https://doi.org/10.17221/7/2025-SWR

Annual dynamics of plant litter calcium and magnesium stocks in a subtropical forest headwater stream

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Citation: Chen W.K., Xiong L., Wu Q.Q., Heděnec P., Peng Y., Zhao Z.M., Yuan C.X., Yuan J., Ni X.Y., Wu F.Z., Yue K. (2025): Annual dynamics of plant litter calcium and magnesium stocks in a subtropical forest headwater stream. Soil & Water Res., 20: 164–177.

Abstract: Forest headwater streams serve as critical interfaces between terrestrial forests and downstream aquatic ecosystems, playing essential roles in the storage and movement of carbon (C) and nutrients. However, despite their importance, our understanding of the dynamics of plant litter calcium (Ca) and magnesium (Mg) stocks within these streams remains limited. In this study, we conducted a quantitative analysis of the spatiotemporal dynamics of plant litter Ca and Mg concentrations and stocks in a subtropical forest headwater stream from March 2021 to February 2022. We found that: (1) the average concentrations of litter Ca and Mg were 9.9 and 0.7 mg/g, respectively, with mean stocks of 8 792.3 and 620.8 mg/m^2, respectively; (2) significant variations in litter Ca and Mg concentrations were observed among non-woody debris (13.1 and 0.9 mg/g), fine woody debris (9.0 and 0.5 mg/g), and coarse woody debris (6.1 and 0.4 mg/g), though plant litter type did not significantly affect the stocks of Ca and Mg; and (3) the stocks of Ca and Mg were positively correlated with factors such as rainfall amount, rainfall frequency, water temperature, flow velocity, water depth, electrical conductivity, and discharge, while negatively correlated with stream water alkalinity and dissolved oxygen levels. These findings highlight the critical role of plant litter in headwater streams as a component of forest nutrient stocks and provide empirical support for incorporating headwater streams into the assessment of nutrient stocks and fluxes in forest ecosystems.

Keywords: environmental drivers; litter decomposition; nutrient stoichiometry; riparian nutrient input; seasonal nutrient dynamics; stream ecosystem function

Supported by by the National Natural Science Foundation of China (32271633, 32201342, 32171641) and Natural Science Foundation of Fujian Province (2022J01642).

https://doi.org/10.17221/7/2025-SWR

Forest headwater streams, particularly those in subtropical regions, serve as crucial connectors between terrestrial forests and downstream aquatic ecosystems. While much of the existing research has concentrated on temperate and boreal forests, our study highlights the unique role of subtropical headwater streams in the storage and cycling of carbon (C) and nutrients (Nuven et al. 2022; Liang et al. 2023; Wei et al. 2023). These streams are integral to the forest ecosystem, where riparian forest canopies help regulate temperature and reduce light, limiting photosynthesis and primary productivity within the stream itself (Sakamaki & Richardson 2013; Colvin et al. 2019; Liang et al. 2023). As a result, plant litter serves as the primary source of material and energy for the heterotrophic food webs in these streams (Schulz et al. 2015; Riskin et al. 2017; Tonin et al. 2017). Nutrient input from plant litter into headwater streams occurs through leaching, abrasion, and microbial decomposition (Liang et al. 2019; Zhang et al. 2019; Carey et al. 2021). Calcium (Ca) and magnesium (Mg) are primarily released into the environment through leaching and the physical breakdown of plant litter. These nutrients actively participate in forest carbon and nutrient cycling, significantly impacting the entire forest ecosystem (Wipfli et al. 2007; Chen et al. 2016). The stocks of Ca and Mg are tightly linked to the processes of litter input, decomposition, and output. Environmental factors such as temperature, moisture, and stream flow regulate the leaching and movement of these nutrients from decomposing litter into the surrounding soil and water, influencing the rate and extent of their release (Chauvet et al. 2016; Lidman et al. 2017; Gao et al. 2022). Ca and Mg are essential for plant growth and metabolic processes, and their presence in plant litter is closely tied to food webs in headwater streams and broader forest nutrient cycling (Guo et al. 2019; Yue et al. 2021; Liu et al. 2023). While most existing studies have focused on carbon and macronutrients (e.g., nitrogen and phosphorus) and often rely on static measurements or short-term observations (Zhang et al. 2015, 2016; Hou et al. 2021), our study provides a year-long analysis of the spatiotemporal dynamics of plant litter Ca and Mg stocks. This approach captures seasonal variations and more comprehensively assesses the impact of environmental factors. Previous studies often examine artificial interventions, such as liming in acidified forests, on litter decomposition and nutrient release (Lin et al. 2015; Allen et al. 2020). While these studies offer insights into nutrient release under manipulated conditions, they do not account for natural spatiotemporal variability. In contrast, our observational approach enables us to assess the natural seasonal and spatial variations of Ca and Mg stocks in headwater streams, filling a critical gap in the literature.

Our research distinguishes itself from studies that focus primarily on vegetation type or soil characteristics by emphasizing the role of stream-specific factors, such as water temperature, flow velocity, and stream morphology, in regulating plant litter Ca and Mg stocks. These physical and chemical stream characteristics, which directly and indirectly mediate litter input, decomposition, and transport, are often overlooked but are key drivers in nutrient cycling (Rosemond et al. 2015; Zhang et al. 2019; Zhao et al. 2023). For example, riparian forest type can influence litter Ca and Mg stocks in multiple ways. It determines both the nutrient composition of plant litter, due to species-specific traits, and the quantity of litter entering the stream (Hu et al. 2023). These differences contribute to spatial heterogeneity in nutrient stocks across stream sections (Jin et al. 2022). Additionally, its effect on bank erosion and deposition alters litter accumulation and decomposition patterns, further shaping Ca and Mg dynamics (Juez et al. 2019; Nelson Mwaijengo et al. 2020). Different types of plant litter also contribute significantly to variations in litter Ca and Mg stocks, as the initial concentrations and input-output dynamics of these nutrients can differ substantially across litter types (Liang et al. 2019). In addition, stream characteristics such as active channel width, water depth, temperature, alkalinity, dissolved oxygen (DO), and electrical conductivity (EC) serve as important moderators of litter Ca and Mg stocks by influencing the distribution and decomposition of plant litter (Ferreira & Chauvet 2011; Pozo et al. 2011; Lidman et al. 2017). Despite the critical role of headwater streams in forest nutrient dynamics, quantitative assessments of plant litter Ca and Mg stocks remain scarce. Most nutrient budget models for forests focus on terrestrial processes, often overlooking the contributions of headwater streams (Matson et al. 2014; Uhlig & von Blanckenburg 2019). By incorporating headwater streams into nutrient stock and flux estimations could offer a more comprehensive understanding of forest nutrient cycling.

Here, we conducted a monthly field investigation to assess the dynamics of Ca and Mg stocks in plant litter within a subtropical evergreen broadleaved forest headwater stream located in the upper reaches of the Minjiang River, Sanming, southeastern China. From March 2021 to February 2022, litter was collected monthly, Ca and Mg concentrations were measured, and their stocks were subsequently calculated. We hypothesised that: (1) litter Ca and Mg stocks would exhibit significant seasonal variation, with the highest stocks occurring in the rainy season and the lowest in the dry season; and (2) multiple factors, including riparian forest type, plant litter type, and physicochemical stream characteristics (closely related to litter input, output, and decomposition processes), would influence the stocks of litter Ca and Mg.

MATERIAL AND METHODS

Study area. The research was conducted at the Fujian Sanming Forest Ecosystem National Observation and Research Station, located in southeast China (26°19'N, 117°36'E). The region experiences a subtropical oceanic monsoon climate, with a long-term mean annual temperature of 19.3 °C and mean annual rainfall of 1 610 mm (Zhao et al. 2023). Based on historical climatic patterns, the rainy season typically occurs from March to August, while the dry season spans from September to February. To assess whether the sampling period (March 2021 to February 2022) reflected typical climatic conditions, we compared precipitation during this period with the five-year average (2018–2022). The total precipitation recorded during the study was 1 262.54 mm, lower than the five-year average of 1 518.83 mm from the ERA5-Land dataset, suggesting relatively dry conditions for that year (Table S1 in Electronic Supplementary Material (ESM)). The terrain is characterised by low mountains and hills, with elevations ranging from 250 to 500 m. The dominant soil type is Ultisols, which are sandy and acidic according to the USDA classification system (Das & Maharjan 2022). Vegetation is primarily subtropical evergreen broad-leaved forest, with dominant species including *Castanopsis carlesii*, *Cunninghamia lanceolata*, and *Pinus massoniana* (Xu et al. 2017).

Experimental design and field measurement. The study was conducted in a subtropical forested watershed of the upper Minjiang River, focusing on a selected headwater stream for monitoring (Figure 1). The stream was divided into 17 sampling reaches (S1–S17), based on specific environmental criteria, including riparian forest type (broadleaved or mixed forests), the presence of tributaries, stream gradient, and active channel width. The boundaries of each reach were delineated through field surveys by identifying changes in riparian forest type, locations of tributary confluences, and significant variations in stream gradient or width. For example, tributary confluences served as the starting points for new sampling reaches, and changes in forest type were used to segment the reaches. Additionally, notable shifts in stream gradient or channel width within short distances were considered further criteria for subdivision. These factors determined the precise boundaries of each sampling reach (Table S2 in ESM). The length of each reach was measured using a handheld GPS device (GPS-A8, ZL, China). To account for spatial heterogeneity, three permanent sampling quadrats (1 m × actual stream width) were randomly established within each reach, and their positions were clearly marked. During the selection of quadrats, we ensured that each quadrat was placed in a location that minimised overlap, ensuring their independence from each other. Plant litter was categorised into three types: non-woody debris (NWD, leaf litter and twigs < 1 cm in diameter), fine woody debris (FWD, 1–10 cm in diameter), and coarse woody debris (CWD, >10 cm in diameter). All plant litter within each quadrat was collected manually or using a 2 mm mesh net to ensure complete removal down to the streambed substratum, continuing until bedrock or sediment layers without litter were reached. Once collected, the litter was sorted into the respective categories. In total, 612 composite samples were collected for both NWD and FWD (12 months × 17 reaches × 3 quadrats per reach). All collected litter from each quadrat was combined into a composite sample by litter type, placed in polyethylene bags, and transported to the laboratory.

Due to the large size and episodic nature of CWD, its sampling was conducted differently. Specifically, CWD was sampled twice: once during the rainy season (July 2021) and once during the dry season (February 2022). During these sampling events, the diameter and length of all CWD within each reach were systematically recorded from downstream to upstream. For each reach, CWD samples from the three quadrats were treated as independent replicates, resulting in a total of 102 composite samples (2 sampling events × 17 reaches × 3 quadrats per reach). Simultaneous stream physicochemical measurements were taken during each monthly sampling. A portable multi-parame-

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ter water quality instrument (YSI Proplus, Xylem, USA) was used to measure stream water temperature, pH, alkalinity, DO, and EC, with five replicates per reach. Flow velocity was measured with a portable current meter (LS1206B, Jiangsu Nan Shui Water and Power Technology Co., Ltd., China), and stream discharge was calculated based on flow velocity, active channel width, and water depth. The active channel width and water depth were measured at each sampling event using a measuring tape, while stream gradient was determined using ArcGIS (Ver. 10.2, 2013) software. Riparian forest type was classified as either broadleaved forests (dominated by *Castanopsis carlesii*) or mixed forests (dominated by *Castanopsis carlesii* and *Pinus massoniana*), and the presence or absence of tributaries was recorded. Free-air rainfall data were continuously recorded using three Tumbler Rain Sensors (SL3-1, Shanghai Meteorological Instrument Factory Co., China), installed in open areas near the study site, each covering approximately 400 m^2. The rain gauges, with a funnel diameter of 20 cm and a tipping bucket resolution of 0.20 mm per tip, logged hourly rainfall data throughout the study period. Rainwater was collected in 5 L polyethylene containers beneath each rain gauge, and rainfall samples were retrieved after each event using 250 mL polyethylene bottles, rinsed twice with deionized water. The total monthly precipitation was calculated, and rainfall frequency was defined as the number of discrete rainfall events per month. A rainfall event was defined as one or more hours of rainfall, with at least 6 consecutive hours of no precipitation before the next event. Detailed physicochemical characteristics of each sampling reach are presented in Table S3 in ESM.

Due to logistical constraints, the study period was limited to one year (March 2021–February 2022). We acknowledge that this short duration may limit the robustness and generalizability of our conclusions. Future studies with longer monitoring periods are recommended to capture broader interannual variability and enhance the reliability of our findings.

Laboratory analyses. The collected litter was first washed with distilled water to remove surface sediments and impurities, then air-dried and weighed.

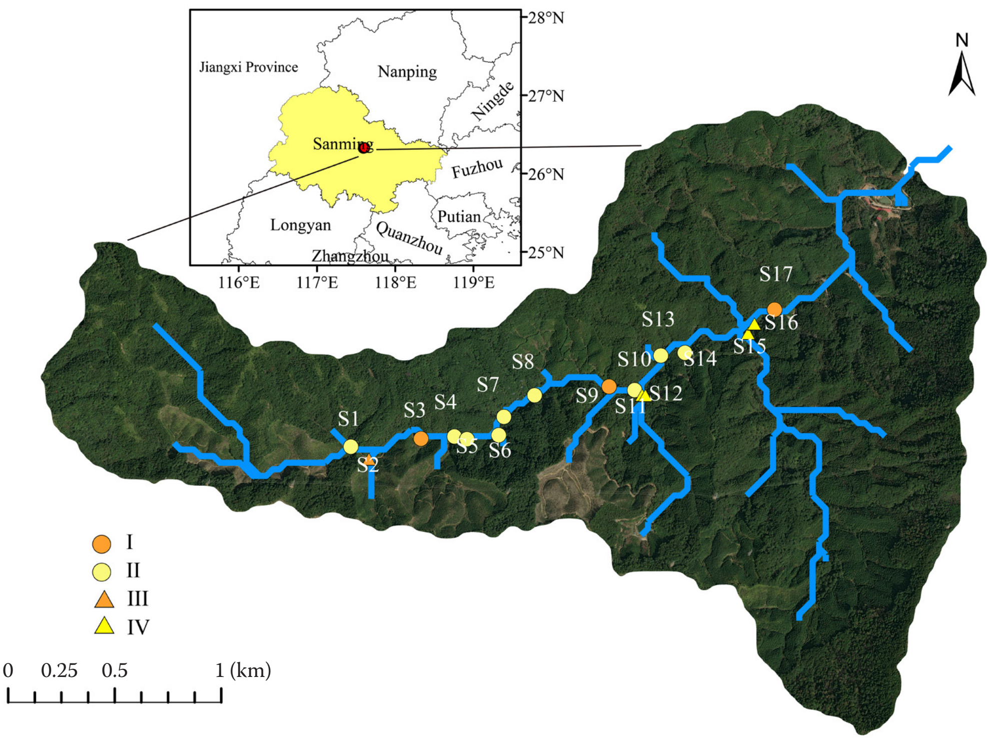

Figure 1. Map of the assessed headwater stream in Sanming, Fujian Province, China; circles and triangles indicate the sampling reaches from the stream source (S1) to the mouth (S17); the inset shows the location of the study area within Fujian Province

I – sampling reaches with mixed riparian coniferous forest and without a tributary; II – sampling reaches with broadleaved riparian forest and without a tributary; III – sampling reaches with mixed riparian coniferous forest and with a tributary; IV – sampling reaches with broadleaved riparian forest and with a tributary

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FWD and CWD were categorized into five decay grades based on previous studies (Burrows et al. 2012; Bataineh & Daniels 2014). Grade I represents fresh debris with mostly intact structure and unchanged wood. Grade II indicates early decomposition, with partial structure breakdown but still relatively hard wood and some bark shedding. Grade III is characterized by significant bark shedding, soft wood, and visible rotting, often accompanied by moss and fungi. Grade IV consists of debris that is easily punctured, with some remaining hardness, no bark, and possibly exhibiting moss, fungi, or invasive roots. Grade V represents completely decomposed debris, where the wood is easily pierced and prone to powdering (Burrows et al. 2012). The sorted litter samples were oven-dried at 65 °C to a constant weight, then ground to pass through a 60-mesh screen. Three grams of the ground samples were digested with a mixture of nitric acid and perchloric acid and subsequently processed in a microwave digestion apparatus (MWD-800, Shanghai Metash Instruments Co., Ltd., China). The Ca and Mg concentrations were determined using an ICAPQ inductively coupled plasma mass spectrometer (ICP-MS, ULTIMA-2, HORIBA Jobin Yvon, France).

Statistical analysis. The storage of plant litter within each sampling reach (M_a, g/m^2) was calculated using the following equation (Wei et al. 2022):

$$M_a = \frac{1}{n}\sum_{i=1}^{3}\frac{m_i}{A}$$

where:
m_i – the dry weight of plant litter in sampling reach i;
A – the area of the sampling quadrat (n = 3).

The storage of Ca and Mg (M_b,g/m^2) within each sampling reach was then calculated according to the following equation:

$$M_b = \sum M_a C$$

where:
C – the concentration of Ca or Mg (mg/g).

Linear mixed-effects models (LMM) were used to assess the effects of factors such as litter type, riparian forest type, and stream characteristics on the storage of plant litter Ca and Mg in headwater streams (Kuznetsova et al. 2017). When a significant effect was detected, Tukey's post-hoc test was applied at α = 0.05. To further evaluate the relative importance of different factors, a model selection approach using maximum likelihood estimation was employed. The importance of each factor was determined by summing the Akaike weights from all models that included that factor, with a threshold of 0.8 used to differentiate the importance of factors (Wagenmakers & Farrell 2004). All statistical analyses were performed using R software (Ver 4.3.1, 2023).

RESULTS

Spatial dynamics of litter Ca and Mg concentrations and stocks. The concentration of litter Ca ranged from 7.3 to 13.3 mg/g, and Mg from 0.5 to 1.0 mg/g across different litter types and sampling reaches (Figure 2). The data indicate a general decline in the stocks of Ca and Mg from the stream source to the mouth, although with some fluctuations. Specifically, the mean Ca stocks in total litter, NWD, FWD, and CWD ranged from 1 672.3 to 15 083.8 mg/m^2, from 1 132.7 to 6 639.7 mg/m^2, from 128.3 to 2 337.3 mg/m^2, and from 5.8 to 8 286.8 mg/m^2, respectively. For Mg, the stocks ranged from 114.4 to 895.4 mg/m^{2,} from 91.4 to 534.5 mg/m^2, from 5.9 to 121.8 mg/m^2, and from 0.6 to 513.8 mg/m^2, respectively.

Temporal dynamics of litter Ca and Mg concentrations and stocks. In the dry season, the concentration of Ca in NWD and FWD was significantly higher than in the rainy season (P < 0.001, n = 17), while Mg concentration in NWD showed an opposite trend, being significantly higher in the rainy season (P < 0.05, n = 17; Figure 3). The total stocks of litter Ca and Mg varied significantly between seasons, with values of 5 430.4 mg/m^2 and 420.0 mg/m^2 in the rainy season, respectively, and 3 302.3 mg/m^2 and 210.9 mg/m^2 in the dry season. Both in the rainy and dry seasons, the stocks of Ca and Mg varied significantly among litter types. NWD contributed the majority of litter Ca (54.5%) and Mg (57.1%) stocks, followed by CWD and FWD (Figure 4A, B).

Factors affecting the stocks of litter Ca and Mg. Decay grade significantly influenced the stocks of Ca and Mg in FWD, with a general decrease from Grade I to V, but did not affect CWD stocks (Figure 4C, D). In contrast, riparian forest type and the presence of tributaries did not significantly affect litter Ca and Mg stocks either as a whole or for individual litter types (Figure 5). Rainfall amount, rainfall frequency, water temperature, discharge, flow velocity, water depth, and EC were all positively associated with total litter Ca and Mg stocks under the relatively dry

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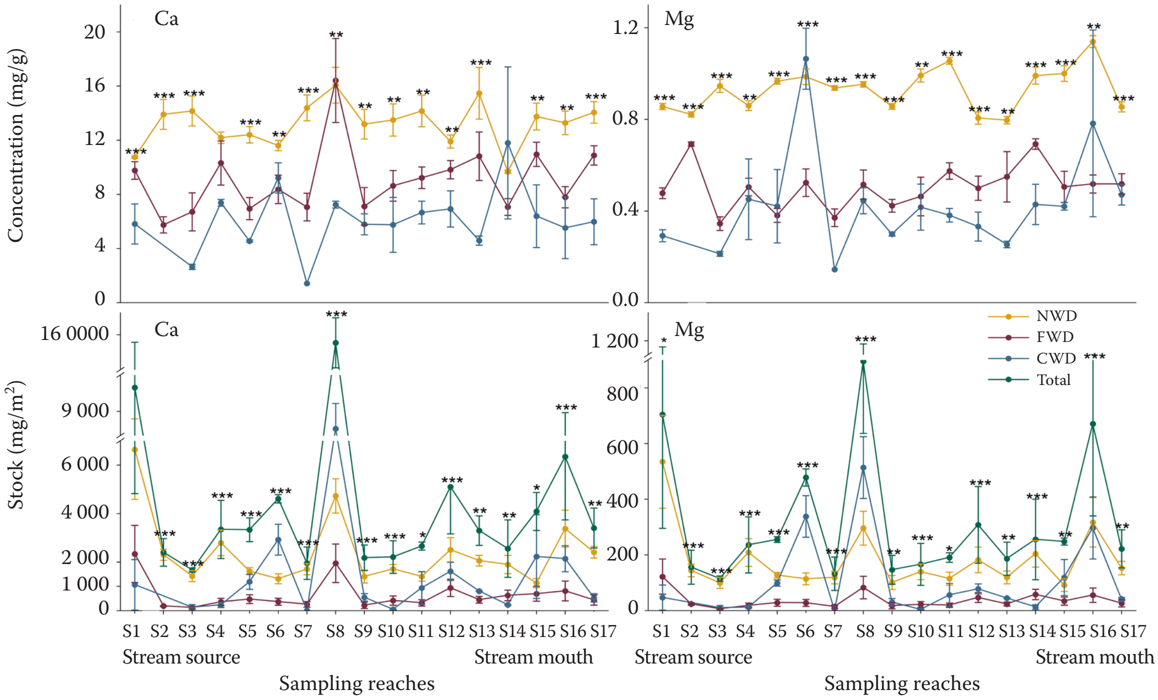

Figure 2. Spatial dynamics of plant litter Ca and Mg concentrations and stocks in the forest headwater stream; S1 to S17 indicate the sampling reaches from the stream source to its mouth; for NWD and FWD, data were based on 12 monthly samples per reach (n = 12); for CWD and total litter, data were based on two seasonal samples per reach (n = 2)

NWD – non-woody debris; FWD – fine woody debris; CWD – coarse woody debris; total – all plant litter; asterisks indicate significant differences between litter types at a specific sampling reach (*, **, ***P < 0.05, 0.01, 0.001); error bars represent the standard error of the mean (± standard error)

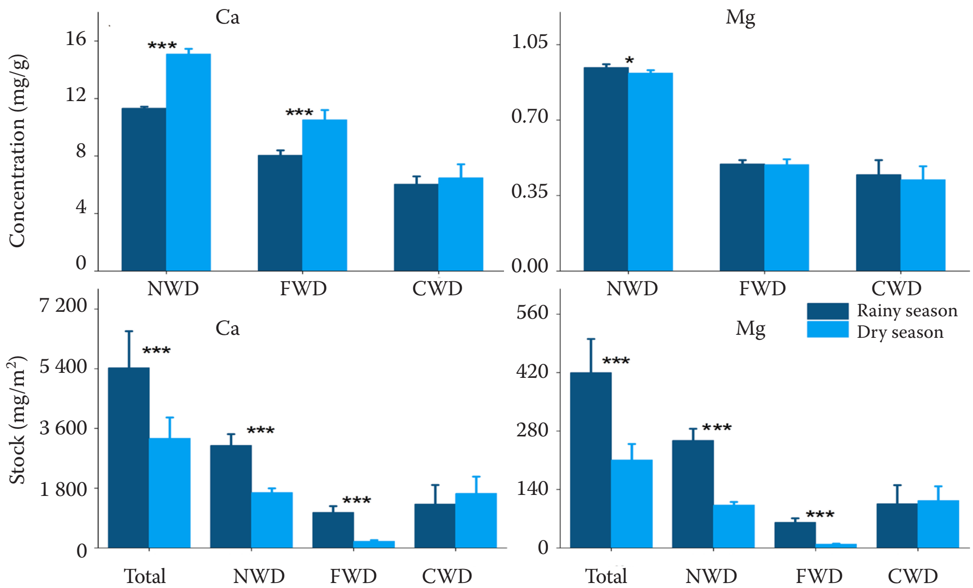

Figure 3. Dynamics of plant litter Ca and Mg concentrations and stocks in the forest headwater stream during the rainy and dry seasons; for NWD and FWD, monthly samples were averaged within each season to obtain one seasonal value per sampling reach; for CWD, samples were collected once per season

NWD – non-woody debris; FWD – fine woody debris; CWD – coarse woody debris; total – all plant litter; asterisks indicate significant differences between seasons for the same litter type (n = 17 reaches per season, *, **, ***P < 0.05, 0.01, 0.001); error bars represent the standard error of the mean (± standard error)

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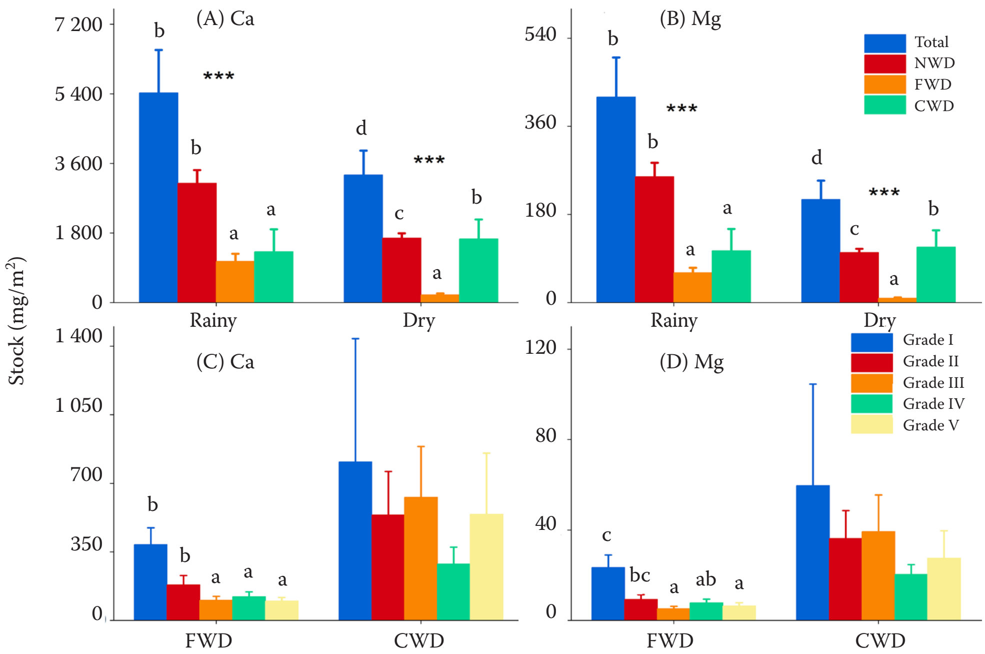

Figure 4. Stocks of litter Ca and Mg among different litter types and decay grades in the headwater stream; lowercase letters indicate significant differences among litter types or decay grades within each panel (α = 0.05); for panels (A) and (B), each litter type includes 17 sampling reaches (n = 17 per season), for panels (C) and (D), sample sizes (n) for each decay grade correspond to the number of sampling reaches in which that specific decay class occurred

NWD – non-woody debris; FWD – fine woody debris; CWD – coarse woody debris; total – all plant litter; asterisks indicate significant differences between rainy and dry seasons for the same litter type (*, **, *** $P < 0.05, 0.01, 0.001$); error bars represent the standard error of the mean (± standard error)

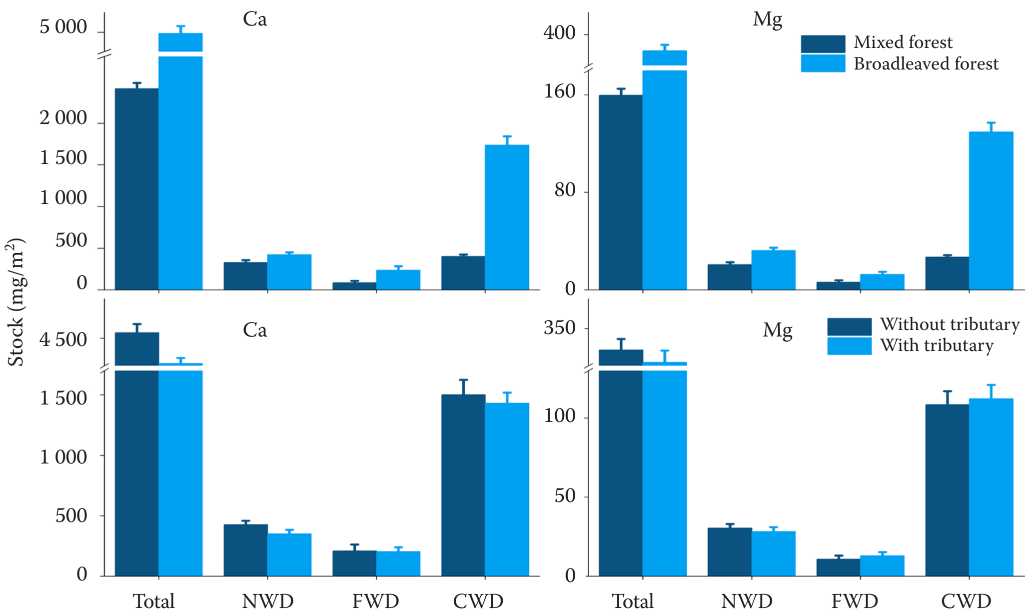

Figure 5. Effects of riparian forest type and the presence of a tributary on the stocks of Ca and Mg in litter as a whole and among different litter types; sample sizes (n) for each group are as follows: broadleaved forest (n = 13), mixed forest (n = 4), with tributary (n = 6), and without tributary (n = 11), based on the number of sampling reaches assigned to each category (Table S2 in ESM)

NWD – non-woody debris; FWD – fine woody debris; CWD – coarse woody debris; total – all plant litter; error bars represent the standard error of the mean (± standard error)

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Table 1. Effects of environmental factors on the stocks of plant litter Ca and Mg in the forest headwater streams as assessed using linear mixed-effect models; estimates (i.e., model slopes) and *P*-values were reported

Factor	Total				NWD				FWD				CWD			
	Ca		Mg		Ca		Mg		Ca		Mg		Ca		Mg	
	slope	*P*	slope	*P*	slope	*P*	slope	*P*	slope	*P*	slope	*P*	slope	*P*	slope	*P*
Rainfall amount (mm)	0.001	< **0.001**	0.001	< **0.001**	0.001	< **0.001**	0.001	**0.012**	0.002	< **0.001**	0.002	< **0.001**	–0.001	**0.020**	–0.001	**0.021**
Rainfall frequency (times/month)	0.03	< **0.001**	0.051	< **0.001**	–0.001	0.862	0.011	0.273	0.113	< **0.001**	0.136	< **0.001**	–0.036	< **0.001**	–0.033	< **0.001**
Water temperature (°C)	0.012	< **0.001**	0.018	< **0.001**	–0.001	0.587	0.015	< **0.001**	0.039	< **0.001**	0.074	< **0.001**	–0.010	< **0.001**	–0.010	< **0.001**
Discharge (L/s)	0.001	< **0.001**	0.001	< **0.001**	0.001	< **0.001**	0.001	< **0.001**	0.001	**0.0013**	0.001	< **0.001**	–0.001	0.254	–0.001	0.062
Flow velocity (m/s)	0.361	< **0.001**	0.545	< **0.001**	0.565	< **0.001**	0.861	< **0.001**	1.486	< **0.001**	1.801	< **0.001**	–0.284	**0.025**	–0.299	**0.011**
Active channel width (cm)	0.001	0.123	0.001	**0.039**	0.001	0.083	0.001	0.505	0.001	0.133	0.001	0.263	–0.001	0.085	–0.001	0.092
Water depth (cm)	0.003	**0.002**	0.004	< **0.001**	0.002	0.560	0.004	0.368	0.029	< **0.001**	0.033	< **0.001**	–0.005	**0.026**	–0.005	**0.012**
Stream gradient (°)	0.330	**0.034**	0.245	0.106	0.247	0.120	0.162	0.265	0.205	0.244	0.115	0.693	0.277	0.455	0.188	0.494
pH	0.022	0.094	0.033	0.085	0.013	0.421	0.302	0.367	0.391	0.095	0.218	**0.041**	–0.002	0.336	–0.010	0.135
DO (mg/L)	–0.001	< **0.001**	–0.011	< **0.001**	–0.007	0.087	–0.026	< 0.001	–0.032	**0.002**	–0.041	< **0.001**	0.006	0.271	0.006	0.244
EC (um/m)	0.296	**0.005**	0.425	**0.002**	–0.170	0.439	0.113	0.904	0.746	0.406	0.763	0.462	–0.218	0.399	–0.298	0.214
Alkalinity (mg/L)	–0.001	< **0.001**	–0.003	< **0.001**	–0.016	< **0.001**	–0.014	< **0.001**	–0.012	**0.002**	–0.015	< **0.001**	–0.001	0.623	–0.003	0.069

Total – all plant litter; NWD –non-woody debris; FWD – fine woody debris; CWD – coarse woody debris; DO – dissolved oxygen; EC – electrical conductivity; bold indicates significant effects

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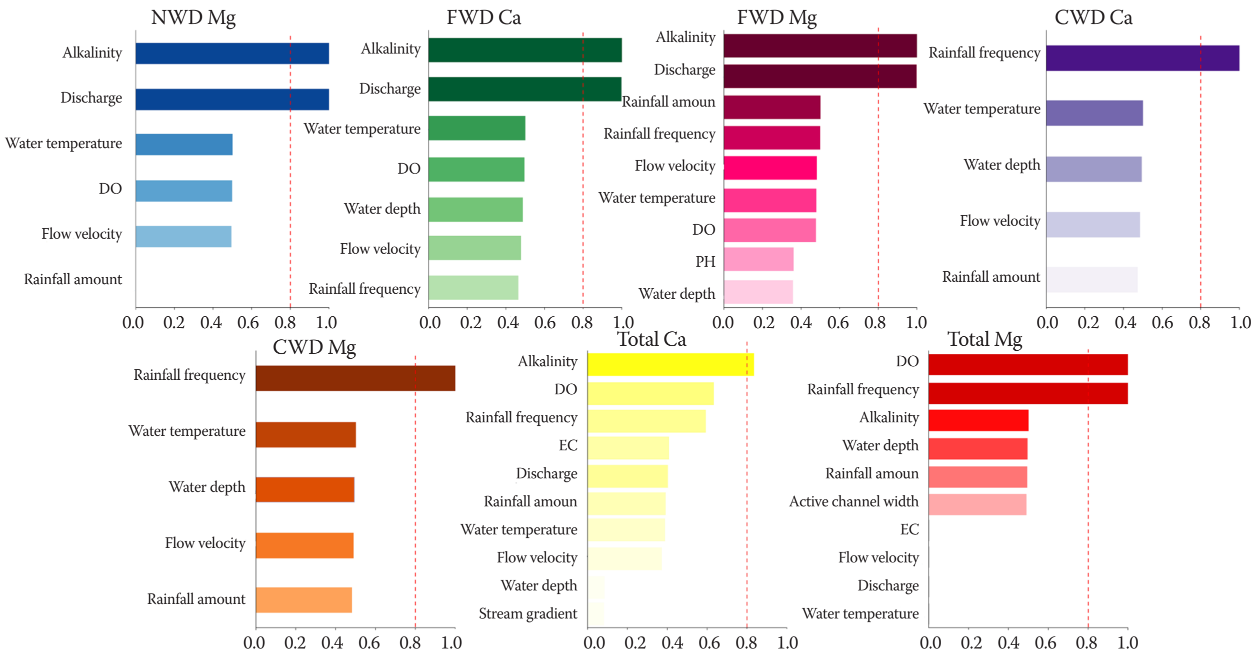

Figure 6. Model-averaged importance of factors influencing the stocks of litter Ca and Mg, assessed using a linear mixed-effect model selection approach; a cutoff value of 0.8 was applied to identify key influencing factors
Colour gradients from dark to light indicate decreasing importance; DO – dissolved oxygen; EC – electrical conductivity; NWD – non-woody debris; FWD – fine woody debris; CWD – coarse woody debris; total – all plant litter

conditions of the study period. These relationships may reflect hydrological and temperature regimes specific to drier years, and their strength or direction may vary under wetter climatic conditions. Conversely, water DO and alkalinity had negative effects on total litter Ca and Mg stocks (Table 1). When analyzing different litter types, similar trends were observed, although the strength of the effects varied among litter types. Among the significant factors, discharge, rainfall frequency, water alkalinity, and DO were identified as the most important variables controlling litter Ca and Mg stocks, both overall and for specific litter types (Figure 6).

DISCUSSION

The dynamics of litter Ca and Mg stocks in headwater streams are influenced by litter input, output, decomposition, and various environmental factors (Renshaw et al. 2022; Hu et al. 2023). As hypothesised, the highest litter Ca and Mg stocks occurred during the rainy season, driven by increased litter inputs from enhanced leaf litter production and higher surface runoff during heavy rainfall (Hart et al. 2013; Tonin et al. 2017; Jin et al. 2022; Wang et al. 2022). However, it is important to note that the precipitation during the study period (March 2021 to February 2022) was lower than the five-year average, suggesting relatively dry conditions. This may result in conservative estimates of seasonal differences compared to wetter years. Our findings support this mechanism, showing positive correlations between rainfall amount and litter Ca and Mg stocks, except for CWD. The negative correlation in CWD may be due to its increased susceptibility to physical transport and removal during high flows in the rainy season (Pye et al. 2023). Spatially, litter Ca and Mg stocks were higher in upstream reaches, likely due to denser riparian vegetation, narrower stream channels, and lower flow velocities that favour litter accumulation (Scarsbrook et al. 2001; Mbaka & Schäfer 2016; Hu et al. 2023). However, riparian forest type did not significantly affect litter Ca and Mg stocks. This may be due to the similar overall litter production rates between broadleaved and mixed forests (Jin et al. 2022) and the frequent alternation of these forest types along the stream, which could dilute potential differences at the reach scale. More pronounced effects may emerge when comparing distinct watersheds dominated by contrasting forest types (e.g., pure coniferous vs. broadleaved systems).

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Stream discharge and flow velocity positively influenced plant litter Ca and Mg stocks across all litter types. Higher discharge and faster flow velocities may enhance both lateral and upstream litter inputs into streams, despite simultaneously increasing litter outputs (Tank et al. 2010; Pye et al. 2023). Additionally, stream characteristics such as water temperature, active channel width, water depth, and stream gradient can affect litter stocks by influencing litter transport and decomposition. For example, higher water temperatures typically accelerate microbial decomposition (Ferreira et al. 2014; Ferreira & Canhoto 2015). Interestingly, we observed a positive relationship between water temperature and litter Ca and Mg stocks, possibly reflecting suppressed microbial decomposition due to reduced DO levels in warmer water (Iñiguez-Armijos et al. 2016; Zhang et al. 2019). This unexpected result may also be influenced by streamflow, as higher discharge could increase litter inputs or promote nutrient retention despite elevated temperatures, thereby contributing to the observed accumulation of Ca and Mg.

Furthermore, stream chemical properties such as pH, EC, and alkalinity influence litter decomposition and regulate Ca and Mg stocks indirectly (Wang et al. 2015; Gomes et al. 2018; Valett & Ely 2019; Wei et al. 2022). Among all environmental variables, rainfall frequency, stream discharge, alkalinity, and DO were the most critical factors controlling litter Ca and Mg stocks. Higher alkalinity may affect the mobility or bioavailability of divalent cations such as Ca^{2+} and Mg^{2+}, influencing their accumulation in litter (Kittaka 2023; Zhao et al. 2023). On the other hand, higher DO generally accelerates microbial decomposition, leading to faster nutrient release (Dangles et al. 2004; Amani et al. 2019). Increased rainfall frequency enhances lateral litter inputs, while stream discharge affects litter transport dynamics. These findings, obtained during a relatively dry year, may be specific to these hydrological and temperature regimes. The relative importance of these factors may change under wetter or more variable climatic conditions. It remains possible that the relative importance of these drivers could shift under wetter or more variable climatic scenarios. A comparative analysis across climatic zones revealed intermediate Ca concentrations in our subtropical mixed forest litter (9.9 mg/g), falling between subalpine coniferous (20.1 mg/g) and tropical broadleaf forests (3.1 mg/g) (Table S4 in ESM). These differences underscore the interaction between temperature, precipitation, and forest type, shaping nutrient retention patterns. Lower Ca concentrations in tropical systems likely result from faster decomposition rates in consistently warm and moist conditions (Dezzeo et al. 1998), while higher concentrations in subalpine coniferous forests reflect slower decomposition and greater nutrient accumulation (Yue et al. 2016). Such cross-biome comparisons highlight distinct nutrient cycling patterns in subtropical headwaters, with important implications for nutrient export to downstream ecosystems. Under projected climate change scenarios, increased rainfall intensity and frequency may amplify these dynamics in different ways depending on litter type. More frequent rainfall events could enhance NWD and FWD inputs through intensified surface runoff (Hart et al. 2013), while extreme rainfall could accelerate CWD removal due to its vulnerability to hydraulic transport (Pye et al. 2023). This differential response emphasises the importance of incorporating litter type-specific responses in climate resilience strategies for headwater ecosystems. Enhanced rainfall frequency, as predicted by the IPCC AR6 report, could increase NWD and FWD stocks, potentially providing more nutrients to downstream environments. Conversely, the depletion of CWD stocks may negatively affect long-term carbon sequestration due to its slower decomposition rate (Wang et al. 2021). Therefore, climate-driven hydrological changes could decouple nutrient (Ca/Mg) cycling from organic matter dynamics, suggesting the need for adaptive management practices, such as riparian buffer maintenance or structural interventions, to mitigate increased litter export.

Finally, we acknowledge two important limitations of this study. First, the relatively short observation period of one year limits the generalizability of our findings. The study period (March 2021 to February 2022) was drier than the recent five-year average, which may have affected litter inputs and hydrological processes. As interannual variability in environmental factors, such as rainfall and temperature, can significantly impact litter dynamics, the results should be interpreted with caution, particularly when extrapolating to wetter or more typical years. Longer-term monitoring is recommended to better capture seasonal and interannual trends, strengthening the conclusions on the spatiotemporal dynamics of Ca and Mg stocks. Second, this study did not consider biotic factors such as microbial communities and macroinvertebrates, which are known to play key roles in litter decomposition. Thus, our understanding

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of decomposition mechanisms is incomplete. Future studies should integrate these biotic components to better characterize their role in nutrient cycling in headwater ecosystems.

CONCLUSION

This study offers valuable insights into nutrient cycling in forest ecosystems by examining the spatiotemporal dynamics of plant litter Ca and Mg stocks in subtropical headwater streams. Our findings revealed significant seasonal and spatial variations, with the highest nutrient stocks occurring in the rainy season due to increased litter inputs and the lowest in the dry season. These results highlight the critical role of headwater streams as hotspots for nutrient storage and cycling.

The study also emphasizes the importance of stream characteristics – such as water temperature, flow velocity, and channel morphology – in regulating nutrient stocks, as well as the influence of climatic factors like rainfall. These relationships provide essential information for developing nutrient management strategies aimed at maintaining soil fertility and forest ecosystem health. Under projected climate change scenarios, more frequent and intense rainfall events may exacerbate fluctuations in nutrient stocks. Specifically, extreme precipitation events could increase NWD and FWD inputs while accelerating CWD loss, which may threaten long-term carbon sequestration. These findings underscore the need for adaptive riparian management strategies to mitigate nutrient export risks associated with hydrological changes.

Our results also highlight the conservation value of headwater streams in sustaining critical nutrient supplies, such as Ca and Mg, which are essential for forest productivity. Given the significant influence of hydrological and environmental factors, further research is needed to explore these interactions under varying climatic conditions.

In conclusion, we provide strong evidence for the importance of subtropical headwater streams in forest nutrient cycling. This research offers practical guidance for sustainable forest management and climate adaptation. However, as the study period (March 2021 to February 2022) coincided with a drier-than-average year, the observed patterns, especially those related to litter input and hydrological processes, may reflect conservative estimates. The identified relationships between environmental drivers and nutrient stocks may also vary under different climatic conditions, so caution is advised when extrapolating these findings to wetter or more extreme years. Therefore, long-term monitoring that accounts for broader interannual variability, along with consideration of additional environmental and biological factors, is recommended to enhance the applicability of these findings and refine our understanding of nutrient dynamics in these ecologically important ecosystems.

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Received: January 28, 2025
Accepted: May 7, 2025
Published online: May 19, 2025