, 1263. https://doi.org/10.1038/ncomms2274

Wohl, E., & Scott, D. (2017). Wood and sediment storage and dynamics in river corridors. *Earth Surface Processes and Landforms*, *42*(1), 5–23. https://doi.org/10.1002/esp.3909

Wondzell, S. (2011). The role of the hyporheic zone across stream networks. *Hydrological Processes*, *25*, 3525–3532. https://doi.org/10.1002/hyp.8119

Xia, X., Zhang, S., Li, S., Zhang, L., Wang, G., Zhang, L., Wang, J., & Li, Z. (2018). The cycle of nitrogen in river systems: Sources, transformation, and flux. *Environmental Science: Processes & Impacts*, *20*, 863–891. https://doi.org/10.1039/C8EM00042E

Yochum, S., Bledsoe, B., David, G., & Wohl, E. (2012). Velocity prediction in high gradient channels. *Journal of Hydrology*, *424-425*, 84–98. https://doi.org/10.1016/j.jhydrol.2011.12.031

Yue, K., García-Palacios, P., Parsons, S., Yang, W., Peng, Y., Tan, B., Huang, C., & Wu, F. (2018). Assessing the temporal dynamics of aquatic and terrestrial litter decomposition in an alpine forest. *Functional Ecology*, *32*, 2464–2475. https://doi.org/10.1111/1365-2435.13143

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*(10), e01523. https://doi.org/10.1002/ecs2.1523

SUPPORTING INFORMATION

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How to cite this article: Liang, Z., Zhuang, L., Yang, J., Yang, F., Yue, K., Ni, X., Xu, Z., Wu, F., Li, H., & Bol, R. (2023). Woody debris dominates the exports of carbon and nitrogen from headwater streams in an alpine forest. *Ecohydrology*, *16*(4), e2531. https://doi.org/10.1002/eco.2531