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Substantial Organic and Particulate Nitrogen and Phosphorus Export from Geomorphologically Stable African Tropical Forest Landscapes

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Abstract

Aquatic losses of nutrients are important loss vectors in the nutrient budgets of tropical forests. Traditionally, research has focused mainly on losses of inorganic nutrient forms, whereas the potential contribution of organic and particulate losses to the total nutrient export budget is much less constrained. In this study, we quantified full aquatic nitrogen (N) and phosphorus (P) exports, including inorganic, organic and particulate forms, from a moist tropical lowland forest and a semi-dry Miombo woodland forest within the Congo Basin. While particulate organic N (PON) was the highest N loss vector in the lowland stream (3.34 kg N ha^{-1} y^{-1}; 44% of TN), dissolved organic N (DON) dominated the export in the Miombo stream (1.41 kg N ha^{-1} y^{-1}; 47% of TN). Aquatic P export was dominated by dissolved organic P (DOP) in both streams, with yields of 0.29 kg P ha^{-1} y^{-1} (65% of TP) in the lowland and 0.24 kg P ha^{-1} y^{-1} (69% of TP) in the Miombo. Storm events were driving those losses, exporting disproportionally high N and P loads during short periods of stormflow conditions (32% and 47% of TN and 20% and 40% of TP in the lowland and Miombo, respectively). Our results highlight the need to take particulate and organic forms into account as important loss vectors in the nutrient balance of tropical forests. This finding is of particular importance considering the projected increasing rainfall intensities in many tropical regions which might exacerbate the export of these nutrient forms in the near future.

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Key words: biogeochemistry; tropical forests; Congo Basin; particulate organic nitrogen; particulate phosphorus; storm events.

Highlights

- An afrotropical lowland forest experienced highest aquatic N loss in particulate form
- An afrotropical Miombo woodland showed highest N losses in dissolved organic forms
- Aquatic P exports were dominated by dissolved organic and particulate forms
- Increased losses of particulate and dissolved organic N and P were observed during storm events

Introduction

Tropical forests play an important role in the global carbon (C) cycle, accounting for roughly 60% of the terrestrial gross primary production (GPP) (Beer and others 2010; Jung and others 2020). High primary production rates are counterbalancing the high respiration rates, resulting in a net C uptake of tropical forests of around 1.7 Pg C per year (Harris and others 2021). The magnitude of both fluxes is partly constrained by the nutrient status of the ecosystem, where nutrient limitation leads in general to lower carbon use efficiencies in forest ecosystems (Fernández-Martínez and others 2014). The main nutrients underpinning these C exchange fluxes are nitrogen (N) and phosphorus (P), but their abundance and availability are highly variable in space and time (Chadwick and others 1999; Hedin and others 2009). Many tropical forests appear to be limited by N and/or P (Wright 2019). A long-lasting paradigm has been that highly weathered soils of tropical forests are abundant in N and limited in rock-derived P, whereas soils in geomorphic active regions are conversely more depleted in N while being rich in P, due to higher soil rejuvenation rates (Hedin and others 2009).

Traditionally, research into nutrient losses has mainly focused on inorganic nutrients, as they are bioavailable for plant uptake. This has resulted in the ''nutrient retention hypothesis'', which states that efficient retention of bioavailable and limiting nutrients leads to minimal losses of those nutrients, resulting an accumulation of those nutrients within the ecosystem. Once these nutrients are not limiting biological processes anymore, the outputs of these nutrients should reflect the inputs into the system (Vitousek and Reiners 1975). Thus, it was postulated that aquatic losses of bioavailable and limiting nutrients can reflect the nutrient status of the ecosystem. The observation of high DON and dissolved organic P (DOP) losses from unpolluted old-growth forests (Hedin and others 1995, 2003; Perakis and Hedin 2002; Vitousek and others 1998) led to the elaboration of the ''leak'' hypothesis, which states that besides the high biological need for nutrients, the export of organic forms of nutrient that are independent of biological demand can lead to long-term nutrient limitations (Hedin and others 2003).

Moreover, this ''DON-leak'' hypothesis was recently complemented by findings of high losses of particulate organic N (PON) forms through erosional processes regulated by hydrological controls (Taylor and others 2015). Nevertheless, particulate nutrients have been widely neglected in biogeochemical research and studies reporting PON or total particulate P (TPP) are scarce due to the challenging nature of quantifying exports of particulates in the tropics during storm events. The few studies that reported PON losses showed that this loss vector can dominate total N (TN) export in a tropical forest (Lewis 1986; Lewis and others 1995; Taylor and others 2015). As the export of organics tends to follow the hydrological regime, storm events have been identified to be an important driver of particulates and dissolved organic species (Clark and others 2013; Hoover and MacKenzie 2009; Lloret and others 2013; Taylor and others 2015; Townsend-Small and others 2008). However, all these studies were conducted in more geomorphologically active landscapes, that is, sites with high erosional potential, due to steep slopes (20–45°) and/or high annual precipitation (3000–5000 mm y^{-1}), but the influence of erosion and storm events on nutrient export on old and more geomorphologically stable landscapes, have not been studied yet. Modeling of PON export from tropical landscapes highlighted higher PON export rates in mountainous regions compared to lowland landscapes, especially for lowlands in central Africa (Taylor and others 2015). However, ground-based measurements from the latter region are inexistent and the relative importance of PON export compared to other dissolved N exports is not known. Thus, a thorough quantification of N and P losses, including the particulate forms, from old geomorphologically stable forested landscapes of the tropics with flat topography, is necessary.

In this study, we assessed the impact of particulate nutrient export on the nutrient budgets of two distinct forest types of the Congo Basin: a lowland tropical forest and a Miombo woodland. These two forest types represent the two most abundant ecosystems of the Congo Basin, with the evergreen lowland forests covering around 35% and the broadleaved deciduous forest (Miombo as a representative type of tropical deciduous forest) covering around 37% (ESA 2017). In particular, we asked the following research questions: (1) how do N and P exports differ in yield in distinct tropical environmental settings? (2) what is the contribution of particulate and organic N and P compared to its inorganic species? and (3) what is the influence of storm events on aquatic N and P losses? To answer these questions, we measured aquatic dissolved and particulate N and P exports from two distinct forest watersheds of the Congo Basin during one hydrological year.

Material and Methods

Study Sites

Aquatic nutrient export and discharge were determined at two representative headwater streams draining a tropical lowland forest and a tropical woodland catchment (Miombo). The lowland forest catchment is situated in the Yoko Forest Reserve 35 km south of the city of Kisangani (Tshopo province, Democratic Republic of the Congo (DRC); 0.291° N, 25.295° E). The whole catchment area consists of pristine primary mixed tropical forest with patches of monodominant forests, where the species *Gilbertiodendron dewevrei* consists of more than 60% of the basal area. Deeply weathered Ferralsols with loamy sand texture is the main soil type in the lowland forest (Baumgartner and others 2020; Van Ranst and others 2010). The lowland forest site experiences two wet seasons, a shorter one from March to May and a more prolonged wet season from August to November with mean annual rainfall of about 1825 mm and mean annual temperature of about 24 °C (Bauters and others 2019; Figure 1). The catchment area was determined using digital elevation models (DEM) derived from the 30 m Shuttle Radar Topographic Mission (SRTM, NASA Jet Propulsion Laboratory). The obtained catchment ranges from 440–475 m a.s.l. and has a mean slope of 4.3° with an area of 311 ha (Baumgartner and others 2021).

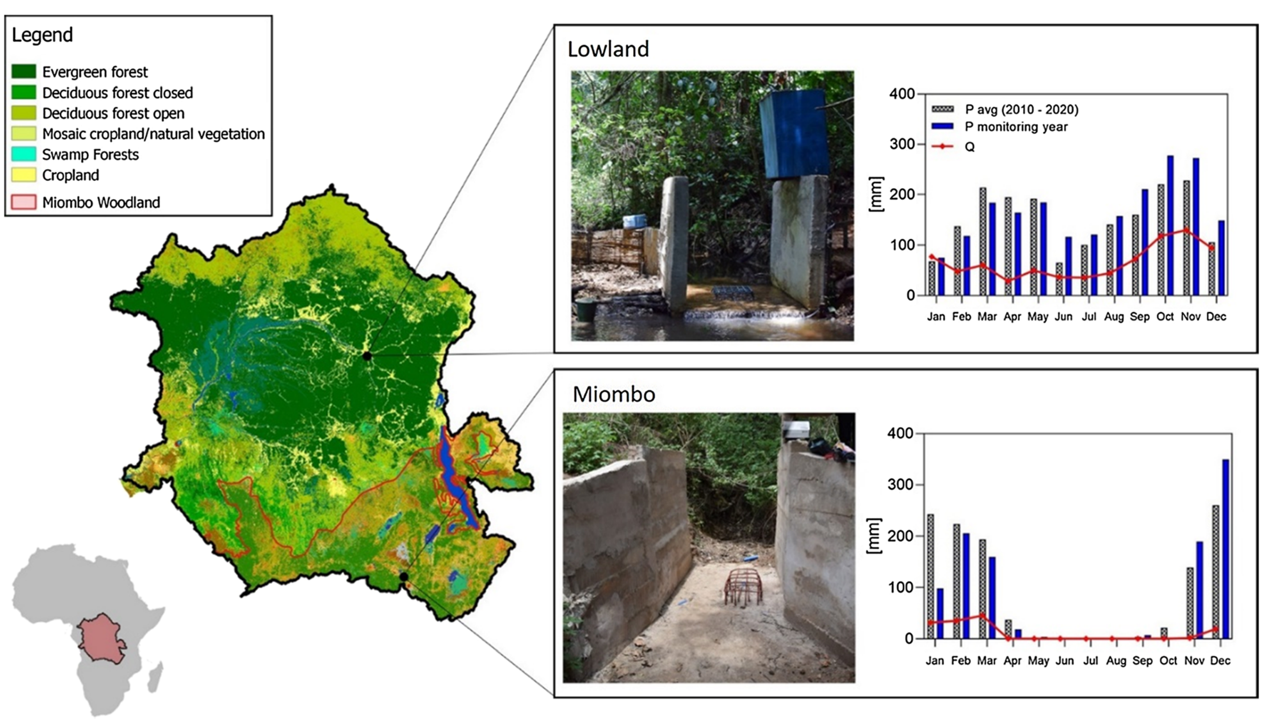

Figure 1. Different ecosystem types within the Congo River Basin and the sampling locations within the lowland forest and the Miombo woodland. Photos show the concrete flumes installed at the two catchments. On the right-hand site are the monthly precipitation rates during the monitoring year (blue) and 10-year average in grey. Precipitation data are derived from GPM satellite data (Huffman and others 2019). The red line is the discharge measured at the flumes. Map adopted from ESA (2017).

The Miombo woodland catchment is situated approximately 50 km north of the city of Lubumbashi (Katanga province, DRC; 11.212° S, 27.233° E). The Miombo woodlands are mosaics of mature forest, shifting cultivation, grazing lands and regrowing forests (Mayes and others 2019); thus, pristine Miombo woodland is scarce in the region. Dominant tree genera in a Miombo woodland are *Brachystegia, Julbernadia* and *Isoberlinia* (Campbell 1996). The site has minor anthropogenic impact, mainly from charcoal production and small-scale agricultural practices, which are representative for the Miombo in the region (Campbell 1996). Moreover, natural and anthropogenic fires during the dry season are common. Soils are classified as Acrisols and Cambisols (Baumgartner and others 2021). The region experiences a single wet season that starts in October and continues until April, with a mean annual precipitation of about 1230 mm and mean annual temperature of about 21 °C (Fick and Hijmans 2017; Figure 1). The selected stream channel only flows with surface water after the onset of the wet season in November until end of the wet season in April and is dry during the rest of the year. We determined the catchment area using a 30 m DEM (SRTM, NASA Jet Propulsion Laboratory). The catchment area is 588 ha with an elevation ranging from 1257 to 1311 m a.s.l. and an average slope of 3.9°.

Monitoring and Sampling Campaigns

At each site, a concrete flume with a fixed width (lowland: 1.6 m; Miombo: 1.4 m) was installed in order to generate high quality water level–water discharge rating curves (Figure 1). Water level was measured in a 5-min interval with a pressure transducer (CS451, Campbell Scientific, UK) connected to a datalogger (CR1000, Campbell Scientific, UK). Bi-weekly (lowland) and weekly (Miombo) manual discharge measurements were carried out to establish a water level–discharge rating curve for each site using a mechanical flowmeter (Model 2030, General Oceanics Inc., USA). Furthermore, in-stream turbidity sensors were installed and set to record at 5-min interval at the Miombo site (OBS 3 + , Campbell Scientific, UK) and at 15-min interval at the lowland site (YSI-EXO2, Xylem, US). At the same time the bi-weekly discharge measurements were conducted, water samples were taken with acid washed 2L-HDPE-bottles. The samples were transported immediately back to the laboratories in Kisangani and Lubumbashi, respectively. In addition to the manual water sampling, autosamplers (6712 Portable Sampler, Teledyne ISCO, USA), equipped with 24 × 1 L PVC bottles, were installed at both sites to obtain water samples during storm event conditions. The autosamplers were connected to the datalogger and triggered when water level reached a certain threshold (0.175 m at the lowland site and 0.35 m at the Miombo site). These thresholds were selected by measuring water level at those streams prior to the monitoring period, which was used to determine water level ranges of the baseflow conditions. Due to logistical constraints, the bottles of the autosampler were only replaced during the bi-weekly or weekly field visits. To minimize biological degradation of the water samples within the autosampler, the empty bottles were prepared with 5 ml of 50% (w/v) $ZnCl_2$ solution to stop biological activity in the water samples.

Dissolved nitrous oxide (N_2O) concentration of the stream water was determined using the headspace equilibrium technique. A 12-ml plastic syringe was used to inject 6 ml of air bubble free water into a N_2-pre-flushed 12 ml exetainer (Labco, UK). The pre-flushed exetainer contained 50 µl of 50% (w/v) $ZnCl_2$ to stop microbial activity after water sample injection. The remaining vial headspace was analyzed for N_2O concentration at ETH Zürich, using gas chromatography (456-GC, Scion Instruments, UK) and dissolved gas concentrations subsequently calculated using Henry's law.

Biweekly water sampling and discharge measurements started in November 2018. Monitoring with the full setup (water level, turbidity and autosampler) was done one hydrological year at both sites (lowland: from 01.04.2019 to 31.03.2020; Miombo: from 01.05.2019 to 30.04.2020, sampling only started at onset of streamflow from 22.11.2019 onward).

Sample Analysis

Immediately upon return to the laboratories in Kisangani and Lubumbashi, the water samples were shaken to resuspend sediments and filtered on pre-combusted (450° C for five hours) glass-fiber filters (0.7 µm GF/F, Whatman, USA). For the analysis of the dissolved nutrients, the filtrate was stored in two acid-washed 250 ml HDPE bottles and were immediately frozen. To determine the total suspended sediment (TSS) concentration, particulate organic C (POC), particulate organic N (PON) and particulate P, the water samples were filtered in duplicates on pre-weighted GF/F filters and stored in the freezer. Due to the limited amount of water sample within the autosampler bottles, storm event samples were only filtered for PON and POC analysis, total particulate phosphorus (TPP) and particulate inorganic phosphorus (PIP) were only determined for baseflow samples. All the samples were returned for laboratory analysis to Europe in batches every two to four months. All filters were dried at 60 °C for 48 h before analysis. TSS concentrations were calculated by dividing the weight difference between the initial and the dried filter after filtration by the amount of water filtered. POC and PON concentrations were determined by measuring the dried GF/F filters on an elemental analyzer (Automated Nitrogen Carbon Analyzer, SerCon; Crewe, UK). To determine TPP and PIP concentrations, the chemical wet oxidation method by Suzumura (2008) was used (see supplementary methods). Dissolved nitrate (NO_3^-), ammonia (NH_4^+) and PO_4^{3-} concentrations were measured colorimetrically from the filtered water samples using a continuous flow autoanalyzer (AA3, Bran and Luebbe, Germany; see supplementary methods). Concentrations of NO_3^-, NH_4^+ and N_2O together are defined as dissolved inorganic N (DIN) and PO_4^{3-} is referred to as dissolved inorganic P (DIP). Total dissolved N (TDN) and total dissolved P (TDP) were measured by converting all N and P in solution into inorganic N and P forms. DON and DOP were determined by subtracting the inorganic forms of N and P from the TDN and TDP concentrations. TPP and PIP concentrations were only obtained for the samples of the biweekly and weekly sampling campaigns.

Export Calculations

To calculate discharge values from the continuously measured water levels, a linear rating curve was applied (Baumgartner and others 2022). TSS concentrations were already calculated for each turbidity and water level measurement using a random forest approach (see detailed description in Baumgartner and others 2022). To calculate total export of the particulate nutrient constituents (PON, TPP and PIP), linear regressions with TSS were applied (Figure S1). Finally, total PON, TPP and PIP export per 5-min interval was calculated by multiplying the obtained particulate nutrient concentration with the instantaneous discharge value integrated over a 5 min period. Yields were calculated by dividing the yearly particulate nutrient export (kg y^{-1}) by the catchment area (ha). This ''double prediction approach'' (TSS via turbidity and then particulate nutrient concentrations via TSS) is leading to higher uncertainty. To validate model performance, we calculated root mean square errors of the predictions (Figure S2).

For dissolved nutrient constituents, a linear model with water discharge was applied (Figure S3). For statistically significant models ($p < 0.05$), the obtained relationship was applied to calculated nutrient concentrations for each discharge measurement. Total exports and yields were then calculated the same way as for particulate nutrient exports and yields. For dissolved nutrient constituents with no significant relation with water discharge, the average concentration was used to calculate annual export and yields, by multiplying the average concentration by the total annual water discharge and yield. Standard errors for the yield calculations include the errors from the double prediction approaches (for particulate nutrients) or the single linear models (for dissolved nutrients) plus the standard error from the uncertainty in the water discharge calculation with the rating curves that were applied. Differentiation between storm event and baseflow conditions was done using a digital filter signal processing technique from the R package *EcoHydRology* (Fuka and others 2015) that separated the discharge hydrograph into event flow and baseflow. A storm event was identified, when peak event flow was at least 10% higher than baseflow and when the event lasted for at least 45 min (Baumgartner and others 2022).

Results

Hydrology

The hydrology and suspended sediment dynamics of the two study sites have been discussed in detail in a previous study (Baumgartner and others 2022). During the 12-month sampling period from April 2019 to March 2020, the lowland forest site received 2030 mm of rainfall, while the stream exhibited a specific discharge of 795 mm. By difference, interception and evapotranspiration totaled to 1235 mm (Figure 1). During the sampling year, 68 distinct storm events were observed (Baumgartner and others 2022). These events comprised 4.7% of the monitoring period and were responsible for 16% of water discharge.

The stream at the Miombo woodland site only flows during five months of the wet season. During the 12-month sampling period, this stream exhibited a specific discharge of 133 mm (all between December 2019 and April 2020). Amid the same wet season, 1036 mm of rainfall was measured, resulting in an interception and evapotranspiration of around 900 mm (Figure 1). Twenty-one storm events were identified at the Miombo stream, exporting 29% of total water discharge during 7.4% of the wet season.

Particulate and Dissolved Nutrient Concentrations

PON concentrations were higher during storm events compared to mean baseflow concentrations in both streams (Figure 2 & Table 1). Mean baseflow TPP concentrations were 55% higher in the Miombo stream than in the lowland stream. While the Miombo stream mainly exported TPP as PIP, the PIP fraction in the lowland stream was only around 41% of the TPP fraction (Table 1). Particulate nutrient concentrations (PON, TPP and PIP) all correlated positively with sediment concentrations (Figure S1). While robust linear relations were obtained for PON at both sites, TPP and PIP correlations with TSS showed higher variability, because no samples for TPP and PIP at high TSS concentrations were available (no storm events).

The lowland stream showed mean measured NO_3^- concentrations that were an order of magnitude higher than the mean measured concentrations within the Miombo stream and both stream experienced higher concentrations during storm events (Table 1). Unlike the lowland stream, the Miombo showed higher concentrations of NH_4^+ than NO_3^-. In both streams the highest dissolved N concentrations were found as DON; however, only the lowland stream showed increased DON concentrations during storm events (Table 1). Only dissolved N species in the lowland site showed a significant positive correlation with water discharge (Figure S3). On the other hand, the Miombo site showed high variability of DON (0.07–5.48 mg DON-N L^{-1}) and DIN (0.01 – 0.75 mg DIN-N L^{-1}) concentrations without a flow dependency (Figure S3). Dissolved N_2O concentrations ranged from 0.28 to 0.56 µg N_2O-N L^{-1} in the lowland stream and from 0.35 to 0.83 µg N_2O-N L^{-1} in the Miombo stream (Figure S6).

At both sites, DIP samples were mainly below detection limit of the colorimetric technique (DL = 0.01 mg P L^{-1}; Figure 2). At the Miombo site, only one sample exceeded the detection limit with 0.02 mg $PO_4{}^{3-}$-P L^{-1} at the onset of the rainy season (Figure 2). At the lowland site, eight samples exceeded the detection limit; however, there was no relationship with water discharge (Figure S3). DOP concentrations in the lowland stream showed low variability, with values ranging from 0.01 – 0.20 mg DOP-P L^{-1}, whereas the Miombo stream showed slightly more pronounced variability with values ranging from 0.04 – 0.60 mg DOP-P L^{-1} (Figure 2).

Nutrient Yields

Total N yields of the lowland forest (7.44 ± 1.35 kg N ha^{-1} y^{-1}) were led by PON (44%; 3.34 ± 0.66 kg N ha^{-1} y^{-1}) and DON (31%; 2.28 ± 0.47 kg N ha^{-1} y^{-1}) yields (Figure 3). The smallest proportion of total the N yield was via the DIN fraction (25%) with 1.82 ± 0.21 kg N ha^{-1} y^{-1} (Fig. 3). Total N yields in the Miombo forest were lower with 2.96 ± 0.90 kg N ha^{-1} y^{-1} (Figure 3). The largest proportion of the TN yield at the Miombo site was the DON fraction (47%; 1.41 ± 0.28 kg N ha^{-1} y^{-1}), which was only marginally higher than the PON yield (44%; 1.28 ± 0.59 kg N ha^{-1} y^{-1}). As in the lowland forest, the smallest proportion of N yields at the Miombo site were comprised by DIN (9%) with 0.28 ± 0.04 kg N ha^{-1} y^{-1} (Figure 3). In the lowland forest catchment, storm events were responsible for 30% of the PON export, 41% of the DON export, and 24% of the DIN export. In the Miombo catchment the storm events were responsible for 65% of the PON export, 32% of the DON export, and 33% of the DIN export (Figure 3). Exports as dissolved N_2O are low and compared to other N exports insignificant. The lowland stream yielded a total of 0.003 kg N_2O-N ha^{-1} y^{-1} and the Miombo stream 0.001 kg N_2O-N ha^{-1} y^{-1}.

Total P yields in the lowland stream (0.48 ± 0.08 kg P ha^{-1} y^{-1}) were dominated by DOP with 0.29 ± 0.02 kg P ha^{-1} y^{-1} (60%). In the particulate P fraction (TPP; 0.14 ± 0.03 kg P ha^{-1} y^{-1}; 29% of TP) more organic P was found than PIP (0.06 ± 0.01 kg P ha^{-1} y^{-1}) (Fig. 3). The Miombo site experienced slightly lower total P yields than the lowland site, with 0.35 ± 0.08 kg P ha^{-1} y^{-1}. The same trend as in the lowland forest was observed in the Miombo woodland, with highest P exports as DOP (0.24 ± 0.05 kg P ha^{-1} y^{-1}, 68%) followed by TPP (0.10 ± 0.05 kg P ha^{-1} y^{-1}, 29%) and only a marginal amount as DIP (0.01 ± 0.01 kg P ha^{-1} y^{-1}, 3%). Particulate P in the Miombo woodland was exclusively exported as PIP (Figure 3). Because the yields for all dissolved P constituents were calculated using average concentrations, the contribution of storm events on P yields reflects the water discharge during storm event conditions: 16% of all P constituent of the lowland stream and 29% of all P constituents of the Miombo stream were exported during storm events. Storm events were responsible for 30% of

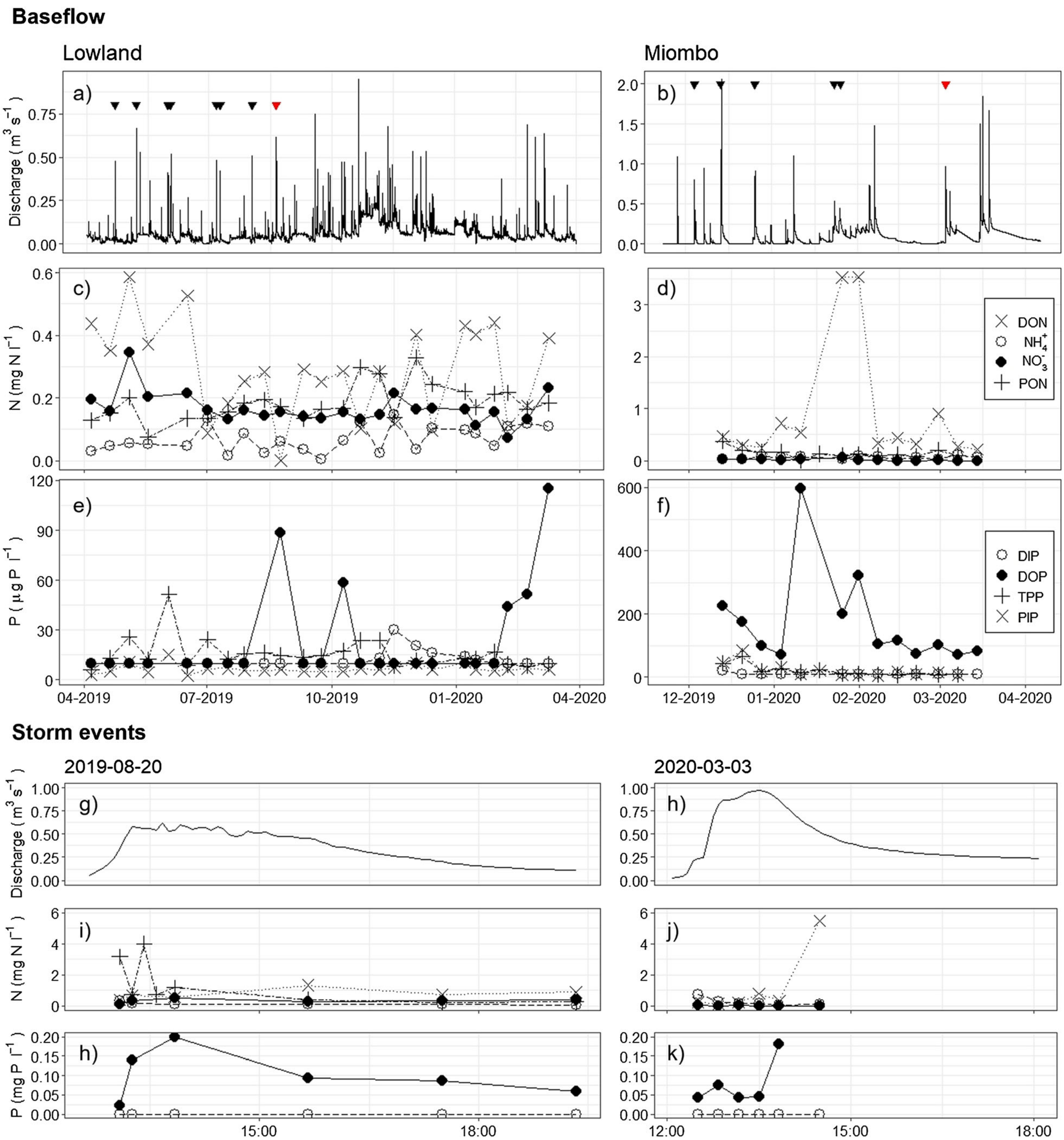

Figure 2. Time series for the lowland (left) and Miombo stream (right). **a**, **b** Time series of water discharge with triangles indicate storm events that got sampled. Red triangles indicate the events that are presented in this figure in the lower panels. The other storm events are presented in Figure S4 and Figure S5. **c**, **d** Time series of all the baseflow N samples: dissolved and particulate N species (dissolved organic nitrogen—DON, ammonium—NH_4^+, nitrate—NO_3^-, particulate organic N—PON). **e**, **f** Timeseries of all the baseflow P samples: dissolved and particulate P species (dissolved inorganic phosphorus—DIP, dissolved organic phosphorus—DOP, particulate inorganic phosphorus—PIP, total particulate phosphorus—TPP). Lower panels (**g–k**): one storm event selected for presentation at each site. **g**, **h** Storm events with water discharge. **i**, **j** Dissolved and particulate N concentrations during storm events. **h**, **k** Dissolved P concentrations during storm events.

Table 1. Number of Samples Taken at Baseflow and Stormflow Conditions for Each Measurement

	N° of Samples		Mean conc. samples		RMSE	Unit
	Baseflow	Stormflow	Baseflow	Stormflow		
Lowland						
TSS	39	49	24.36 ± 1.35	116.88 ± 18.60	48.39[1]	mg L^{-1}
PON	29	24	0.17 ± 0.01	2.28 ± 0.34	0.68	mg L^{-1}
DON	39	16	0.33 ± 0.03	1.05 ± 0.29	0.77	mg L^{-1}
NO_3^-	39	16	0.17 ± 0.01	0.31 ± 0.04	0.12	mg L^{-1}
NH_4^+	39	16	0.07 ± 0.01	0.12 ± 0.02	0.06	mg L^{-1}
TPP	39	0	12.25 ± 1.00	n.a	6.5	µg L^{-1}
PIP	39	0	5.58 ± 0.41	n.a	2.1	µg L^{-1}
DOP	39	16	21.74 ± 5.85	75.21 ± 13.25	n.a	µg L^{-1}
PO_4^{3-}	39	16	7.31 ± 0.87	7.47 ± 2.47	n.a	µg L^{-1}
Miombo						
TSS	18	55	34.89 ± 7.17	271.89 ± 45.33	117.6[1]	mg L^{-1}
PON	18	42	0.12 ± 0.02	1.20 ± 0.30	1.1	mg L^{-1}
DON	19	11	0.81 ± 0.24	0.85 ± 0.47	n.a	mg L^{-1}
NO_3^-	19	11	0.02 ± 0.00	0.08 ± 0.02	n.a	mg L^{-1}
NH_4^+	19	11	0.05 ± 0.01	0.23 ± 0.06	n.a	mg L^{-1}
TPP	18	0	22.28 ± 3.67	n.a	37	µg L^{-1}
PIP	18	0	17.54 ± 4.87	n.a	42	µg L^{-1}
DOP	19	11	139.82 ± 32.30	119 ± 30	n.a	µg L^{-1}
PO_4^{3-}	19	11	6.48 ± 0.90	5 ± 0	n.a	µg L^{-1}

[1] TSS model from Baumgartner and others (2022).
Middle columns show the mean values ± standard error of the baseflow and stormflow samples. Root mean square error (RMSE) of model predictions for the constituents which were modeled for yield calculations (see Figure S2 and Figure S3).

the total PIP and TPP export in the lowland stream and for 65% of the total PIP and TPP export in the Miombo stream (Figure 3), even though those predictions might be conservative due to missing TPP and PIP concentration measurements during storm events.

Discussion

Nitrogen Export is Dominated by Dissolved and Particulate Organic Nitrogen

Studies reporting PON or TPP yields from pristine tropical headwater streams are scarce, and relevant studies are presented in Table 2. Across the tropics, reported PON yields (n = 8) are generally less or equal to the PON yields we found for the lowland forest of the Congo Basin (Table 2). Only for a lowland forest in Costa Rica were reported PON yields significantly larger than those from our lowland site (Taylor and others 2015); however, with uplift rates from 1.7 up to 8.5 mm y^{-1} (Weintraub and others 2015), this lowland forest in the Osa Peninsula is far more geomorphologically active than a typical lowland forest sites within the Congo Basin. DON yields from all studies fell within a similar range and varied between 1.21 (lowland forest in Brazil, Lewis (1995)) and 4 kg ha^{-1} y^{-1} (Montane forest in Venezuela, Lewis (1986)). Both sites within the Congo Basin lay well within all these reported values (Table 2).

Lowland

Within the DIN losses of the lowland forest, around 70% is exported as NO_3^- and only 30% as NH_4^+. Higher losses as NO_3^- are expected, as NH_4^+ is more immobile and usually quickly nitrified to NO_3^- (Figure 2) whereas NO_3^- is more soluble and thus more mobile in soil solution, which makes it prone to leaching (Brookshire and others 2012). NO_3^- concentrations were stable throughout the year, indicating no shifts in microbial activity (such as nitrification and denitrification) and plant uptake in upslope soils. An increase in NO_3^- concentration was only visible during elevated discharge events (Figure S3), which has been attributed to periodically higher groundwater tables during storm events, leading to increased leaching of soluble N and a subsequent increase of lateral NO_3^- transport. This process may act independently of bio-

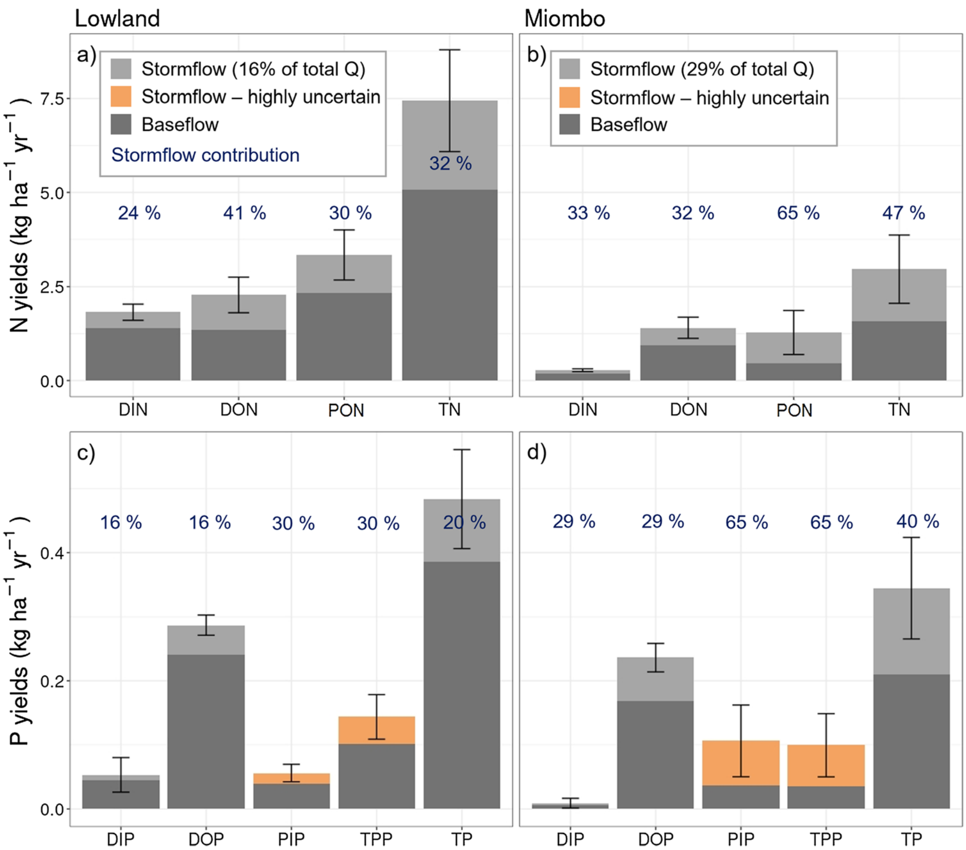

Figure 3. Top: Yields of dissolved inorganic N (DIN), dissolved organic N (DON), particulate organic N (PON) and total N (TN) during storm- and baseflow conditions at the lowland (**a**) and Miombo (**b**) site. Bottom: Yields of phosphate (DIP), dissolved organic P (DOP), particulate inorganic P (PIP), total particulate P (TPP) and total P (TP) during storm- and baseflow conditions at the lowland (**c**) and Miombo (**d**) site. Error bars indicating the standard error of calculated yields. Percentages indicate the share of constituent export during stormflow conditions. Storm event contributions of PIP and TPP are colored in orange, since those contributions are only based on TPP/PIP baseflow samples and total suspended sediment (TSS) storm event samples and thus highly uncertain.

logical control (Bruijnzeel 1991; Saunders and others 2006).

Our results from the lowland forest in the Congo Basin are the first to demonstrate the importance of PON export in apparently low erosive systems and we can show that even for old stable landscapes, sediment export from pristine forests is an important factor for nutrient budgets and biogeochemical cycles. The long-standing paradigm of N-rich lowland tropical forest was mainly justified by high DIN losses from these ecosystems compared to DON losses (Hedin and others 2003, 2009; Lewis and others 1999; Neill and others 2001). However, more recent observations found the opposite pattern: organic losses dominate over inorganic forms in N-rich ecosystems (Bauters and others 2019; Taylor and others 2015). We found the same trend during our year-long monitoring of the lowland forest in the central Congo Basin: only 24% of the total N was yielded as DIN, whereas organic forms (including PON) were responsible for 76% the TN export. Our results corroborate the findings by Bauters and others (2019) that even in N rich systems, inorganic N forms are cycled tightly and thus, aquatic DIN losses are not the best predictor for the N status of the ecosystem.

Miombo

Dissolved N in the Miombo were dominated by DON, while DIN concentrations were low throughout the wet season, even during storm events. DIN concentrations were more than three times lower in the Miombo compared to the lowland forest (Table 1) and reflects the lower N availability of dry tropical forests and savannah systems compared to the wet lowland forest (Mayes and others 2019). DON concentrations were stable throughout the wet season, with two samples exceeding the usual range of concentrations

Table 2. Literature Values of Particulate and Dissolved Nitrogen and Phosphorus Yields From Tropical Forested Watersheds

Country	Forest type	Yields (kg ha^{-1} y^{-1})			References
		PON	DON	DIN	
Costa Rica	Lowland	14.6	1.37	0.32	Taylor and others (2015)
Brasil	Lowland	0.7	2.87	0.2	Lesack (1993)
Brasil	Lowland	0.02–2.44	1.21–2.48	0.67–2.04	Lewis and others (1995)
Brasil	Montane	2.03–3.9	1.3	1.3–2.4	Lewis and others (1995)
Venezuela	Montane	0.75	2.35	2.07	Lewis and Saunders (1989)
Venezuela	Montane	3.64	4	2.38	Lewis (1986)
Puerto Rico	Montane	1.26	3.78	2.32	McDowell and Asbury (1994)
Kenya	Montane	4			Stenfert Kroese and others (2021)
DRC	Lowland	3.25	2.28	1.82	this study
DRC	Miombo	1.28	1.41	0.28	this study
Country	**Forest type**	**Yields (kg ha^{-1} y^{-1})**			**References**
		TPP	**DOP**	**DIP**	
Malaysia	Lowland	0.05			Malmer (1996)
Malaysia	Lowland	0.1			Malmer (1996)
Venezuela	Montane	0.23	0.177	0.06	Lewis (1986)
Mexico	dry forest	0.004		0.06	Campo and others (2001)
Puerto Rico	Montane	0.12			Pett-Ridge (2009)
DRC	Lowland	0.16	0.29	0.05	this study
DRC	Miombo	0.08	0.24	0.01	this study

(0.2 – 0.9 mg l^{-1}) by a factor of 4 (Figure 2). On closer examination, it is obvious that these two samples were collected just hours after the peak discharge of two different storm events. The time lag between the discharge and concentration peak indicates that DON rich waters, sourced from upper soil layers, probably take other flow paths (with slower response times) than bulk water. Similar to the lowland site, organic forms (that is, DON and PON) at the Miombo site dominate the N export (Figure 3); however, the overall DON and PON yields are lower than from the lowland forest. Although similar total sediment exports from both sites were reported (Lowland: 0.25 t ha^{-1} y^{-1}; Miombo: 0.24 t ha^{-1} y^{-1}; Baumgartner and others 2022), the PON export at the Miombo site was 60% lower compared to the lowland site. This reflects to a general lower N content within the suspended sediments (0.5% vs. 1.3%, respectively), mirroring the overall lower general productivity found in the Miombo, given by the lower density of vegetation and lower overall N inputs (see section Impact on Nutrient Budgets).

Dissolved Organic Phosphorus as the Major Loss Vector, Followed by Particulate Phosphorus

Studies that cover dissolved and particulate forms of organic P export from tropical forest ecosystems are even more scarce than studies covering organic N export (Table 2). Reported TPP values range from 0.004 kg ha^{-1} y^{-1} in a dry forest of Mexico (Campo and others 2001) up to 0.23 kg ha^{-1} y^{-1} in a montane forest of Venezuela (Lewis 1986). All reported values for TPP are within the same order of magnitude as the two measured sites of this study except the dry forest site in Mexico, which is an order of magnitude lower than the Miombo woodland.

Lowland

Roughly 36% of the total P yield of the lowland forest is attributed to particulate P (Figure 3). More than two thirds of this TPP are particulate organic P (POP), whereas only one third is PIP. PIP concentrations were quite stable during the year (Figure 2) and only showed a marginal increase with increasing water discharge (Figure S1), POP, and thus TPP, increased more strongly at high flowing conditions. This is an indication that PIP is predominantly exported with baseflow, while event-flow adds mainly POP to the suspended sediment fraction.

DOP is the most important fraction of TP exported from the lowland forest site. Unlike DON, DOP showed no significant correlation with water discharge (Figure S3). Because a decoupling of these dissolved organic nutrient pools is highly unlikely, this might be an artifact of analytical sensitivity, as DOP concentrations were generally low and close to the detection limit of the measurement.

The DIP concentrations were below the detection limit of 0.01 mg l^{-1} throughout the year, except for six samples at the end of the year 2019, and were not correlated with water discharge, resulting in not detectable concentrations even during storm events (Figure 2 & Figure S3). The observed concentrations near the detection limit of our method result in high uncertainty of the total DIP export. Low DIP concentrations are expected in old weathered tropical forest soils, due to the low mobility of PO_4^{3-} ions and their fixation by oxides (Sollins and others 1988).

Miombo

In contrast to the lowland forest, all TPP exported from the Miombo woodland was PIP (Figure 3). PIP concentrations were slightly higher than TPP concentrations for four sampling points (Figure 2), likely because TPP and PIP extractions were done from different filters of the same water sample. Nevertheless, the almost 1:1 correlation between TPP and PIP confirmed that the extraction methods worked well and that mainly PIP is present in TPP (Figure S7). PIP can be in the form of P containing minerals or inorganic P bound to secondary minerals. However, in old-weathered soils of the tropics P inputs from parent material weathering is negligible (Reed and others 2011) and mobilization of particulate P only occurs through surface runoff (Slomp 2012). Thus, it is likely that mainly mineral particles and not organic particles were removed from surface soils during rainfall events because export was dominated by PIP. Moreover, in contrast to the highly weathered Ferralsols in the lowland forest, the Acrisols of the Miombo do not show a well-developed organic horizon, leaving the mineral associated P more susceptible to erosion. Soil organic matter accumulation in Miombo woodlands is hindered by seasonal fires and the volatilization of N and P compounds (Campbell 1996). Furthermore, seasonal fires can cause higher soil mineral P concentration through pyomineralization of P, which has a light density and thus can be eroded more easily (Butler and others 2018).

DOP was the most important P loss vector in the Miombo woodland (Figure 3), while DIP concentrations were generally low and often below detection limit, hindering a robust quantification of DIP exports (Figure 2). In contrast to DIP losses, which are expected to be low in a tropical forest ecosystem on old-weathered soils, DOP losses do not reflect the P status of an ecosystem and can be high even in a P-limited system (Hedin and others 2003). We observed a generally lower P export compared to the lowland forest. However, the TN losses were even more reduced in the Miombo, resulting in a lower N:P ratio of total nutrient losses from the Miombo (8.5) than from the lowland forest (15.5), which may indicate that the Miombo site is relatively more limited in N than in P, compared to the lowland forest site (see ''Impact on nutrient budgets'' chapter).

Storm Events Disproportionally Affect N and P Losses

Yields of all N and P constituents at both sites are mostly driven by intense storm event conditions (Figure 3), although these storm conditions only take up a very short time during the whole hydrological year. The influence of short but intense storm events on sediment and on particulate organic matter (POM) exports of tropical montane forests has been shown (Clark and others 2013; Lloret and others 2013; Townsend-Small and others 2008). Furthermore, also dissolved organic C (DOC) has been reported to be driven by a few storm events in temperate forests (Raymond and Saiers 2010). The influence of storm events on PON export has been reported for temperate forests (Correll and others 1999) and in geomorphic active sites of the tropics (Hoover and MacKenzie 2009; Taylor and others 2015). However, the influence of storm events on dissolved and particulate forms of N and P in more geomorphologically stable regions of the tropics are lacking. In this study we showed that lowland forest storm conditions of short duration (4.7% of the time) are responsible for 41% of annual DON and 30% of annual PON export (Figure 3). In the Miombo this trend is even more pronounced with events exporting 65% of PON during 6.5% of the time. The Miombo experienced far fewer events than the lowland stream, leading to a few intense discharge pulses of accumulated material, while the more regular storm events in the lowland forest resulted in a more constant sediment export. The same trends are to some extend visible for P exports, although there TPP and PIP are more driven by storm events compared to DOP (Figure 3). However, it is important to state, that TPP and PIP exports were calculated without any storm event samples and are only based on the measured TSS exports, leading to a high uncertainty in those values. The high proportional export of organic constituents also corroborates the idea that there is limited biological control on organic losses and these forms of N and P are mainly transport limited. Thus, particulate, and organic forms of N and P are highly controlled by the hydrological regime, this very much highlights the susceptibility of these systems to possible changes in rainfall patterns. Predictions of future precipitation patterns in central Africa show an increase of heavy rainfalls under all climate scenarios (Haensler and others 2013), meaning that intensities of single rainfall events are increasing and that the stormflow conditions become even more dominating compared to baseflow conditions. All nutrient forms that are mainly transport limited will tend to follow hydrological regimes and increased aquatic exports of these nutrients are expected with increasing rainfall intensities, possibly increasing the importance of aquatic organic N and P exports under changing climate.

Impact on Nutrient Budgets

Nitrogen Budget

The majority of N inputs and outputs of the same lowland forest in the DRC have been quantified thoroughly by Bauters and others (2019) and is now complemented by a full quantification of aquatic losses by this study. Bauters and others (2019) observed high N deposition rates in the lowland forest (18.2 – 53.1 kg ha^{-1} y^{-1},Table 3) which was attributed to fire derived and mainly organic forms of N originating from savanna fires (Bauters and others 2018). Uncertainty in this value is derived from the difficult distinction between dry deposition and canopy leaching. If we include the complete aquatic N exports from this study, N_2O outgassing of 1.38 kg N-N_2O ha^{-1} y^{-1} (Barthel and others 2022), N_2 outgassing estimated at 7.1 kg ha^{-1} y^{-1} (Gallarotti and others 2021) and NO emissions of 7.6 kg N ha^{-1} y^{-1} (Holtgrieve and others 2006; Koehler and others 2009), the high imbalance toward N input is still prominent (− 5.2 to 29.7 kg N ha^{-1} y^{-1}, Table 3). While we conclude that PON, although neglected regularly in ecological and biogeochemical research, is an important N loss vector and indeed the highest loss term in aquatic N losses, it cannot close the N budget of the lowland forest within the Congo Basin. The amount of N received as wet and dry deposition is immensely high, especially considering the remoteness of this site and probably leads to an accumulation of N in this forest.

Although there are no studies available that cover biogeochemical research within the same Miombo ecosystem, reported atmospheric deposition (Bobbink and others 2010) and N_2-fixation rates (Houlton and others 2008) from other Miombo forests show that total N inputs into the Miombo likely range from 5 to 11 kg N ha^{-1} y^{-1} (Table 3). Aquatic TN export of 2.97 kg N ha^{-1} y^{-1} measured in this study together with reported N_2O emissions of 1.6 kg N ha^{-1} y^{-1} (Rees and others

Table 3. Nitrogen and Phosphorus Budgets From the Lowland Forest and Miombo Woodland Site

	Deposition	Fixation	Inputs	TDN	PON	N_2O	N_2	NO	Outputs	*Imbalance*
Nitrogen										
Lowland	18.2–53.1[1]	0[2]	**18.2–53.1**	4.1	3.3	1.43	7.1[4]	7.6[5]	**23.5**	*−5.3 to 29.6*
Miombo	3.0–5.0[5]	2.0–6.0[6]	**5.0–11.0**	1.7	1.3	1.2 [7]	*NA*	*NA*	**4.2**	*0.8–6.8*
	Deposition		**Inputs**	**DIP**	**DOP**	**TPP**			**Outputs**	***Imbalance***
Phosphorus										
Lowland	3.1[8]		**3.1**	0.05	0.29	0.16			**0.5**	*2.6*
Miombo	0.8–1.6[9]		**0.8–1.6**	0.01	0.24	0.08			**0.33**	*0.47–1.27*

All values are in kg ha^{-1} y^{-1}. References used: [1] Bauters and others (2019); [2] Bauters and others (2016); [3] Barthel and others (2022); [4] Gallarotti and others (2021); [5] Holtgrieve and others (2006), Bobbink and others (2010); [6] Houlton and others (2008); [7] Rees and others (2006); [8] Bauters and others (2021); [9] Wang and others (2017). Bold values are the sum of the values and italics are the difference between output and input

2006) is almost counterbalancing the N inputs (Table 3), even with N_2 and NO outgassing not been accounted for yet. Furthermore, seasonal fires cause N losses through volatilization and soil N mining is occurring through ongoing agricultural practices and charcoal production (Campbell 1996; Mayes and others 2019; Vitousek and others 2009). Therefore, the Miombo site is potentially more prone to N limitations compared to the lowland forest site, which can also be seen in the low DIN losses (Figure 3).

Phosphorus Budget

P budgets are less complicated than N as there is no major gaseous form of P. There are only two inputs of P into a forest ecosystem: via weathering of P-containing rocks and through atmospheric deposition. Rates of P input via weathering are not known for the study area, but we assume that those inputs are negligible as these soils are already old and deeply weathered (Reed and others 2011). High atmospheric P deposition sourced from fires has been found in the lowland forests of the DRC (Bauters and others 2021). As with N, the observed rates of aquatic P losses are too low to counterbalance high deposition rates (Table 3). The imbalance in the P budget toward higher inputs indicates that—contrary to widely held assumption—lowland tropical forests of the Congo Basin are likely not P limited.

P deposition for Miombo was obtained from a global modeling study by Wang and others (2017) and is thus highly uncertain. Even if assuming a conservative P deposition of 0.8 kg ha^{-1} y^{-1}, the aquatic loss term still only accounts for around 40% of the P input into the Miombo ecosystem (Table 3). However, an important landscape-level loss vector within the Miombo ecosystems was not accounted for in this study: seasonal understory fires and resulting loss of dust particles that transport organic forms of N and P from Savanna regions into the central tropics. This is likely a significant loss term, given the observed high N and P deposition within the lowlands which originates from savanna fires (Bauters and others 2018; Bauters and others 2021).

Conclusion

Our study highlights the importance to include aquatic losses of organic and particulate N and P constituents in biogeochemical research of tropical forest ecosystems. Even in geomorphologically stable landforms, such as the lowland forest and Miombo woodland within the Congo Basin, sediment transport had an important influence on the aquatic losses of N and P. Organic and especially particulate forms of N and P are under limited biological control, compared to inorganic forms, and thus those exports follow more the hydrological regime. Therefore, short but intense storm events are driving significant parts of TN and TP exports in both of our study sites, due to the high exports of particulate and dissolved organic forms of N and P. This is especially important in light of the predicted increase in rainfall intensity with climate change for the Congo Basin and thus has the potential to strongly impact N and P exports and impact nutrient cycling in those ecosystems. Moreover, although some systems such as the lowland forest experience high nutrient inputs through atmospheric deposition, inorganic aquatic losses are minimal compared to organic losses, which challenges the current paradigm that nutrient-rich systems encounter high losses of inorganic and bio-available nutrients. Our results are based on the monitoring efforts at two small headwater catchments within the Congo Basin. However, to get a better sense on nutrient exports from forests of the whole Congo Basin, more spatial coverage of measurements is necessary.

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DATA AVAILABILITY

Data are available at: https://doi.org/10.5281/zenodo.6586018.

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