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Research Article

Detritus in small streams of the Tatra mountains – the role of abiotic factors

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The quantity and quality of detrital input to alpine and forested mountain streams depends mainly upon the type of adjacent riparian vegetation: from alpine meadows to lower mountain forests. Benthic organic matter (BOM) and transported organic matter (TOM) content were quantified in six streams flowing in different vegetation zones of the Tatra Mountains. Annual BOM ranged from 0.1 g AFDM m^{-2} in the alpine meadow zone to 5.9 g AFDM m^{-2} in the lower mountain zone, and the coarse fraction of BOM was generally greatest. Similarly, average annual seston (particles <100 μm) concentrations increased from 0.1 to 0.4 mg AFDM l^{-1} in consecutive studied zones. VFPOM constituted 97% of total TOM. In the Tatra Mountains, stream BOM storage and the amount of TOM were negatively related to altitude and stream gradient and positively related to stream width and order. Very fine fractions of TOM in Tatra streams were negatively correlated with stream gradient. The performed analysis revealed some discrepancies concerning relation of BOM and TOM to stream gradient and order with that published for North American temperate zone streams from undisturbed forested catchments.

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1 Introduction

Allochthonous organic matter plays a central role in low order streams [1], including alpine and mountain streams, mostly as the energy base that supports heterotrophic stream organisms such as microorganisms, invertebrates, and fish. The quantity and quality of detrital materials entering streams depend upon the adjacent riparian zone [2] and are key parameters, determining both the density and composition of the stream ecosystem [3]. In alpine streams riparian vegetation is sparse, and the annual allochthonous input and storage is much more lower compared to the streams below the tree line that receive large amounts of organic matter in the form of leaves and wood [4]. Those authors assume that in alpine streams the role of allochthonous organic matter seems to be lower compared with autochthonous ones.

Allochthonous material (leaves, wood) that falls into the water can be stored on the bottom as benthic organic matter (BOM) or may be transported downstream (transported organic matter (TOM)). Since 1986, there have been numerous publications (~180) focusing on organic matter budgets in streams published in the major aquatic journals [5]. Among them were many studies performed in various regions of the world on the organic matter dynamics mostly in mountain streams, while high mountain streams were investigated only occasionally. Alpine (high mountain, above tree line) and forested mountain streams are characterized by geomorphic and hydrologic variables that create common patterns of organic matter processes. Forested mountain streams constitute a transition between forest and downstream ecosystems and are exceptionally effective in detritus retention and processing. In the Tatra Mountains, the highest mountains in Poland, benthic detrital storage and transport has been measured in several streams by the author and co-workers [6–10]. All the obtained results concerning BOM and TOM were used here for regression analysis with various abiotic factors

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such as altitude, stream width, order, and gradient to find out if there are changes along altitudinal gradients. Such a comparison was done for various forested streams in North America [11, 12] and there are data on BOM and TOM from alpine ones [4, 13]. This paper is the first attempt to establish relationships of benthic and transported particulate organic matter contents in Polish Tatra alpine and mountain streams with some local abiotic factors such as altitude, stream gradient, order, and width.

2 Materials and methods

2.1 Study site

The study was conducted in the Polish Tatra Mountains in the Western Carpathians. Although they are much lower than the Alps, they display a typical alpine character and landscape. The climate is cool and moderately wet. The annual precipitation is the highest in Poland and reaches 1800 mm $year^{-1}$ [14]. Above 1550 m dwarf pine (*Pinus mugo* L.) and individual stone pines (*Pinus cembra* L.) are present. The Carpathian subalpine forest represents an association of *Plagiothecio piceetum* and it is dominated by Norway spruce (*Picea abies* (L.) Karst.), where forest stands are unevenly aged and spruces 150- to 200-year-old dominate. The coniferous forest streams show a more even distribution of inputs throughout the year.

The studied streams are: the unnamed stream connecting Zadni and Długi Staw lakes (ZD), Czarny Potok (CP), Sucha Woda (SW), Biały (BI), Kościeliski (KO), and Bystra (BY) stream (Fig. 1). The first three are situated in High Tatra, where the substratum of the catchments is built of granitic bedrock, while the others are located in Western Tatra, with catchments composed of metamorphic rocks and dolomites (Fig. 1).

The streams flow through several vegetation zones: alpine meadow (above 1800 m), dwarf pine zone (1550–1880 m), upper montane forest (1250–1550 m), and lower montane zone (below 1250 m). On each stream two sampling stations (A, B) were studied, always located in the same vegetation zone with the distance from 50 to 150 m between them (Table 1). All the studied streams have rhithral character, fed by rainfall and snowmelt.

The Tatra Mountains streams are characterized by high slope gradient (>0.15%) and by high water oxygen saturation. Other water chemistry parameters such as pH, conductivity, and Ca concentration were related to their different catchment geology (Table 1, Fig. 1).

2.2 Benthic organic matter (BOM)

BOM standing crops from Zadni-Długi, Czarny Potok, Sucha Woda, and Bystra streams were collected using a 0.006 m^2 plastic traps. Four to eight of them were placed randomly on the stream bottom in riffles and pools and left for 1 wk [7, 8, 10]. For the highest altitude streams, in the region of the bare rocks and alpine meadows, plastic traps were left on the bottom for 2 wk. All collected materials were preserved on ice until analyzed in the laboratory,

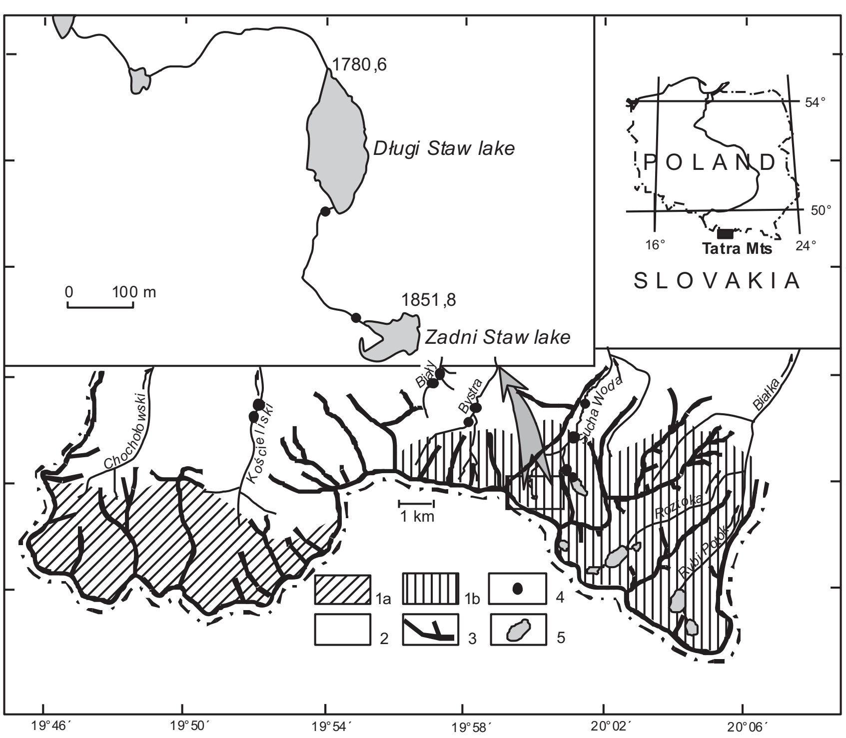

Figure 1. Locations of the streams in Polish Tatra; (1a) metamorphic rocks, (1b) granitoids, (2) limestone, dolomites, sandstones, (3) mountain ranges, (4) sampling stations, (5) lakes.

Table 1. Ranges of physical and chemical parameters of the studied streams in Tatra Mountains

Stream	Stream connecting two lakes	Czarny Potok	Sucha Woda	Biały	Bystra	Kościeliski
Acronymus	ZD	CP	SW	BI	BY	KO
Vegetation zone	Alpine meadow	Dwarf pine	Upper montane/lower montane	Upper montane/lower montane	Lower montane	Lower montane
Dominant plant species in the catchment	*Juneus trifidus*, *Oreochloa disticha*	*Pinus mugo*, *Sorbus aucuparia*	*Picea abies*	*Picea abies*	*Picea abies*	*Picea abies*, *Abies alba*
Permanent/temporary	Temporary (VI–IX)	Temporary (V–X)	Permanent	Permanent	Permanent	Permanent
Altitude (m)	1852–1784	1620–1435	1672–826	1390–838	1220–813	1317–878
Length (km)	0.1	1.44	10.0	4.6	7.3	10.9
Catchment area (km^2)	0.5	3.15	26.9	3.26	–	37.5
Gradient (%)	20–35	13–35	6.6–10	19	5.6	4.0
Width (m)	1.0–2.0	2.0–3.0	4.5–6.5	2.5–4.0	2.5–5.0	3.0–5.0
Mean discharge ($m^3 s^{-1}$)	–	0.95	0.55	1.20	1.15	1.61
Temperature (°C)	0.2–4.5	0.4–5.0	0.1–5.5	1.1–10.4	4.5–6.5	3.4–7.2
pH	4.9–6.2	5.5–7.7	6.3–6.8	8.2–8.5	6.7–8.4	7.0–7.6
O_2(%)	75–82	82–89	84–93	85–90	89–114	88–136
Ca (mg L^{-1})	0.6–5.0	2.0–3.4	3.3–8.6	28–34.7	15–18	11.4–26.6
Conductivity ($\mu S\ cm^{-1}$)	29–55	19–21	21–69	249–283	98–211	83–202

where macroinvertebrates were removed under a stereoscopic microscope and remaining material was sorted by a 1 mm net into coarse POM (CPOM, >1 mm) and fine POM (FPOM, <1 mm).

Samples of deposited POM from pool sections of Kościeliski and Biały streams were collected with a core sampler (e.g., [15–17]). Within each of the sampling stations, three to four samples of organic matter were collected from randomly chosen points located in the riffles and pools using a 13 cm^2 polyethylene core, which was driven into the substratum to a depth of $\approx$4 cm. Sediment was removed and preserved on ice until analyzed in the laboratory, where benthic fauna were removed from the samples, and the remaining material was separated through 1.0 mm sieve into CPOM and FPOM. All materials from both plastic traps and core samplers were dried at 105°C to a constant mass, weighed, and ashed at 500°C for 4 h, and reweighed to determine ash free dry mass (AFDM). The results of BOM standing crop were expressed as g AFDM m^{-2}.

2.3 Transported organic matter (TOM) measurements

Transported particles of FPOM and CPOM were measured during macroinvertebrate drift sampling [18] using four to six 0.3 mm mesh nets with 1 m length and 400 cm^2 inlet area, placed in the central, most turbulent part of the stream for 0.5 h [7–10]. Water flow was measured at each sampling station by the current meter (Global Water FP 201). In the laboratory, fauna (drift) was removed under a microscope, and the remaining material was separated through nested sieves (1.0 mm, 0.3 mm) into CPOM and FPOM and finally through 0.45 μm glass filters Whatman GF/C. Three samples of very fine particles (VFPOM 0.45–100 μm) were determined in four streams (Table 1) by filtering 25 L of water through a 100 μm net and then vacuum-filtering through pre-washed Whatman GF/C glass-fiber filters. All material was oven dried, weighed, and ashed to determine AFDM. The results of fine and coarse organic matter are expressed in mg m^{-3}, and VFPOM is expressed as mg L^{-1}.

Samples of TOM were taken at the same time as BOM samples, always once per month in the following months: ZD in VI, VII, VIII; CP in VI, VII, VIII, IX, and X; SW throughout the whole year; BI in III, V, VIII, X; BY in IV, VI, VIII, X; KO in III, VI, IX, and XII (sampling per year in Table 2).

Water temperature, pH, and conductivity were measured in situ using a portable instrument (Elmetron pH-meter CX-742). Water samples for oxygen analysis were taken in glass bottles and measured in the laboratory by

Table 2. Average annual organic matter content (± SD) in the sampling stations of the studied streams; number of replications in parenthesis

Streams	ZD	CP	SW	BI	BY	KO
Vegetation zone	Alpine meadow	Dwarf pine	Upper montane	Upper montane	Lower montane	Lower montane
Elevation (m a.s.l.) of sampling						
Station A	1850	1595	1460	1000	1150	1020
Station B	1780	1517	1330	950	1000	970
Stream order	1	1	2	2	5	3
Sampling per year	3	5	12	4	4	4
Bottom						
FPOM g m^{-2} A	0.32 ± 0.22 (10)	0.65 ± 0.60 (24)	1.01 ± 0.94 (12)	0.37 ± 0.36 (12)	1.11 ± 1.07 (12)	3.58 ± 4.00 (20)
CPOM g m^{-2} A	0.22 ± 0.15 (10)	0.76 ± 1.20 (24)	1.47 ± 1.87 (12)	2.45 ± 2.94 (12)	1.81 ± 1.49 (12)	3.55 ± 5.90 (18)
FPOM g m^{-2} B	0.43 ± 0.33 (12)	0.38 ± 0.59 (15)	2.35 ± 3.32 (12)	0.53 ± 0.73 (12)	1.84 ± 1.31 (12)	2.53 ± 2.46 (20)
CPOM g m^{-2} B	0.91 ± 1.69 (12)	1.64 ± 2.80 (13)	2.26 ± 2.55 (12)	3.32 ± 5.25 (12)	4.70 ± 4.54 (12)	2.16 ± 2.30 (20)
Transported						
VFPOM mg L^{-1}	A 0.09 ± 0.04 (8)	0.28 ± 0.30 (5)	0.32 ± 0.12 (9)	–	–	0.25 ± 0.10 (9)
VFPOM mg L^{-1}	B 0.14 ± 0.07 (8)	0.11 ± 0.02 (9)	0.34 ± 0.25 (9)	–	–	0.47 ± 0.27 (9)
FPOM mg m^{-3}	A 0.53 ± 0.22 (16)	1.67 ± 1.62 (20)	3.99 ± 5.45 (12)	0.49 ± 0.59 (16)	2.47 ± 2.59 (15)	4.78 ± 4.25 (12)
CPOM mg m^{-3}	A 1.34 ± 3.17 (16)	1.84 ± 1.68 (20)	6.06 ± 8.49 (12)	2.69 ± 6.79 (14)	6.63 ± 8.72 (15)	7.66 ± 9.06 (12)
FPOM mg m^{-3}	B 3.36 ± 0.66 (16)	3.25 ± 3.54 (12)	3.59 ± 4.74 (12)	1.54 ± 1.37 (14)	1.46 ± 1.52 (15)	3.26 ± 2.10 (12)
CPOM mg m^{-3}	B 2.06 ± 1.35 (16)	6.65 ± 4.93 (12)	5.04 ± 6.95 (12)	14.04 ± 14.81 (14)	5.12 ± 7.15 (15)	5.22 ± 4.45 (12

the Winkler method, Ca^{2+} content was also measured both according to Apha [19].

The relationships between BOM (FPOM + CPOM), TOM (VFPOM, FPOM + CPOM) concentrations, and abiotic parameters such as altitude, slope gradients, stream order (inferred from maps), and width were analyzed using linear regressions. Some data were logarithmically transformed if such transformation gave a better fit of the regression line.

3 Results and discussion

3.1 Benthic organic matter storage in streams

The quantity and quality of BOM in streams is directly related to the detritus input from adjacent riparian vegetation. The lowest amount of BOM (FPOM + CPOM) in the Tatra streams was in an alpine stream (ZD), where the only source of organic matter are fragments of vegetation from alpine meadow such as grass and lichens. BOM in this zone averaged only 1 g m^{-2} (Table 2). In the dwarf pine zone, BOM amounted to on average 1.62 g m^{-2}, but in the upper and lower montane zones, BOM increased to 3.3 and 5.9 g m^{-2}, respectively. These values are much lower than measurements made in the Western and Easter United States streams flowing through coniferous and deciduous forests [11, 20, 21]. The largest components of terrestrial detritus in the forested montane streams were leaves, cones, and twigs from *P. abies* or *Abies alba*, and the CPOM fraction was the main pool of BOM (62–83%).

In this study, BOM in was negatively related to altitude ($r^2 = 0.75$, $P<0.001$; Fig. 2A) and stream gradient ($r^2 = 0.82$, $p<0.001$) (Fig. 2B). From the studied sampling stations the values obtained on station B (located downstream) were always higher than those for station A (Table 2). This difference was statistically significant (*t*-test, $p<0.05$). Organic matter standing crops from selected 1st and 2nd order, montane North American streams, located in both coniferous and deciduous forest basins, also showed negative relationships between BOM and

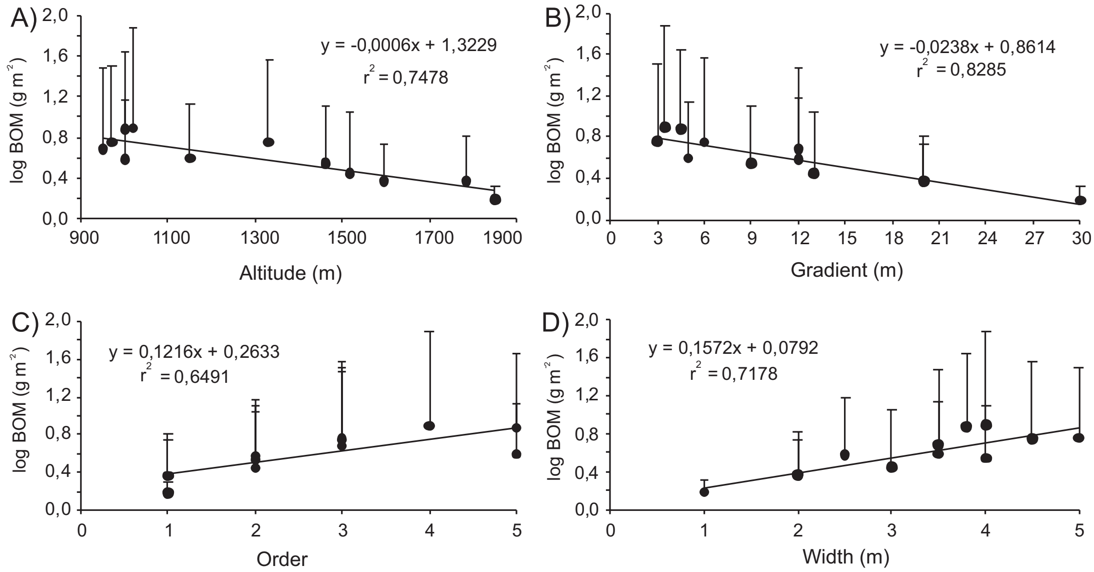

Figure 2. The relationship of BOM to: (A) altitude, (B) gradient, (C) stream order, and (D) stream width; black dots represent average annual BOM + SD.

altitude (based on [15, 17, 22–24]). Jones [11] compared organic matter storage in North American temperate zone streams and found that BOM stocks were higher in streams with higher gradients. The studied Tatra streams do not appear to fit that relationship: high-gradient but low BOM storage, similarly as high-gradient streams in Panama [25]. The relationship between gradient and BOM observed by Jones [11] could have been confounded with the presence of wood, since large amounts of wood were present in some of the high-gradient headwater sites included in his analyses. In sites studied here, the presence of large wood was almost negligible as a result of frequent removal of this material during floods.

Study of streams in the southern Appalachian Mountains revealed that steep streams accumulated significantly less CPOM than less steep streams [16]. The storage of BOM in streams is not only dependent on terrestrial organic matter input but is also related to channel morphometry and is regulated by retention structures such as debris dams which facilitate retentions [11, 26] or boulders and large wood [27].

In the studied Tatra streams, as their order and channel width increased the BOM storage also enlarged ($r^2 = 0.65$, $p<0.01$) and ($r^2 = 0.72$, $p<0.001$; Fig. 2C and D), however as predicted by River Continuum Concept [3], CPOM should decrease downstream as channel become larger and riparian influences decline [11, 24]. In spite of this for the majority of Western US streams, there was no significant relationship between BOM and stream order, only an increasing trend of fine material accumulation was significant [21]. The increase in BOM with stream order stated in this study may be due to the additional sources of organic matter input [23, 28]. In the lower montane zone, as a stream increases width and order, its canopy disappears. This results in a lower amount of leaves falling into the water, whereas the fine fraction increases due to mechanical fragmentation and the action of benthic fauna.

3.2 Transported organic matter

The transport of materials in water links upstream and downstream communities into one integrated ecosystem [3, 29]. Numerous studies of detritus dynamics in different streams have revealed that allochthonous detritus falling into streams as coarse particles (leaves, needles, and wood) is transported primarily as very fine particles (50–100 μm) [30, 31]. In all vegetation zones of the Tatra streams, transported fine particles composed 97% of the total TOM. In stream ZD, flowing in the alpine meadow zone, the mean values of VFPOM at two sampling stations were 0.09 and 0.14 mg L^{-1}, respectively (Table 2), similar to those in rhitral streams of the Alps flowing above tree line [13, 32]. In the forested zones, from dwarf pine to lower montane, VFPOM was higher and ranged from 0.28 to 0.47 mg L^{-1}. The very fine fraction in the Tatra streams was weakly negatively related to altitude ($r^2 = 0.55$, $p<0.1$; Fig. 3A) as well as to stream gradient ($r^2 = 0.52$, $p<0.1$).

Although allochthonous CPOM is the greatest source of organic matter input to small, high-gradient streams, leaves, and twigs generally represent only 2–4% of TOM [33]. Coarse particles are transported only over small distances [34] and quickly settle near their point of entry [26, 35] particularly in small streams that can act as collecting zones [12]. TOM has rarely been measured in

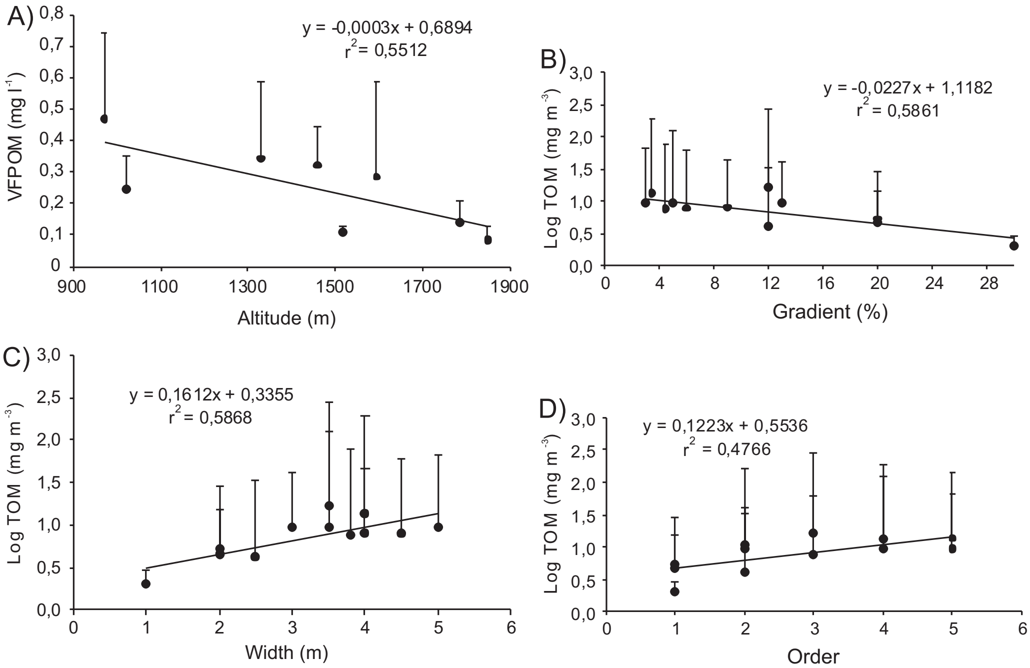

Figure 3. The relationship of (A) transported organic matter (VFPOM fraction) and stream altitude, (B) TOM and stream gradient, (C) TOM, and stream width, (D) TOM and stream order; black dots represent average annual VFPOM and TOM + SD.

alpine streams. In the rhithral streams in Swiss Alps, Hieber et al. [13] found TOM ranging from 0.02 to 0.13 mg L^{-1}. In the Appalachian headwater stream TOM concentration ranged from 0.53 to 6.68 mg L^{-1}, with no significant changes between elevations 1245 and 610 m a.s.l. [31]. In North American montane streams, with similar gradient, width and order to Tatra streams, Golladay [12] reported higher values of TOM than those for Tatra streams (Table 2). However, in this study the size range of transported fine and coarse particles taken into account was 300–1000 and >1000 μm, whereas in American investigations ranging from 50 to 300 μm that often make up the greatest percentage of the total TOM [30, 31]. These frequently occurring differences in the size of particles actually measured by various authors do not allow for making comparisons of TOM content published for various streams.

The amount of transported POM in North American 1st and 2nd order streams flowing in coniferous and deciduous forests was negatively correlated with stream gradient [12]. The investigations performed on non-forested and forested Tatra streams also suggested an inverse relationship between TOM and stream gradient ($r^2 = 0.58$, $p = 0.1$; Fig. 3B). In the Tatra streams, TOM also seemed to be positively related to stream width ($r^2 = 0.58$, $p = 0.1$; Fig. 3C) and stream order ($r^2 = 0.48$, $p = 0.1$; Fig. 3D). The relationship between TOM and stream order were not established by Golladay [12] in various non-forested USA streams, while in the eastern US streams Webster et al. [21] found a significant positive relation between TOM concentration and stream order. Such discrepancies are the result of differences in sampling methods used among other possible factors.

Detritus that enters a stream is either retained or transported – both depend on physical variables of the stream such as gradient, width, and order, that together with altitude appear to be the most important abiotic parameters involved in storage and transport of organic matter in high mountain and forested Tatra mountain streams. However, the influence of these variables is mostly indirect through their effects on terrestrial vegetation. High altitude streams, i.e., those with sparse vegetation, need more study, especially of their organic matter storage and transport. In conclusion, it would be useful to repeat the suggestion of Tank et al. [5] for further collection of data from different streams, including alpine and mountain streams, to obtain a more comprehensive synthesis of stream organic matter budgets.

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