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High precipitation causes large fluxes of dissolved organic carbon and nitrogen in a subtropical montane *Chamaecyparis* forest in Taiwan

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Abstract Fluxes of dissolved organic carbon (DOC) and nitrogen (DON) may play an important role for losses of C and N from the soils of forest ecosystems, especially under conditions of high precipitation. We studied DOC and DON fluxes and concentrations in relation to precipitation intensity in a subtropical montane *Chamaecyparis obtusa* var. *formosana* forest in Taiwan. Our objective was, to quantify DOC and DON fluxes and to understand the role of high precipitation for DOC and DON export in this ecosystem. From 2005 to 2008 we sampled bulk precipitation, throughfall, forest floor percolates and seepage (60 cm) and analyzed DOC, DON and mineral N concentrations. Average DOC fluxes in the soil were extremely high (962 and 478 kg C ha^{-1} year^{-1} in forest floor percolates and seepage, respectively) while DON fluxes were similar to other (sub)tropical ecosystems (16 and 8 kg N ha^{-1} year^{-1}, respectively). Total N fluxes in the soil were dominated by DON. Dissolved organic C and N concentrations in forest floor percolates were independent of the water flux. No dilution effect was visible. Instead, the pool size of potentially soluble DOC and DON was variable as indicated by different DOC and DON concentrations in forest floor percolates at similar precipitation amounts. Therefore, we hypothesized, that these pools are not likely to be depleted in the long term. The relationship between water fluxes in bulk precipitation and DOC and DON fluxes in forest floor percolates was positive (DOC $r = 0.908$, DON $r = 0.842$, respectively, Spearman rank correlation). We concluded, that precipitation is an important driver for DOC and DON losses from this subtropical montane forest and that these DOC losses play an important role in the soil C cycle of this ecosystem. Moreover, we found that the linear relationship between bulk precipitation and DOC and DON fluxes in forest floor percolates of temperate ecosystems does not hold when incorporating additional data on these fluxes from (subtropical) ecosystems.

Keywords Dissolved organic nitrogen · Dissolved organic carbon · Precipitation · Fluxes · Forest floor · Subtropical montane forest

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Introduction

Dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) often play a prominent role in the C and N cycle of forest soils. Both DOC and DON represent measures for dissolved organic matter (DOM), which is operationally defined as molecules that are smaller than 0.45 µm (Thurman 1985). However, DOC and DON do not behave similar in soils and should to be investigated separately (Michalzik et al. 2001). The concentrations and fluxes of DOC and DON in forest ecosystems often vary substantially which can be seen from the temporal dynamics and spatial patterns of the DOC/DON ratio (Michalzik and Matzner 1999; Prechtel et al. 2000).

Most of the research on the soluble organic forms of C and N has been conducted in temperate ecosystems (Kalbitz et al. 2000; Michalzik et al. 2001; Perakis and Hedin 2002; Aitkenhead-Peterson et al. 2005; Park and Matzner 2006). In (sub)tropical ecosystems, DOC and DON concentrations and fluxes have received less attention, especially in forest floor percolates, although the forest floor is known to be an important source of DOM (Kalbitz et al. 2000). Of these studies, only two investigated both DOC and DON fluxes and concentrations in throughfall, forest floor percolates and soil water seepage under (sub)tropical conditions (Schwendenmann and Veldkamp 2005; Chang et al. 2007). Other papers on DOC and DON in (sub)tropical ecosystems only focused on throughfall or seepage data (Tobón et al. 2004a; Schrumpf et al. 2006; Heartsill-Scalley et al. 2007; Fang et al. 2009), concentrations instead of fluxes (Wilcke et al. 2001; Guo et al. 2005; Möller et al. 2005; Goller et al. 2006; Zimmermann et al. 2007), or either DOC or DON (McDowell 1998; Hafkenscheid 2000; Liu and Sheu 2003; Oyarzún et al. 2004; Tobón et al. 2004b; Fang et al. 2008; Fujii et al. 2009).

In (sub)tropical regions, DOC fluxes in throughfall ranged from 97 to 232 kg C ha^{-1} year^{-1} (Schwendenmann and Veldkamp 2005; Fujii et al. 2009) and DON fluxes from 5.5 to 20.1 kg N ha^{-1} year^{-1} (Oyarzún et al. 2004; Fang et al. 2008). Chang et al. (2007) observed very high fluxes of DOC and DON in forest floor percolates (1,400 and 16.5 kg ha^{-1} 15 months^{-1}, respectively) and even high fluxes in seepage (653 and 4.6 kg ha^{-1} 15 months^{-1}, respectively) in a high precipitation mountain forest in Taiwan. Organic N fluxes in the soil exceeded those of mineral N by far. This finding is supported by other studies that reported a dominance of DON over mineral N in N-limited forest ecosystems (Qualls 2000; McDowell 2001; Perakis and Hedin 2002). In contrast, Schwendenmann and Veldkamp (2005) found, that the flux of mineral N with litter leachates was extremely high (200 kg ha^{-1} year^{-1}) as compared to the DON flux (13 kg ha^{-1} year^{-1}). They concluded that a high proportion of N_2-fixing legumes at their site in Costa Rica may have been responsible for the high inorganic N fluxes.

The flux of water is a major control of the dynamics of DON and DOC in temperate forest soils (Michalzik et al. 2001; Qualls et al. 2002). Therefore, it can be assumed that in (sub)tropical regions, fluxes of DOC and DON should be high, as these ecosystems are often subject to high amounts of precipitation due to frequent heavy storms (hurricanes, cyclones, typhoons). Two contrasting scenarios concerning the relationship between DOC and DON concentrations and water fluxes have been reported. On the one hand, concentrations of DOM increased with increasing discharge (Jardine et al. 1990; Easthouse et al. 1992; Dosskey and Bertsch 1994; Boyer et al. 1997; Hagedorn et al. 2000; Buffam et al. 2001), due to limited contact of organic solutes with possible sorption sites (Luxmoore et al. 1990; Edwards et al. 1993; Riise 1999). This positive relationship has not only been reported for runoff from catchments or seepage from the mineral soil, but also for forest floor leachates of temperate and tropical forests (e.g. Michalzik et al. 2001; Solinger et al. 2001; Goller et al. 2006). On the other hand, some studies found a dilution effect on DOC concentrations due to increasing water fluxes (McDowell and Wood 1984; Easthouse et al. 1992). Tipping et al. (1999) concluded, that the export of DOC only increases with increasing water fluxes in soils with large pools of potential DOM. Potential DOM is defined as organic material, which can possibly enter the soil solution, depending on its interaction with the solid soil phase (Tipping 2002). One important source for potential DOM is the forest floor (Qualls 2000; Park and Matzner 2003). In (sub)tropical ecosystems with high amounts of precipitation, a positive relationship between DOC and DON concentrations in forest floor percolates and water fluxes should therefore point to large pools of potential DOM. These pools are hard to deplete, even under these conditions of high precipitation. On the other hand, a negative relationship between DOC and DON concentrations in forest floor percolates and water fluxes should point to small pools of potential DOM (dilution effect), that can be depleted fast.

Our objective was, to quantify DOC and DON fluxes in relation to precipitation intensity and to understand the role of high precipitation for DOC and DON export in this poorly studied subtropical ecosystem over 4 years.

Materials and methods

Site description

The Chi-Lan Mountain site is located in northern Taiwan (24°35′N, 121°24′E). Altitude varies from 1,400 to 1,800 m above sea level with a mean annual air temperature of 13°C and annual precipitation from 2,000 to more than 5,000 mm depending on the number and strength of storms (Chang et al. 2007). Fog is very frequent and plays an important role for nutrient and water input. The average relative humidity of the atmosphere is 90% (Chang et al. 2007).

Vegetation is dominated by *Chamaecyparis obtusa* var. *formosana*, planted about 50 years ago, with a density of 1,820 trees ha^{-1} and 82% of the total basal area. Understory vegetation comprises species such as *Illicium philippinense* (Merr.) and *Rhododendron formosanum* (Hemsl.). The total annual litterfall of *C. obtusa* var. *formosana* amounts to 5,722 kg dry mass ha^{-1} $year^{-1}$ (Chang et al. 2007). The above-ground biomass of this species is 140 t dry mass ha^{-1} (12% leaves, 12% twigs, 76% stems) (Chang, unpublished data).

The soil is a poorly developed Lithic Leptosol (FAO 1998) with a loamy texture, developed from metamorphic slate and quartzite of a former landslide. Due to a very high content (about 90 vol%) of coarse material (>2 mm), there is no surface runoff, even during very high precipitation events (Chang et al. 2007). Because of intensive rooting the stratification of the well developed forest floor is poor. Thickness of the forest floor varies between 7 and 10 cm and C and N contents amount to 340 and 20 g kg^{-1}, respectively. The C/N ratio of the total forest floor is 17 and the pH (H_2O) is 3.5. The pH ($CaCl_2$) of the mineral soil varies between 2.8 (A horizon) and 3.2 (40 cm depth). The soil is very poor in nutrient cations (Ca^{2+}, Mg^{2+}, K^{+}), which are largely restricted to the O and A horizon. The soil is permanently moist due to continuously high precipitation over the year (Chang et al. 2007). Soil C stocks in the complete profile amount to 27.3 t C ha^{-1}, of which 32% is stored in the O horizon and 48% in the A horizon (Chang et al. 2008).

Sample collection and analysis

Samples from throughfall, forest floor percolates and seepage (60 cm) were taken once every 2 weeks for 4 years (January 2005–December 2008). Bulk precipitation was collected in three samplers of 20 cm diameter in an open field. Throughfall was collected with 12 20 l PE bottles and 20 cm diameter funnels, which were installed in a systematic grid. Samples were then aggregated to three replicates by volume-weighted mixture of each four collector solutions. Forest floor percolates were sampled by free draining lysimeters (January 2005–March 2007) and by PVC lysimeters with PE membranes (pore size 3 μm) of about 500 cm^2 (April 2007–December 2008) established in four replicates at the border of the O and A horizon. At 10 min intervals, suction was applied to the membrane of the PVC lysimeters to collect the sample into a PE bottle and to avoid water logging.

Soil water seepage was collected by eight ceramic suction cups installed at about 60 cm depth. Each sampling device for seepage water was comprised of two suction cups, therefore, seepage water was collected in four replicates per sampling date. The suction cups were evacuated at about −0.2 bar.

Before analysis, all samples were filtered (0.45 μm) and then analyzed for DOC, DON and mineral N. NH_4^+, NO_3^- and TDN (total dissolved N) were determined using a flow injection analyzer (Lachat, QuikChem 8000 series, USA). Dissolved organic N was calculated as TDN−(NO_3^- + NH_4^+). Dissolved organic C was analyzed using high temperature combustion (Elementar, High TOC II, Germany).

Calculations

For 5% of all sampling dates, no data for bulk precipitation from the field samplers was available.

For these dates, we used data from an additional rain gauge, installed in some distance from our sampling site. Values obtained from the rain gauge were comparable to values from our site ($r = 0.99$, $p < 0.01$, $n = 96$, Pearson correlation). If the amount of precipitation exceeded the uptake capacity of throughfall samplers, throughfall fluxes were calculated using a regression equation derived from the relation of bulk precipitation and throughfall (at 5% of all sampling dates). For the regression equation, we used throughfall fluxes and bulk precipitation data since 20 November 2002 ($r = 0.98$, $p < 0.01$, $n = 147$, Pearson correlation). The calculation of solute fluxes in bulk precipitation and throughfall was done by multiplying measured water fluxes by measured concentrations.

Soil water fluxes were calculated using the transpiration of the stand and the distribution of fine roots in the soil. Transpiration was measured by using the sap flow method (Chang et al. 2007) and amounts to about 160 mm year^{-1}. Evaporation was assumed to be negligible (Chang et al. 2007). Compared to annual precipitation amounts, transpiration rates were very low and were assumed to be evenly distributed over the year. Therefore, we calculated the transpiration loss from the forest floor for each sampling date by dividing the total transpiration by the number of sampling dates per year. Forest floor percolate fluxes of water for each sampling date were calculated using the fine root distribution in the forest floor. As 34% of fine roots are located in the forest floor (Chang et al. 2007), transpiration losses amount to 34 and 66% from the forest floor and the mineral soil, respectively. Therefore, we subtracted 34% of transpiration at each sampling date from respective throughfall fluxes to obtain forest floor percolate fluxes of water. Seepage fluxes of water were calculated by subtracting 66% of transpiration at each sampling date from respective forest floor water fluxes.

Statistical analyses

Concentrations and fluxes are presented as arithmetic means with standard errors if not stated otherwise. Normality was tested with the Kolmogorov–Smirnov test, and correlation analysis was carried out using Spearman rank or Pearson correlation, depending on whether the data were normally distributed. To meet the requirements for linear regression analysis, data were log-transformed. Mann–Whitney Rank Sum tests or t tests were carried out at $p < 0.001$. Significant effects were determined at $p < 0.05$ unless stated otherwise. All statistical analyses were performed with SigmaStat (version 3.5, Systat Software, Inc., Chicago, IL, USA).

Results

Figure 1 gives an overview over the bulk precipitation at each sampling date. Mean annual precipitation (years 2005–2008) amounted to 4,815 mm (±617 mm, standard deviation), the mean annual water flux in throughfall, forest floor percolates and seepage to 4,169, 4,115 and 4,009 mm, respectively (Table 1).

Concentrations of NH_4^+ and NO_3^- in all solutions were very low during the sampling period (Table 2). While concentrations of inorganic N decreased with passage through the ecosystem, DOC and DON behaved differently. In throughfall, DOC and DON concentrations were low, increased clearly in forest floor percolates and decreased again in seepage (Table 2). In throughfall DON concentrations were similar to NO_3^- concentrations, but in forest floor percolates, DON concentrations were considerably higher than inorganic N concentrations. In seepage, inorganic N concentrations were still lower than DON concentrations, but the difference was not as prominent as in forest floor percolates (Table 2).

Mean annual DOC and DON fluxes were highest in forest floor percolates and seepage (Table 1) with

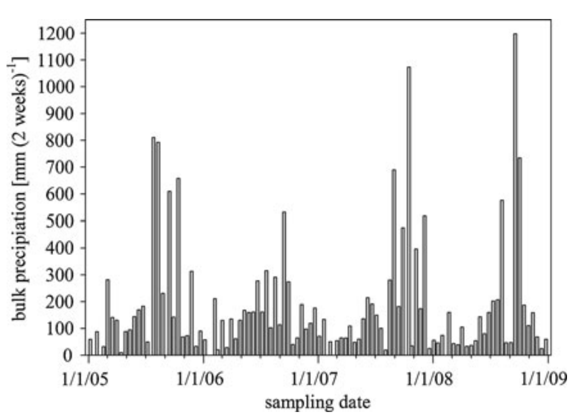

Fig. 1 Bulk precipitation at the study area from January 2005 until December 2008

Table 1 Annual and mean annual fluxes of water, NO_3^-, NH_4^+, DON and DOC in throughfall, forest floor percolates and seepage (60 cm)

Year	Water (mm)	NO_3^- (kg N ha^{-1} $year^{-1}$)	NH_4^+	DON	DOC (kg C ha^{-1} $year^{-1}$)
Throughfall					
2005	4,587	2.3	1.5	1.8	140
2006	3,503	1.8	2.2	2.8	93
2007	4,560	4.6	2.3	4.7	97
2008	4,026	2.5	1.6	4.4	94
Mean	4,169 (±257)	2.8 (±0.6)	1.9 (±0.2)	3.4 (±0.7)	106 (±11)
Forest floor percolates					
2005	4,533	2.9	0.9	12.6	894
2006	3,448	0.6	0.8	12.7	745
2007	4,506	3.2	2.1	21.0	1135
2008	3,972	1.5	2.1	16.4	1073
Mean	4,115 (±257)	2.1 (±0.6)	1.5 (±0.4)	15.7 (±2.0)	962 (±89)
Seepage (60 cm)					
2005	4,427	1.6	0.6	5.7	561
2006	3,343	1.3	0.7	5.3	411
2007	4,400	3.3	2.6	7.3	512
2008	3,866	2.8	1.3	7.7	477
Mean	4,009 (±257)	2.3 (±0.5)	1.3 (±0.5)	6.5 (±0.6)	490 (±32)

Sampling: once every 2 weeks from January 2005 to December 2008, numbers in parentheses indicate standard errors of the mean

Table 2 Mean annual concentrations of NO_3^-, NH_4^+, DON and DOC in throughfall, forest floor percolates and seepage (60 cm)

	NO_3^- (mg N l^{-1})	NH_4^+	DON	DOC (mg C l^{-1})
Throughfall	0.13 (±0.03)	0.08 (±0.01)	0.13 (±0.03)	3.9 (±0.2)
Forest floor percolates	0.06 (±0.01)	0.06 (±0.02)	0.46 (±0.06)	28.4 (±3.5)
Seepage (60 cm)	0.06 (±0.02)	0.04 (±0.01)	0.15 (±0.01)	12.3 (±0.3)

Sampling: once every 2 weeks from January 2005 to December 2008, numbers in parentheses indicate standard errors of the mean

exceptionally high DOC fluxes in forest floor percolates. Mineral N fluxes were similar to DON fluxes in throughfall, but significantly lower than DON fluxes in forest floor percolates and seepage. Again, the difference between DON and inorganic N fluxes was most prominent in forest floor percolates (Table 1).

There was no clear relationship between DOC and DON concentrations in throughfall, forest floor percolates and seepage and bulk precipitation per 2-week interval (Fig. 2). Most of the bulk precipitation per 2 weeks interval was in the range of 10–200 mm $(2\ weeks)^{-1}$. Within this range, DOC and DON concentrations in forest floor percolates were highly variable at similar amounts of bulk precipitation.

On the contrary, there was a linear relationship between bulk precipitation per 2 weeks interval and DOC and DON fluxes in forest floor percolates (Fig. 3). Here, water fluxes explained 79.9% of DON fluxes and 82.3% of DOC fluxes (linear regression on log-transformed data). The relationship between DOC and DON fluxes in forest floor percolates and bulk precipitation per 2 weeks interval was significant (DOC: $r = 0.908$, DON: $r = 0.842$, $n = 100$, $p < 0.01$, Spearman rank correlation). The same was

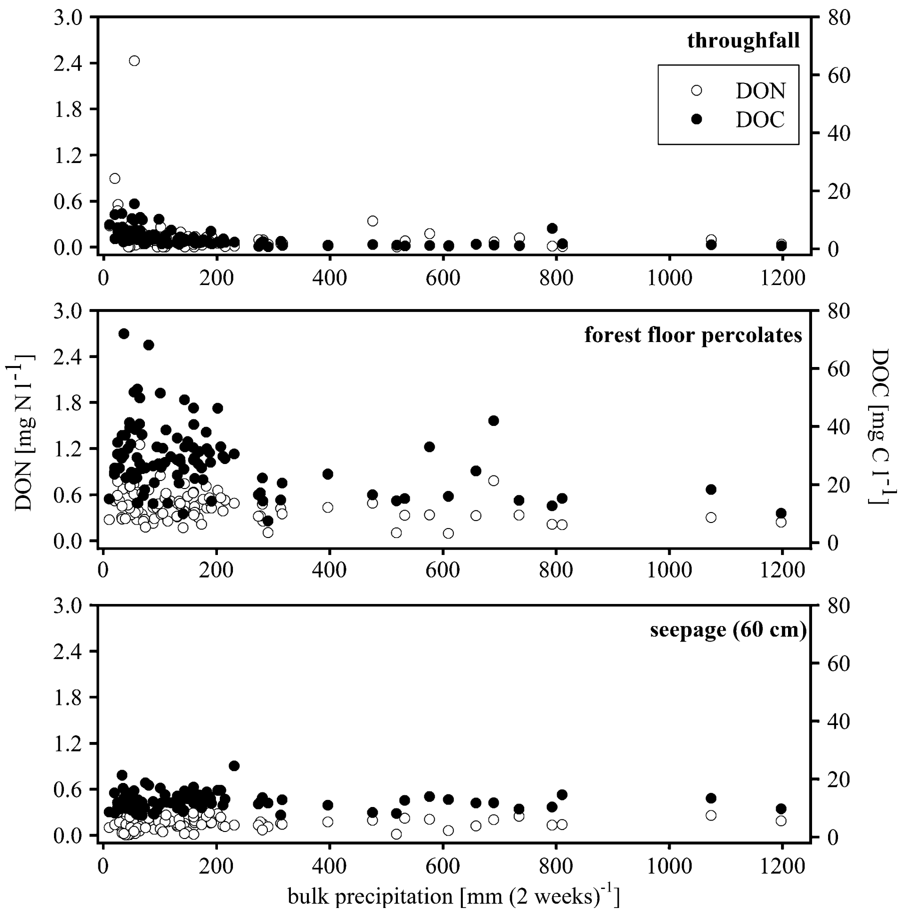

Fig. 2 Relationship between bulk precipitation and DOC and DON concentrations in throughfall, forest floor percolates during and seepage (60 cm). *Black dots* are DOC concentrations, *white dots* are DON concentrations

true when correlating organic solute fluxes in seepage and bulk precipitation per 2 weeks interval (DOC: $r = 0.980$, DON: $r = 0.866$, $n = 100$, $p < 0.01$, Spearman rank correlation).

Discussion

Solute concentrations in forest floor percolates can be influenced by lysimeter type. At our site, the lysimeter type was changed from zero-tension to suction-operated lysimeters in April 2007. For DOC, differences between zero-tensions and suction-operated lysimeters have been reported, but the results were not consistent among studies, probably due to differences installation depth and other factors (Reynolds et al. 2004; Buckingham et al. 2008). In our study, both DOC and DON concentrations increased significantly after installing new lysimeters (DOC Mann–Whitney Rank Sum Test, DON *t* test; $n = 56$ before installation of new lysimeters, $n = 44$ after installation of new lysimeters). The effect on fluxes was moderate: average DOC fluxes increased from 819 (2005–2006) to 962 kg C ha^{-1} year^{-1} (2005–2008) while average DON fluxes increased from 12.6 (2005–2006) to 15.7 kg N ha^{-1} year^{-1} (2005–2008). The observed increase might not only be due to the change of lysimeter type but also due to the large heterogeneity of the soil which makes it difficult to assess actual differences between lysimeter types in the field (Hendershot and Courchesne 1991; Neff and Asner 2001). Our results corroborate the finding, that there is a general source of uncertainty associated to flux measurements using lysimeters, as different lysimeter types collect different pools of water (Lajtha et al. 1999).

Mean annual fluxes of DOC and DON in throughfall and DON fluxes in forest floor percolates were well within the range of values reported in the literature, while DOC fluxes in forest floor percolates and

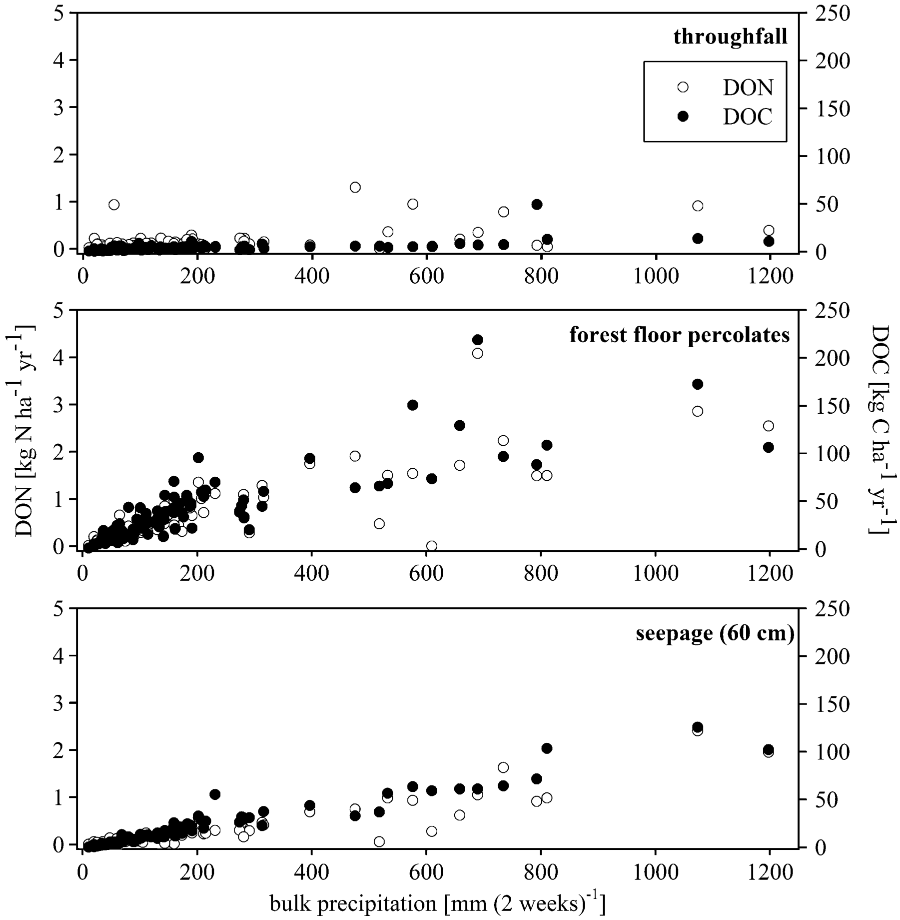

Fig. 3 Relationship between bulk precipitation and DOC and DON fluxes in throughfall, forest floor percolates during and seepage (60 cm). *Black dots* are DOC concentrations, *white dots* are DON concentrations

seepage at our site were exceptionally high (Table 3). The magnitude of DOC and DON fluxes might be explained by several different factors. First, fresh litter contributes significantly to DOC production in forest floors (Kalbitz et al. 2000) and the input of litter is large at our site due to frequent typhoons (Rees et al. 2006). However, decomposition rates are low at our site due to the poor litter quality of *Chamaecyparis* leaves (Rees et al. 2006) and due to very low pH values. The subsequent accumulation of Oa material can also lead to high DOC fluxes from the forest floor, as Oa material can play an even more important role in DOC release from the forest floor than fresh litter (Fröberg et al. 2003; Müller et al. 2009).

Second, rooting is very intensive at our study site with a total mass of living fine roots of 2,074 kg ha^{-1} in the forest floor (Chang et al. 2007). Yano et al. (2005) showed in a laboratory study that below-ground litter can strongly add to DOC and DON production as root litter produced ten times more water extractable DON and than needle litter and twice as much DOC. This finding suggests, that the decay of fine roots might significantly contribute to DON fluxes under field conditions.

Third, bryophytes are abundant in the understory vegetation at our site. Research on leaching of DOC and DON from bryophytes and the decomposability of bryophyte species is lacking, therefore, it still has to be investigated if bryophytes significantly contribute to DOC and DON fluxes in forest ecosystems.

Fourth, Kalbitz et al. (2006) reported increasing DOM production (DOC is the main constituent of DOM) during the later phase of litter decomposition in samples with relatively large lignin degradation. They concluded that lignin can be an important source for DOM from decomposing litter. However, the lignin content of fresh *C. obtusa* var. *formosana* litter is low, amounting to 13.8% (Rees et al. 2006), but the actual role of lignin in the DOC production of *C. obtusa* var. *formosana* litter has not been investigated yet.

When assessing the role of DOC export from the forest floor in the C cycle of this ecosystem, sources and sinks of DOC in the forest floor need to be considered. Input of C to the forest floor at our site can occur via throughfall, above- and belowground litter and root exudates. The total annual aboveground litterfall at the Chi-Lan Mountain site amounts to 3,059 kg C ha^{-1} $year^{-1}$ (Chang et al. 2007), while throughfall input of DOC is 105.8 kg ha^{-1} $year^{-1}$. No data on root litter and root exudate input of C is available for our site. Losses of DOC from the forest floor at our site will mainly occur via mineralization or leaching. Mineralization to CO_2 is the most important fate of organic matter supplied to the O horizon of forest soils, while export to the mineral soil as DOC is less important (McDowell and Likens 1988; Zech and Guggenberger 1996). In this study, losses of DOC from the forest floor were very high (962 kg C ha^{-1} $year^{-1}$), while soil respiration amounts to 17.6 kg C ha^{-1} $year^{-1}$. Therefore, we conclude, that the high losses of DOC from the forest floor play an important role in the soil C cycle of this forest ecosystem.

The passage of organic solutes through the mineral soil often leads to a decrease in DOC and DON concentrations in seepage as compared to the forest floor, as DOC and DON are adsorbed onto mineral surfaces (Guggenberger et al. 1998; Kaiser and Zech 1998, 2000) or mineralized (Yano et al. 2000; Kalbitz et al. 2003; Marschner and Kalbitz 2003). The decrease in DOC and DON concentrations between forest floor percolates and seepage (Table 2) was not as prominent as compared to the results of Schwendenmann and Veldkamp (2005) as both sorption and decomposition are probably less important at our site. At the Chi-Lan Mountain site, the soil is very shallow and stony and also partly water-saturated. Consequently, the availability of iron oxides as sorption sites for DOC and DON is limited. In anaerobic soils, clay minerals can contribute significantly to sorption, if available iron oxide pools are small (Fiedler and Kalbitz 2003). The clay content at our site is 13% in the first 5 cm of the mineral soil and increases to 20% below 5 cm.

As DOC and DON in water extracts from litter of the Chi-Lan Mountain site were recalcitrant to microbial decay in a laboratory experiment (Schmidt, unpublished data), decomposition probably only plays a minor role in these soils. Therefore, we suspect that at our site, sorption of DOC and DON is more important than decomposition. Both iron oxides and clay minerals may contribute to sorption, depending on the redox state of the soil.

Dissolved organic N played an important role for N losses from this ecosystems as compared to mineral N. The contribution of DON to total N fluxes was 42% in throughfall, 81% in forest floor percolates and 65% in seepage (60 cm) (Table 1). Hafkenscheid (2000) found similar contributions in a montane rain forest in Jamaica, where DON fluxes amounted to 67–79% of total N fluxes in litter percolates and to 54–71% in the Ah horizon, while Schwendenmann and Veldkamp (2005) reported a lower contribution of DON fluxes to total N fluxes in a tropical wet forest ecosystem in Costa Rica. At their site, mineral N fluxes were very high due to the high proportion of N_2-fixing legumes. Fang et al. (2008) also found, that the contribution of DON fluxes to total N fluxes was low in three subtropical forests in China. At their site, the total N flux in precipitation was very high (50 kg N ha^{-1} $year^{-1}$) and mineral N fluxes in throughfall amounted to 23–32 kg N ha^{-1} $year^{-1}$. As revealed by small throughfall fluxes of mineral N (averaging 4 kg N ha^{-1} $year^{-1}$), N deposition was low at our site. This corroborates the finding, that DON is dominant over mineral N in N-limited forest ecosystems receiving low anthropogenic N inputs (Qualls 2000; Perakis and Hedin 2002; Park and Matzner 2006).

Michalzik et al. (2001) correlated published data on a broad range of annual precipitation (500–1,800 mm) and DOC and DON fluxes in the forest floor percolates of temperate forest ecosystems and found a strong positive linear relationship. We collected additional data on these parameters from (sub)tropical forest ecosystems (see Table 3). Moreover, additional data on DOC and DON fluxes in forest floor percolates of 12 temperate ecosystems were included (Table 4). Three of these studies were not included in Michalzik et al. (2001) although they were published before (Qualls et al. 1991; Zech and Guggenberger 1996; Markewitz and Richter 1998), while the other nine studies have been published afterwards (Solinger et al. 2001; McDowell et al. 2004; Yano et al. 2004; Fröberg et al. 2005, 2006; Fujii et al. 2008; Jones et al. 2008; Kleja et al. 2008; Rosenqvist et al. 2010). Although some studies were conducted at the same forests in Sweden, we included all of them, as they measured fluxes in different years. In addition, we included annual fluxes from our study, as annual precipitation was highly variable

Table 3 Fluxes of DOC and DON in throughfall, forest floor percolates and seepage (60 cm) in (sub)tropical forest ecosystems

Location	Precipitation (mm)	Fluxes (kg ha^{-1} year^{-1})						References
		Throughfall		Forest floor percolates		Seepage		
		DON	DOC	DON	DOC	DON	DOC	
Chi-Lan Mountains (Taiwan)	4,815	3.4	105	15.7	962	6.5 (60 cm)	490 (60 cm)	This study
Luquillo Mountains (Puerto Rico)	3,482[a]	–	127	–	–	–	92 (40 cm) 43 (80 cm)	McDowell (1998)
Blue Mountains (Jamaica)	2,850	–	–	17.6	–	1.0	–	Hafkenscheid (2000)
Guandaushi forest (Taiwan)	2,300–2,700 (three sites)	–	167–231	–	–	–	–	Liu and Sheu (2003)
Valley Antillanca (Chile)	7,111	5.5	–	8.2	–	–	–	Oyarzún et al. (2004)
Pena Roja (Colombia)	3,400 (four sites)	–	148–190	–	–	–	–	Tobón et al. (2004a)
Araracuara (Colombia)	3,400	–	–	–	217–369	–	–	Tobón et al. (2004b)
La Selva Biological Station (Costa Rica)	4,200	9.0	232	13	277	3.0 (20 cm) 2.0 (40 cm) 1.0 (80 cm)	95 (20 cm) 64 (40 cm) 44 (80 cm)	Schwendenmann and Veldkamp (2005)
Kilimanjaro (Tanzania)	1,840 (three sites)	7.3–9.2	120–200	–	–	–	–	Schrumpf et al. (2006)
Luquillo Mountains (Puerto Rico)	3,482[a]	8.8	132	–	–	–	–	Heartsill-Scalley et al. (2007)
Dinghushan Reserve (China)	1,927 (three sites)	14.6–20.1	–	–	–	6.5–16.9 (20 cm)	95–198 (20 cm)	Fang et al. (2008, 2009)
East Kalimantan (Indonesia)	2,187/2,427 (two sites)	–	182/97	–	470/562	–	54/54 (30 cm)	Fujii et al. (2009)

[a] Taken from Heartsill-Scalley et al. (2007)

Table 4 Fluxes of DOC and DON in forest floor percolates in temperate forests in publications not included in Michalzik et al. (2001)

Location	Precipitation (mm)	Fluxes in forest floor percolates (kg ha^{-1} $year^{-1}$)		References
		DON	DOC	
Coweeta Hydrologie Laboratory (USA)	1,770	–	482	Qualls et al. (1991)
Fichtelgebirge (Germany)	1,150	–	231	Zech and Guggenberger (1996)
Calhoun Experimental Forest (USA)	1,230	–	317	Markewitz and Richter (1998)
Steigerwald (Germany)	752	–	271	Solinger et al. (2001)
Harvard Forest (USA)	Two sites 1,100	8.0/10.9	288/402	McDowell et al. (2004)
H.J. Andrews Experimental Forest (USA)	2,370	–	482	Yano et al. (2004)
Asa (Sweden)	688	–	317	Fröberg et al. (2005)
Asa, Knottäsen, Flakaliden (Sweden)	688	–	263	Fröberg et al. (2006)
Mt. Yatsugatake, Tango Peninsula, Mt. Yoshida (Japan)	Three sites 1,422–1,782	–	35–344	Fujii et al. (2008)
North Wales (United Kingdom)	2,000	4.5	109	Jones et al. (2008)
Asa, Knottäsen, Flakaliden (Sweden)	Three sites 523–688	–	140–930	Kleja et al. (2008)
Tönnersjöheden (Sweden)	Two sites 800–1,000	7.9/9.3	252/309	Rosenqvist et al. (2010)

depending on the number and strength of typhoons (4,014–5,312 mm).

Annual DOC fluxes in forest floor percolates from our site fitted the linear correlation found by Michalzik et al. (2001) (Fig. 4). The same was true for additional data from temperate forest ecosystems (Table 4; Fig. 4). On the contrary, most of the DOC fluxes reported from other (sub)tropical ecosystems (Table 3) were lower than one could expect from the linear relationship reported by Michalzik et al. (2001) (Fig. 4). One explanation for this phenomenon could be that higher temperatures in (sub)tropical regions enhance decomposition and forest floors are often thinner than in temperate forest ecosystems. As soils in (sub)tropical ecosystems are often poor in nutrients and deeply weathered, the nutrients that enter the forest floor with litterfall, throughfall and stemflow need to be retained efficiently. Therefore, the forest floor is virtually "leak-proof" (Richards et al. 1996) and losses of DOC and DON will be minimized. Also, a high proportion of the nutrient stock is held in aerial tissues (Richards et al. 1996). These nutrients will not enter the forest floor and therefore will not be subject to leaching losses.

Mean annual DON fluxes from temperate forest ecosystems (Table 4) also fitted the linear relationship found by Michalzik et al. (2001) (Fig. 4). Again, additional DON flux data from (sub)tropical ecosystems was lower than one could expect from the observed linear relationship (Fig. 4). In contrast to DOC fluxes, DON fluxes from our site did not fit the linear correlation (Fig. 4). For DON, there seems to be a precipitation threshold above which DON fluxes no longer increase. This phenomenon might also be explained by the efficient nutrient retention mechanisms of (sub)tropical ecosystems (Richards et al. 1996). As N is a very important nutrient in forest ecosystems, the retention mechanisms for organic N might be even better developed than for DOC, e.g. via direct uptake of DON by plants in the forest floor. For example, ectomycorrhizal associations, which can enhance nitrogen uptake (Högberg 1989) can be found in many tropical plant families (Richards et al. 1996).

One objective of this study was to understand the role of high precipitation for DOC and DON export in this ecosystem. We found, that the relationship between DOC and DON concentrations in forest floor percolates and water fluxes was weak (Fig. 2), while DOC and DON fluxes in forest floor percolates were governed by the flux of water to a large extent (Fig. 3). No dilution effect was visible as concentrations did not decrease with increasing water fluxes. At the same time, there was also no positive relationship

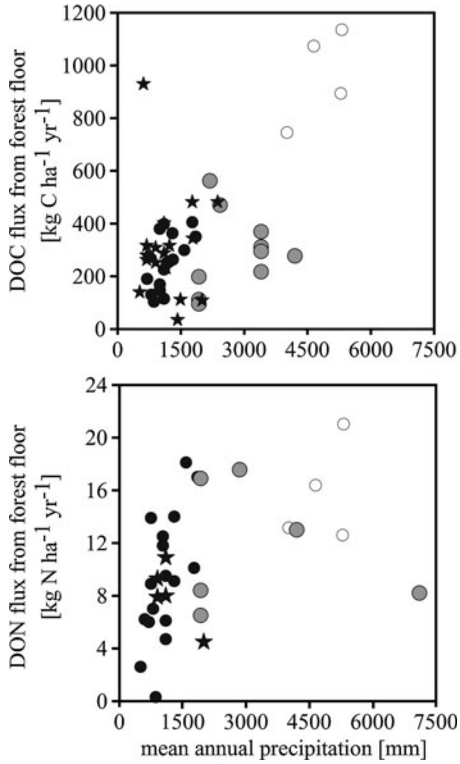

Fig. 4 Fluxes of DOC (*top*) and DON (*bottom*) from forest floor percolates and mean annual precipitation. *Black dots* are data from temperate forest ecosystems published by Michalzik et al. (2001), *black stars* are data from temperate forest ecosystems not included in Michalzik et al. (2001) (Table 4), *grey dots* are data from (sub)tropical ecosystems (Table 3), *white dots* are annual values from this study

between DOC and DON concentrations and water fluxes, which would indicate a large pool of potentially soluble DOM. Other studies also reported, that there was no correlation between DOC and DON concentrations in forest floor percolates and water fluxes (Guggenberger and Zech 1994a; Michalzik et al. 1998; Michalzik and Matzner 1999; Hilli et al. 2008). This implies, that a depletion of the pool of potentially soluble DOM is rather unlikely. However, our sampling frequency could have been too low to detect a relationship as the response of DOC and DON concentrations will occur within hours or days after rainfall (Michalzik et al. 1998).

Another possible explanation for the independence of DOC and DON concentrations from the flux of water might be, that at some times the pool of potentially soluble DOM was larger than at other times, leading to different concentrations of DOC and DON in forest floor percolates at similar precipitation amounts. The pool size of potentially soluble DOM is not constant, as it is governed by different factors. For example, decomposition conditions before rainfall can influence the amount of potentially soluble DOM that is available during rainfall, as microorganisms decompose soil organic matter to DOM (Guggenberger and Zech 1994b; Park et al. 2002), that can be lost from the forest floor. A strong increase in DOC and DON concentrations due to rewetting the soil after a dry period as reported by Goller et al. (2006) for a montane forest in Ecuador, is not likely to occur under the conditions at the our site. Although the importance of drying–wetting events on the release of soluble organic compounds is well known (Christ and David 1996; Hentschel et al. 2007; Borken and Matzner 2009), this process is not likely to play an significant role at our site, as the soil is permanently moist due to high continuous precipitation and frequent fog (Chang et al. 2008).

Also the amount of substrate available for decomposition might need to be considered when assessing the depletion risk of the potentially soluble DOM pool in the forest floor. The Chi-Lan mountain site is subject to frequent typhoons which cause large additions of fresh litter to the forest floor. Chang et al. (2007) showed in a litter manipulation experiment, that DOC concentrations increased after litter addition at our site. This implies, that the pool of potentially soluble DOM is probably quickly replenished, e.g. by DOM released by microorganisms during decomposition.

Conclusions

Precipitation plays a crucial role for DOC and DON losses in this forest ecosystems as fluxes are directly related to the amount of precipitation. These losses are important for the soil C and N cycle of this ecosystem. We conclude, that a depletion of potentially soluble DOM pools in the forest floor is unlikely. If these pools are depleted during a storm, they will probably quickly be replenished, e.g. by DOM released by microorganisms during decomposition. More research on DOC and especially DON fluxes from the forest floor of (sub)tropical ecosystems is needed, to better understand the relationship of these fluxes and the amount of bulk precipitation on a global scale.

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