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Fluxes and concentrations of dissolved organic carbon and nitrogen – a synthesis for temperate forests

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Abstract. Dissolved organic carbon (DOC) and nitrogen (DON) represent an important part of the C and N cycles in forest ecosystems. Little is known about the controls on fluxes and concentrations of these compounds in soils under field conditions. Here we compiled published data on concentrations and fluxes of DOC and DON from 42 case studies in forest ecosystems of the temperate zone in order to evaluate controls on a larger temporal and spatial scale. The focus was on annual fluxes and concentrations in throughfall, forest floor leachates and soil solutions. In all compartments considered, concentrations and fluxes differed widely between the sites. Highest concentrations of DOC and DON were generally observed in forest floor leachates and in A horizons. Highest fluxes occurred in forest floor leachates. The fluxes of DOC and DON in forest floor leachates increased with increasing annual precipitation and were also positively related to DOC and DON fluxes with throughfall. Variation in throughfall fluxes could explain 46% and 65% of the variation in DOC and DON fluxes from the forest floor, respectively. No general difference in DOC and DON concentrations and fluxes in forest floor leachates was found when comparing coniferous and hardwood sites. Concentrations of DOC in forest floor leachates were positively correlated to the pH of the forest floor. Furthermore, there was no relationship between organic C and N stocks, soil C/N, litterfall or mineral N inputs and concentrations and fluxes of DOC and DON in forest floor leachates. Including all compartments, fluxes of DOC and DON were highly correlated. Ratios of DOC to DON calculated from fluxes from the forest floor were independent of the amount of annual precipitation, pointing to a similar response of DOC and DON to precipitation conditions. A decrease in the ratio of DOC to DON with soil depth as observed on a plot-scale, was not confirmed by data analysis on a large scale. The controls observed on annual fluxes and concentrations of DON and DOC at regional scale differed from those reported for smaller time and space scales.

Introduction

Dissolved organic matter (DOM), including dissolved organic forms of carbon (DOC), nitrogen (DON) and phosphorus (DOP), is often described as solutes passing filter $< 0.70\ \mu$m in pore size. Dissolved organic matter consists of a continuum of organic substances ranging from defined small molecules to highly polymeric humic substances. The importance of DOM for processes in forest ecosystems is beyond question: Dissolved organic matter contributes significantly to carbon, nitrogen, phosphorus and nutrient budgets (Qualls & Haines 1991; Michalzik & Matzner 1999), its mobilisation and transport is of central importance to soil-forming processes (Dawson et al. 1978; Petersen 1976) and transport of heavy metals (Guggenberger et al. 1994a). In the absence of strong inorganic acids, DOM production is a key driver for soil and water acidification (Driscoll et al. 1989).

In forest ecosystems, the forest floor has been identified as a primary source for DOM (Cronan & Aiken 1985; Qualls et al. 1991; Currie et al. 1996). Microbial degradation of soil organic matter (SOM) followed by desorption of organic substances from soil solids, leaching of organic substances from fresh litter are thought to be the most important processes causing the release of DOM (Qualls & Haines 1991; Guggenberger et al. 1994b; Currie et al. 1996). The identification of factors regulating the release of DOC and DON from the forest floor is crucial for the prediction of organic C and N pools in soils and their development under varying environmental conditions. Controls on the dynamics of DOC and DON appear to encompass biological, chemical and physical processes, which interact by antagonistic and synergistic mechanisms. Still, the relevance of each process for the description of DOM dynamics under field conditions is unclear (Kalbitz et al. 2000). Furthermore, the disagreement of results on the dynamics of DOM derived from laboratory experiments and plot-level field studies points to the idea that controls change with both, temporal and spatial scale (Kabitz et al. 2000). So far, information about DOM response to changes in temperature, soil moisture, waterflux, pH, ionic strength, throughfall and soil chemistry is mainly derived from laboratory experiments and most often restricted to DOC. Under laboratory conditions, the release of DOC from forest floors generally increased with temperature and soil moisture (Clark & Gilmour 1983; Christ & David 1996a; Gödde et al. 1996), decreasing ionic strength (Vance & David 1989), increasing sulfate concentrations (Evans et al. 1988), increasing C/N ratio of the solid phase, increasing leaching frequency (Gödde et al. 1996) and decreasing metal saturation of DOC (Tipping 1998). With regard to the influence of pH results are inconsistent. Chang and Alexander (1984) and Vance and David (1989) observed a positive relationship between the release of DOC and increasing pH of the extraction solution, whereas

Cronan (1985) reported no differences in the amounts of mobilized DOC within a pH range between 3.5 and 5.7.

How far these laboratory findings are transferable to the patterns of concentrations and fluxes of DOC under field conditions is still an open question. Compared to laboratory studies, findings from field monitoring often led to contradicting results. As an example, significant relationships between DOC and solution pH found in laboratory experiments were not confirmed by field data (McDowell & Likens 1988; Michalzik & Matzner 1999).

It is unclear to what extent the dynamics of DON are linked to those of DOC (Michalzik & Matzner 1999). The effect of the dominant vegetation type on DOM fluxes from the forest floor is also still uncertain. Currie et al. (1996) studied DOC and DON fluxes in coniferous and hardwood forests simultaneously and found higher fluxes of both from the forest floor under coniferous vegetation, Matzner (1988) observed no differences in DON fluxes from the forest floor of a beech and spruce forest stand.

Only few investigations focused on the effects of regulating factors, such as temperature and water flux, on DOM dynamics under field conditions. In the field, a temperature dependence was found for DOC concentrations in forest floor leachates but not for DOC and DON fluxes (Guggenberger 1992; Michalzik & Matzner 1999). McDowell and Likens (1988) found no control of the water regime on DOC concentrations in throughfall. However in the subsoil, they observed a negative relation between DOC concentrations and seepage volume. Currie et al. (1996) found a weak, but significant relation between water fluxes and DOC concentrations in the forest floor, which was not valid for DON concentrations. In a field experiment Tipping et al. (1999) observed significant increases in the export of DOC with increasing water input from 2 out of 3 soils. Reasons for the discrepancy between field and laboratory findings on controls of DOM could be a bias in temporal or spatial scales of observation, unknown synergistic effects, non-consideration of hydrologic conditions or differences in microbiology.

The aim of the present paper was to compile and synthesize published data on concentrations and annual fluxes of DOC and DON along a vertical profile in forest ecosystems and to evaluate the relevance of DOC and DON for the overall C and N turnover. We used data from 42 field studies from mostly temperate forest ecosystems in the northern hemisphere to assess controlling factors on the concentrations and fluxes of DOC and DON on a larger temporal and spatial scale.

Methods

Data base

The present paper is based on 42 ecosystem studies, which were carried out during the last two decades mainly in North America and Europe. The majority of the studies (38) encompassed temperate forest ecosystems. Additionally, one boreal and three subalpine forest sites are included. The ecosystems are located between 60 and 3500 m a.s.l. with mean annual temperatures ranging from 1 to 16 °C and mean annual precipitation ranging from 500 to 1900 mm. The studies cover 26 coniferous, 14 deciduous, one mixed forest site and one peat site with stand ages ranging from 30 to 250 years. The dominant soil types according to Soil Survey Staff (1992) are spodosols (19) and cambisols (10) followed by ultisols (6), inceptisols (5), alfisols (1) and histosols (1). For the statistical analysis, data sets from both coniferous and deciduous forest sites were combined. Therefore, one might argue that some interpretations are misleading due to environmental conditions, which were reflected by the type of vegetation. However, we found the distribution of coniferous and hardwood stands independent from climatic conditions such as annual precipitation, mean annual temperature and altitude a.s.l.. For data evaluation and interpretation it therefore appeared reasonable to include observations from both vegetation types. Just four studies (Qualls et al. 1991; Arthur & Fahey 1993; Cortina et al. 1995; Gallardo & Vicente Esteban 2000) presented data about DOP fluxes and concentrations. Therefore, a synthesis on DOP was not possible. Data were left out in Table 1 and were only mentioned in the text.

From studies including manipulations we only included data from the reference or control plots. Sampling of forest floor leachates was done by zero tension or suction lysimeters. Whenever information from both methods was available we preferred zero tension data. Soil solutions from the mineral soil were collected by suction lysimeters in all cases. Length of sampling periods and sampling frequency vary considerably among studies, but most periods cover two or more years. Calculation of water fluxes in the soils were carried out by water budget models or by the use of sampling volumes. We only considered mean annual concentrations and mean annual fluxes as given in the reference and did not calculate fluxes from average concentrations and water fluxes. In one case (Currie et al. 1996), C and N concentrations for different seasons were given and we calculated the arithmetic mean. Information on water flow regime, e.g. consideration of preferential flow, storm events and stem flow were sparse and was not further used here.

Filtration sizes vary considerably between the studies ranging predominantly from < 0.45 μm up to 1.2 μm (26 studies). Eight studies used a filtration

Table 1. Solution concentrations and fluxes of DOC and DON in throughfall, forest floor percolates and soil solutions of the mineral soil

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC		DON		Reference[6]
					Concentration[4] [mg l^{-1}]	Fluxes[5] [kg ha^{-1} a^{-1}]	Concentration[4] [mg l^{-1}]	Fluxes[5] [kg ha^{-1} a^{-1}]	
Adirondack Park,	Temperate,	Northern	Series of	**Oa layer** of					Cronan and
New York State,	1000 mm a^{-1};	hardwood forest,	Spodosols	Site 1	32 ± 7[a]	—	—	—	Aiken, 1985
U.S.	5 °C; 174, 122	Fa, Ac, B, Ts,	Haplorthods,	Site 2	21 ± 6	—	—	—	
	and 561 m a.s.l.	Pic, Pin,	Fragiorthods,	Site 3	27 ± 5	—	—	—	
			Haplaquods	**B horizon** of					
				Site 1	7 ± 2[a]	—	—	—	
				Site 2	5 ± 1	—	—	—	
				Site 3	7 ± 1	—	—	—	
Medicine Bow	Subalpine,	Coniferous forest	Cryocrepts to	**Throughfall**	—	—	0.58	1.2	Fahey et al.,
Mountains, SE	600 mm a^{-1}	Pin	Cryoboralfs	**O-layer**	—	—	1.48[b]	6.2	1985
Wyoming, U.S.				**B horizon** (40 cm)	—	—	0.48	1.2	
				C horizon (180 cm)	—	—	0.08	0.1	
Study site of	Temperate,	Hardwood forest	Cambisols	**Throughfall**					Matzner,
Solling project,	1032 mm a^{-1};	Fa		Hardwood	—	—	0.95	7.0[b]	1998
Niedersachsen,	6.4 °C;	Coniferous forest		Coniferous	—	—	1.28	9.6	
Germany	500 m a.s.l.	Pic		**O layer**					
				Hardwood	—	—	2.03	12.5	
				Coniferous	—	—	1.64	11.8	
				C horizon (90 cm)					

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC Concentration[4] [mg l^{-1}]	DOC Fluxes[5] [kg ha^{-1} a^{-1}]	DON Concentration[4] [mg l^{-1}]	DON Fluxes[5] [kg ha^{-1} a^{-1}]	Reference[6]
				Hardwood	—	—	0.38	2.2	
				Coniferous	—	—	0.52	2.2	
Hubbard Brook	Temperate,	Hardwood forest,	Series of	**Throughfall**	11.95	47.3	—	—	McDowell
Experimental	1310 mm a^{-1};	Fa, B, Ac, Pic, Ab	Spodosols	**O layer**					and Likens,
Forest, New	550–790 m			mull like	28.0[b]	263	—	—	1988
Hampshire, U.S.	a.s.l.			mor	37.5	—	—	—	
				B horizon					
				Upper B	5.9	54.5	—	—	
				30 cm depth	3.0	23.0	—	—	
Maglehems Ora,	Temperate,	Hardwood forest,	Cambisols to	**Throughfall**	9.9	41.1	—	—	Bergkvist
South-Sweden	602 mm a^{-1};	Fa	Arenosols	**B horizon** (30 cm)	12.2	37.8	—	—	and Folkeson,
	80 m a.s.l.								1992
Mount St. Hilaire,	Temperate,	Hardwood forest,	Dystric to	**A horizon** of 2 sites					Dalva and
Quebec, Canada	988 mma^{-1};	Ac, Fr, Fa, Q	Eutric	Hardwood forest	46.0[b]	—	—	—	Moores,
	5.5 °C;	Mixed forest,	Cambisols	Mixed forest	49.2	—	—	—	1991
	240–280 m	Ts, Fa, Pin, Q	Dystric	**B horizon**					
	a.s.l.		Cambisols to	Hardwood	16.6	—	—	—	
			Ferric Podzols	Mixed	19.4	—	—	—	

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC		DON		Reference[6]
					Concentration[4] $[\text{mg l}^{-1}]$	Fluxes[5] $[\text{kg ha}^{-1}\ \text{a}^{-1}]$	Concentration[4] $[\text{mg l}^{-1}]$	Fluxes[5] $[\text{kg ha}^{-1}\ \text{a}^{-1}]$	
Whiteface Mountain, Wilmington, New York, U.S.	Subalpine, 1300 mm a^{-1}; 2 °C; 970–1100 m a.s.l.	Coniferous forest Ab, Pic	Spodosols (Cryohumods, Cryorthods)	**Throughfall**	—	—	0.25[a]	3.5	Friedland et al., 1991
				Oa layer	—	—	0.81	9.1	
				AB horizon (30 cm)	—	—	0.22	2.1	
				B horizon (45–60 cm)	—	—	0.15	1.5	
Southern Appalachians, North Carolina, U.S.	Temperate, 1770 mm a^{-1}; 700–1000 m a.s.l.	Hardwood forest, Q, C, Ac	Inceptisols to Ultisols (Dystrochrept, Hapludult)	**Throughfall**	9 ± 2[c]	130 ± 20[a]	0.25 ± 0.05[c]	39 ± 0.2[a]	Qualls et al., 1991
				Oi layer	33 ± 3	410 ± 30	0.80 ± 0.07	10.2 ± 0.6	
				Oa layer	33 ± 4	405 ± 50	0.80 ± 0.11	10.1 ± 1.0	
Loch Vale Rocky Mountain, Watershed, National Park, Colorado, U.S.	Subalpine, 1000 mm a^{-1}; 1.5 °C; 3100–4000 m a.s.l.	Coniferous forest, Pic, Ab	Lithic Cryoboralf	**Oi layer** (above rooting zone)	28.3[b]	—	0.41[b]	—	Arthur and Fahey, 1993
				B horizon (below rooting zone)	26.1[b]	—	0.5[b]	2.95	
Fichtelgebirge, Bavaria, Germany	Temperate, 1000 mm a^{-1}; 6 °C; 680–750 m a.s.l.	Coniferous forest, Pic	Spodosols to Inceptisols (Haplorthod, Dystrochrepts)	**Throughfall** of Site 1	10.0 ± 5.9[a]	70 ± 2[b]	—	—	Guggenberger, 1992
				Site 2	11.7 ± 10.0	93 ± 14	—	—	
				Site 3	21.4 ± 11.3	128 ± 81	—	—	

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC Concentration[4] [mg l^{-1}]	DOC Fluxes[5] [kg ha^{-1} a^{-1}]	DON Concentration[4] [mg l^{-1}]	DON Fluxes[5] [kg ha^{-1} a^{-1}]	Reference[6]
				Oa layer of					
				Site 1	27.7 ± 11.7	146 ± 49[b]	—	—	
				Site 2	26.7 ± 11.9	169 ± 51	—	—	
				Site 3	54.4 ± 43.5	380 ± 178	—	—	
				B horizon (30 cm)					
				Site 1	2.6 ± 0.8[a]	9.6 ± 1.8 [b]	—	—	
				Site 2	3.8 ± 1.2	28 ± 14	—	—	
				Site 3	31.2 ± 12.1	187 ± 54	—	—	
				B horizon (90 cm)					
				Site 1	1.7 ± 0.9[a]	5.4 ± 2.1[b]	—	—	
				Site 2	22 ± 0.7	11.0 ± 4.2	—	—	
				Site 3	10.1 ± 4.4	66.0 ± 24	—	—	
Sta. Coloma de Farners, Spain	Temperate, 750 mm a^{-1}; 200 m a.s.l.	Coniferous forest, Pin	Dystric Xerochrepts	**Forest Floor**	—	—	—	13.9	Cortina et al., 1995
Howland Integrated Forest Study site, east-central Maine, U.S.	Temperate, 1063 mma^{-1}; 60 m a.s.l.	Coniferous forest Pic, Ab	Haplaquods to Haplorthods	**Oa**	77.6 ± 15.1[e]	—	—	—	Fernandez et al., 1995
				B horizon					
				Bh (10 cm)	9.0 ± 0.5[e]	—	—	—	
				Bs (25 cm)	3.8 ± 0.4	31.2 ± 7.0[e]	—	—	

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC Concentration[4] [mg l^{-1}]	DOC Fluxes[5] [kg ha^{-1} a^{-1}]	DON Concentration[4] [mg l^{-1}]	DON Fluxes[5] [kg ha^{-1} a^{-1}]	Reference[6]
Harvard Forest,	Temperate,	Coniferous forest,	Typic	**Throughfall**					Currie et al.,
Massachusetts,	1100 mma^{-1};	Pin	Dystrochrepts	Coniferous	13–37	139	0.35–1.1	3.48	1996
U.S.	220–410 m a.s.l.	Mixed hardwood		Hardwood	11–60	117	0.24–1.1	2.68	
		forest, Q, B, Ac		**Oa layer**					
				Coniferous	14–75[a]	398	0.28–1.8[a]	9.5	
				Hardwood	5.7–45	225	$<$0.13–1.4	6.1	
				B horizon (60 cm)					
				Coniferous	26 ± 5.2[d]	167[c]	0.78 ± 0.28[d]	5.4[c]	
				Hardwood	21 ± 3.9	123	0.63 ± 0.23	3.2	
Calhoun	Temperate,	Coniferous forest	Ultisols	**Throughfall**	7.5	—	—	—	Richter and
Experimental	1170 mm a^{-1};	Pin		**O-layer**	34	251	—	—	Markewitz,
Forest South	16 °C			**E horizon** (15 cm)	24	154	—	—	1996
Carolina, U.S.				**Bt horizon** (60 cm)	1.5	9	—	—	
				C horizon (600 cm)	0.6	4	—	—	
Cape Blanco,	Temperate,	Coniferous forest,	sites 1+ 2:	**Throughfall**					Bockheim
South/West	1780 mm a^{-1};	sites 1–3: Pic	Series of	Site 1:	8.8	—	—	—	and Langley-
Coastal Oregon,	11.3 °C	site 4: Pt	Inceptisols	Site 2:	7.3	—	—	—	Turnbaugh,
U.S.	site 1–3: 60–70 m,	site 5: Ts, Pt	to Ultisols	Site 3:	4.3	—	—	—	1997
5 marine	site 4: 200 m and		sites 3+ 4:	Site 4:	2.7	—	—	—	
terraces sites	site 5: 300 m a.s.l.		Spodosols	Site 5:	4.4	—	—	—	

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC Concentration[4] [mg l^{-1}]	DOC Fluxes[5] [kg ha^{-1} a^{-1}]	DON Concentration[4] [mg l^{-1}]	DON Fluxes[5] [kg ha^{-1} a^{-1}]	Reference[6]
			site 5: Ultisol	**A and B horizon**					
				Site 1: A3 (40 cm)	74.2[c]	—	—	—	
				Site 2: A2 (25 cm)	54.1	—	—	—	
				Site 3: AE2 (35 cm)	52.4	—	—	—	
				Site 4: E2 (20 cm)	57.4	—	—	—	
				Site 5: Bh (25 cm)	15.5	—	—	—	
				B horizon					
				Site 1: 2Bsv (80 cm)	14.7	—	—	—	
				Site 3: 2Bt1(100cm)	19.3	—	—	—	
				Site 4: 2Bt2 (95 cm)	5.8	—	—	—	
				Site 5: Bt3 (70 cm)	5.3	—	—	—	
Upper Atlantic Coastal Plain, South Carolina, U.S.	Temperate, 1210 mm a^{-1}; 80 m a.s.l.	Mixed pine-oak forest, Pin, Q, C	Series of Coarse Ultisols,	**Throughfall**	35.0 ± 21.8[a]	—	—	—	Dosskey and Bertsch, 1997
				A horizon (10 cm)	25.5 ± 7.1 [a]	128	—	—	
				E_1 horizon (30 cm)	13.7 ± 6.1[a]	55	—	—	
				E_2 horizon (75–100 cm)	1.8 ± 0.3	6			
Sor catchment, Galicia, NW Spain	Temperate, 1600 mm a^{-1}; 11 °C, 580 & 685 m a.s.l.	Sanche site Hartdwood: Q, Be Piocorto site Coniferous: Pin	Humic Cambisols and Haplumbrepts	**Throughfall**					Fernandez-Sanjurjo et al., 1997
				Sanche site	6.5	—	—	—	
				Piocorto site	13.4	—	—	—	
				Ah horizon					
				Sanche site	36.7	—	—	—	

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC		DON		Reference[6]
					Concentration[4] [mg l^{-1}]	Fluxes[5] [kg ha^{-1} a^{-1}]	Concentration[4] [mg l^{-1}]	Fluxes[5] [kg ha^{-1} a^{-1}]	
				Piocorto site	21.2	—	—	—	
				AB horizon					
				Sanche site	6.1	—	—	—	
				Piocorto site	4.6	—	—	—	
				B horizon					
				Sanche site	3.8	—	—	—	
				Piocorto site	4.0	—	—	—	
Slavkov Forest, Lysina site, Pluhuv Bor site, Czech Republic	Temperate, 950 & 850 mm a^{-1}; 5.0 & 6.0 °C; 890 & 850 m a.s.l.	Coniferous forest Pic	Cambisols Lysina: Dystric Pluhův Bor: Eutric	**Oa layer**					Krám et al., 1997
				Lysina	32.4 ± 18.0[a]	—	—	—	
				Pluhův Bor	87.6 ± 61.2[a]	—	—	—	
				E horizon Lysina	20.4 ± 8.0[a]	—	—	—	
				A horizon Plu. Bor	34.8 ± 16.8[a]	—	—	—	
Northern Pennine Uplands, UK	Temperate 1880 mm a^{-1}; 5.1 °C 560 m a.s.l.	Peat catchment Calluna, Eriophorum	Histosols	**H horizon**					Adamson et al., 1998
				10 cm depth	—	—	0.52 ± 0.01[e]	—	
				50 cm depth	—	—	0.38 ± 0.01[e]	—	
Tegernsee Alps, Bavaria, Germany	Temperate, 1800–2000 mm a^{-1}; 5°C; 1220 m a.s.l.	Mixed mountain forest, Pic, Ab, Fa	Inceptisols to Spodosols	**Mineral soil**					Bäumler and Zech, 1998
				10 cm	10.5 ± 13.5[c]	—	—	—	
				30 cm	2.7 ± 4.4	—	—	—	
				50 cm	2.1 ± 1.3	—	—	—	

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC Concentration[4] $[\mathrm{mg\ l^{-1}}]$	DOC Fluxes[5] $[\mathrm{kg\ ha^{-1}\ a^{-1}}]$	DON Concentration[4] $[\mathrm{mg\ l^{-1}}]$	DON Fluxes[5] $[\mathrm{kg\ ha^{-1}\ a^{-1}}]$	Reference[6]
NITREX experimental sites, Klosterhede (KH), Denmark, Aber (AB), Wales UK, Speuld (SP) and Ysselsteyn (YS), the Netherlands	Temperate, KH 860 mm a^{-1}; AB 1850 mm a^{-1}; SP 800 mm a^{-1}; YS 700 mm a^{-1}; 8.8 °C–9.3 °C	Coniferous forest, Pin, Pt	Series of Spodosols	**Forest floor**					Gundersen et al., 1998
				Klosterhede	—	103	—	0.3	
				Aber	—	350	—	17.0	
				Spleud	—	130	—	7.0	
				Ysselsteyn	—	190	—	6.0	
				Below rooting zone					
				Klosterhede	—	51	—	0.5	
				Aber	—	43	—	1.6	
				Spleud	—	23	—	1.2	
				Ysselsteyn	—	190	—	9.4	
Eastern Finland	Boreal, 502 mm a^{-1}; 1.0 °C; 220 m a.s.l.	Mixed boreal forest, Pic, Pin, Bet	Ferric podzols	**Throughfall**	—	—	0.35 ± 0.03[d]	1.8 ± 0.4[b]	Piirainen et al., 1998
				Oa layer	—	—	0.85 ± 0.23[d]	2.6 ± 0.8[b]	
				E horizon	—	—	0.71 ± 0.18[d]	1.1 ± 0.2[b]	
				B horizon	—	—	0.25 ± 0.15	0.14 ± 0.15	
PROTOS experimental site: Coulissenhieb, Waldstein, Bavaria, Germany	Temperate, 1100 mm a^{-1}; 5 °C; 780 m a.s.l.	Coniferous forest, Pic	Dystric Cambisols to Podzols	**Throughfall**	15.2 ± 0.4[e]	84.1	0.75 ± 0.04[e]	3.4	Michalzik and Matzner, 1999
				Oi layer	35.7 ± 2.7	172.7	1.33 ± 0.13	7.1	
				Oe layer	38.2 ± 2.2	154.8	1.28 ± 0.10	6.0	
				Oa layer	37.8 ± 1.4	114.7	1.22 ± 0.05	4.7	
				B horizon (20 cm)	24.7	85.8	0.15	0.2	
				C horizon (90 cm)	5.0	16.5	$<$ d.l.	$<$ d.l.	

Table 1. Continued

Location	Climate[1]	Dominant vegetation[2]	Soil[3]	Compartment	DOC Concentration[4] [$mg\ l^{-1}$]	DOC Fluxes[5] [$kg\ ha^{-1}\ a^{-1}$]	DON Concentration[4] [$mg\ l^{-1}$]	DON Fluxes[5] [$kg\ ha^{-1}\ a^{-1}$]	Reference[6]
PROTOS	Temperate,	Coniferous forest,	Podzols to	**Throughfall**	13.1[e]	161	0.50 ± 0.05[e]	4.3	Mulder and
experimental site:	1300 mm a^{-1};	Pic	Cambisols	**Oa layer**	47.8 ± 14.7	363	2.00 ± 0.60	14.0	Clarke, 2000
Birkenes, Norway	5.3 °C;			**E horizon**	22.4 ± 8.4	174	1.06 ± 0.50	9.2	(in preparation)
	250 m a.s.l.			**B horizon** (45 cm)	6.2 ± 0.7	63	0.37 ± 0.11	4.4	
PROTOS	Temperate,	Hardwood forest,	Humic	**Throughfall**	5.6 ± 1.2[e]	104	0.62 ± 0.10[e]	11.5	Gallardo and
experimental Site:	1580 mm a^{-1};	Q	Cambisols	**Oa layer**	20.3 ± 2.8	299	1.22 ± 0.10	18.1	Vicente Esteban,
Navasfrias, Spain	14.1 °C;			**Ah1 horizon**	12.5 ± 1.3	176	1.10 ± 0.04	16.2	2000
	960 m a.s.l.			**B horizon** (70cm)	3.8 ± 1.7	57	0.57 ± 0.03	7.9	(in preparation)
Steinkreuz,	Temperate,	Hardwood forest,	Cambisols	**Throughfall**	13.6	74	1.11	5.7	Solinger, 2000
Steigerwald,	750 mm a^{-1};	Fa, Q		**Forest Floor**	79.6	274	2.45	8.9	(in preparation)
Bavaria, Germany	7.5 °C;								
	460 m a.s.l.								

[1]Climate: annual precipitation, mean annual temperature, height a.s.l.
[2]Vegetation: Ab, *Abies*; Ac, *Acer*; C, *Carya*; Fa, *Fagus*; Fr, *Fraxinus*; Pic, *Picea*; Pin, *Pinus*; Q, *Quercus*; Ti, *Tilia*; Ts, *Tsuga*.
[3]Soil classification referring to U.S. Soil Taxonomy or FAO Classification.
[4]Concentrations: [a]arithmetic mean and standard deviation; [b]volume or flux weighted mean; [c]flux weighted mean and standard error; [d]volume weighted and standard deviation; [e]arithmetic mean and standard error.
[5]Fluxes: [a]area-weighted mean and standard error; [b]arithmetic mean and standard deviation; [c]fluxes calculated from volume weighted concentrations.
[6]References arranged in chronological order.

size $\leq$ 25 μm and in 8 cases authors did not give details about sample preparation, but denoted data as ‘dissolved’. For the forest floor leachates we found no correlation between DOC or DON concentrations and filtration sizes up to 25 μm. Thus, we decided to include all data for further evaluation. In general, DON was determined as the difference between mineral N and total N. Inorganic N species were analyzed colorimetrically or by ion chromatography. Methods to measure total N encompassed Kjehldahl method, persulfate digestion procedures and thermal oxidation. In some studies micro-Kjehldahl was used to determine organic N plus ammonium, calculating organic N by subtracting ammonium after separate determination. For DOC two analytical procedures were mostly applied measuring DOC as CO_2 after thermal oxidation or persulfate-UV-digestion.

Classification of data and statistical analysis

Concentrations and fluxes of DOC and DON were assigned to a vertical profile through the ecosystem as follows: bulk precipitation (bulk); throughfall (TF); leachates of the forest floor from the litter layer (Oi), fermented layer (Oe), humic layer (Oa); soil solutions of the A, B and C horizons of the mineral soil. Information about N and C fluxes with litterfall and throughfall, solution and soil pH (H_2O), soil C/N ratio, stocks of and C and N were used for data analysis and interpretation. T-test was used for comparison of means. Depending on normally or non normally distributed data correlation analysis was carried out by Pearson and Spearman correlations, respectively. Due to violations of assumptions for linear (multiple) regression analysis, such as normal distribution of variables and residuals, and limited numbers of cases (mostly $n < 15$) multiple regressions could not be calculated. Statistical analysis was carried out with SPSS for Windows, version 7.5.

Results

Concentrations and fluxes of DOC and DON

Most data on concentrations of DOC are available for throughfall, Oa leachates and soil solutions from A and B horizons (Figure 1(a); Table 1). In throughfall solution, mean annual concentrations of DOC are between 3 and 35 mg l^{-1}. The fluxes of DOC with throughfall range from 40 to 160 kg DOC ha^{-1} y^{-1}. Mean annual concentrations of DOC in solutions of the Oa layer vary between 20 and 90 mg l^{-1} and in B horizons between 2 and 35 mg l^{-1}. Largest fluxes of DOC occur in the Oa layer leachates and vary between 100 to 400 kg ha^{-1} y^{-1}, while 10 to 200 kg ha^{-1} y^{-1} are reported for seepage

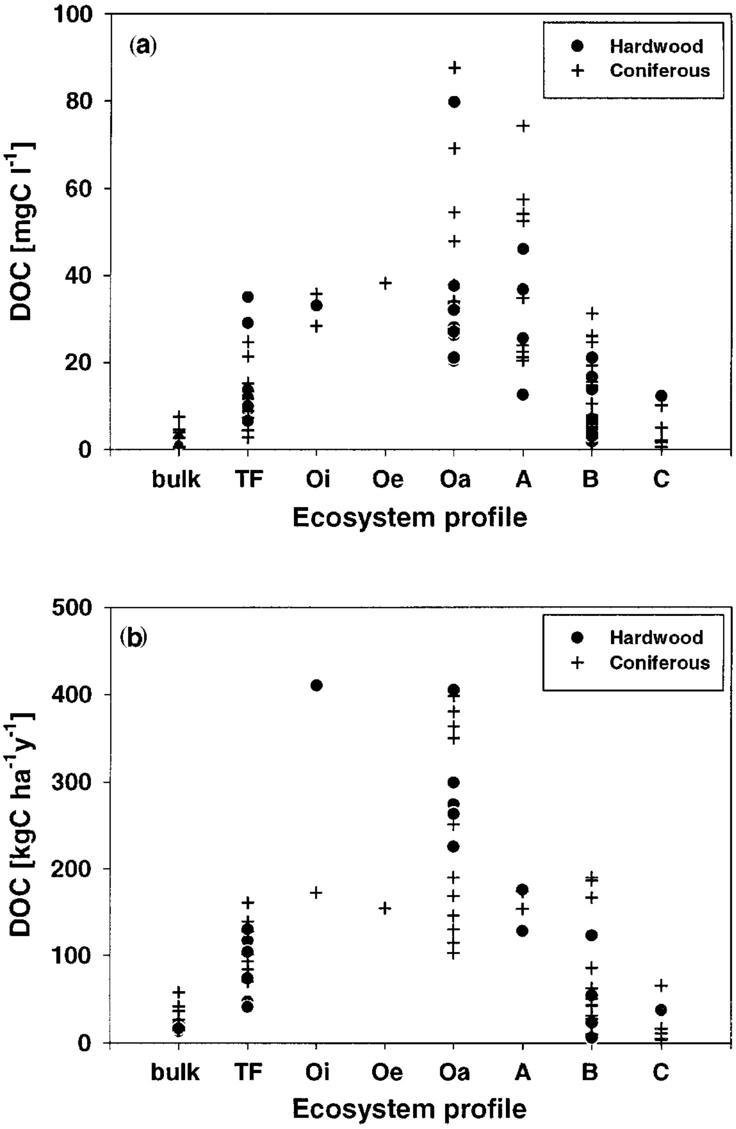


Figure 1. (a) Mean annual concentrations of DOC and (b) annual fluxes of DOC along a vertical profile in forest ecosystems (bulk = bulk precipitation; TF = throughfall precipitation; Oi = litter, Oe = fermented, Oa = humic layer; A, B and C = horizons of the mineral soil).

fluxes in the B horizon (Figure 1(a)). Concentrations of DOC clearly decrease from the A horizon to the B horizon, whereas fluxes of DOC decrease rapidly from the forest floor to the A horizon, where fluxes are within the range of those in B and C horizons (Figure 1(b)).

Only few data are available on fluxes of DOC and DON in the upper layers of the forest floor (Oi and Oe layers) and in the A horizon representing the transitional zone between the C-rich forest floor and the deeper mineral soil. In the A horizon, the concentrations of DOC are highly variable ranging from 18 to 75 mg l^{-1}, which is similar to DOC concentrations in Oa leachates.

Similar to the DOC dynamics, most data on DON are available for throughfall, Oa layer leachates and soil solution from the B horizon. Mean annual concentrations of DON range from 0.25 to 1.11 mg l^{-1} in throughfall, from 0.4 to 2.45 mg l^{-1} in the forest floor and from 0.2 to 1.1 mg l^{-1} in the mineral soil horizons (Figure 2(a)). Fluxes of DON with throughfall range from 1.2 to 11.5 kg ha^{-1} y^{-1}. In the Oa layer and the B horizon fluxes vary considerably between 0.2 and 18.0 kg ha^{-1} y^{-1} and 0.1 and 9.4 kg ha^{-1} y^{-1}, respectively (Figure 2(b)).

Four studies present data on DOP in forest floor leachates and soil solutions. The authors observed concentrations of DOP between 0.2 and 0.3 mg l^{-1} in the forest floor and 0.03 mg l^{-1} in den B horizon and fluxes of about 0.30 to 0.43 kg ha^{-1} y^{-1} and 0.2 kg ha^{-1} y^{-1}, respectively.

Controls on the DOC and DON concentrations and fluxes in forest floor leachates

Compared with bulk precipitation the canopy functions as a source for DOC and DON in forest ecosystems (Figure 1(b) and 2(b)). In contrast to the forest floor, the annual fluxes of DOC and DON in throughfall are not correlated with the mean annual precipitation. The DON fluxes from the canopy are positively related to fluxes of NH_4-N and NO_3-N in throughfall ($r = 0.92$; $p = 0.000$ and $r = 0.85$; $p = 0.002$ for $n = 10$, respectively).

The annual fluxes of DOC and DON in leachates of the Oa layer are positively correlated to annual precipitation ($r = 0.59$; $n = 16$; $p = 0.016$ for DOC and $r = 0.63$; $n = 17$; $p = 0.007$ for DON) (Figure 3(a) and (b)). The ratios of DOC to DON calculated from annual fluxes in leachates of the Oa layer appear to be independent from the amount of the annual precipitation. There is no significant dilution effect of the precipitation on concentrations of both DON and DOC in Oa leachates.

Fluxes of DON in the forest floor leachates (Oa) show a positive correlation with those of DON in throughfall ($r = 0.81$, $p = 0.001$, $n = 12$) (Figure 4(b)). The same is true for DOC with $r = 0.68$ ($p = 0.022$ and $n = 11$) (Figure 4(a)). Variation in throughfall fluxes can explain 46% and 65% of the vari-

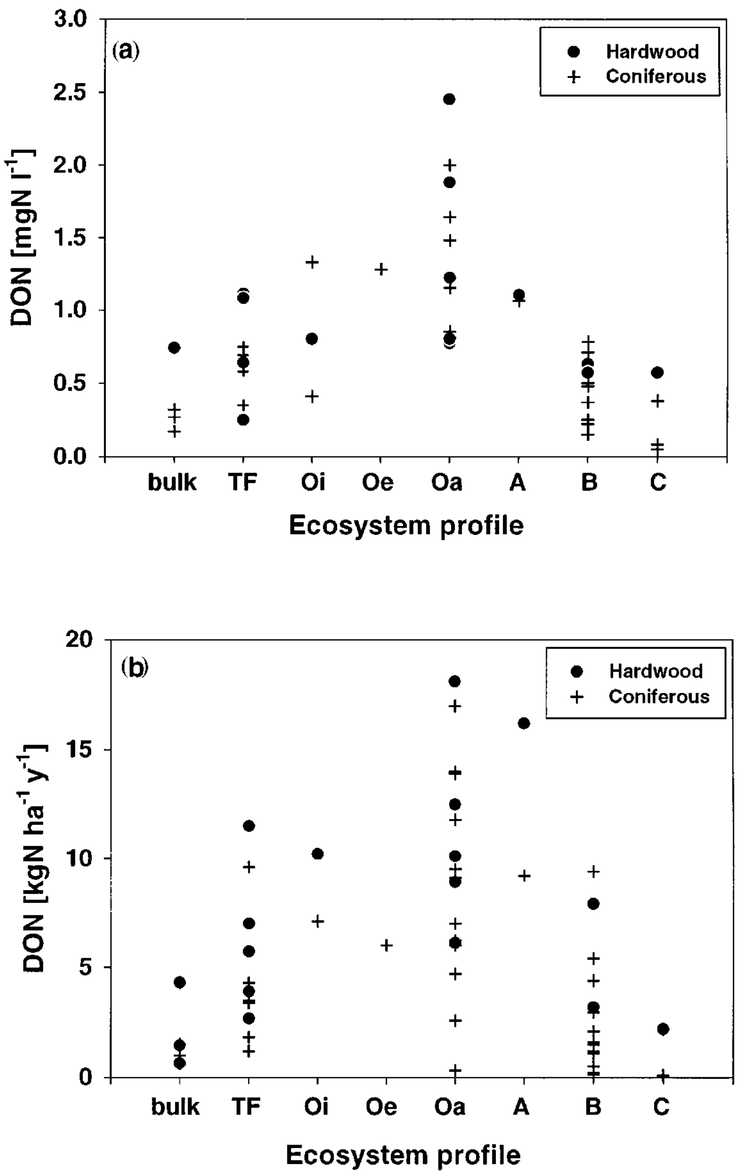
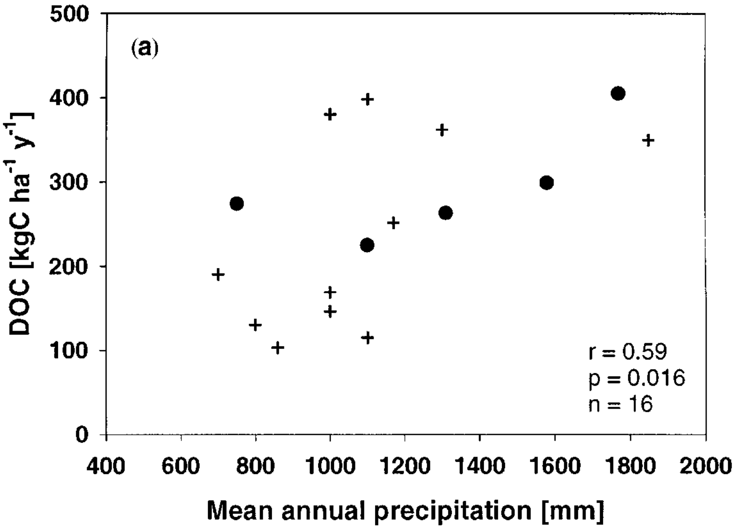


Figure 2. (a) Mean annual concentrations of DON and (b) annual fluxes of DON along a vertical profile in forest ecosystems (bulk = bulk precipitation; TF = throughfall precipitation; Oi = litter, Oe = fermented, Oa = humic layer; A, B and C = horizons of the mineral soil).



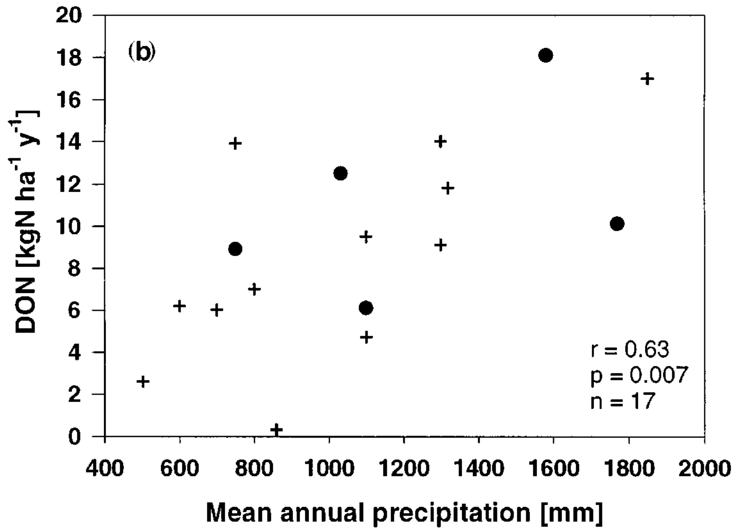


Figure 3. Mean annual fluxes of (a) DOC and (b) DON from the Oa versus mean annual precipitation. (•) indicate hardwood (✚) coniferous forest ecosystems.

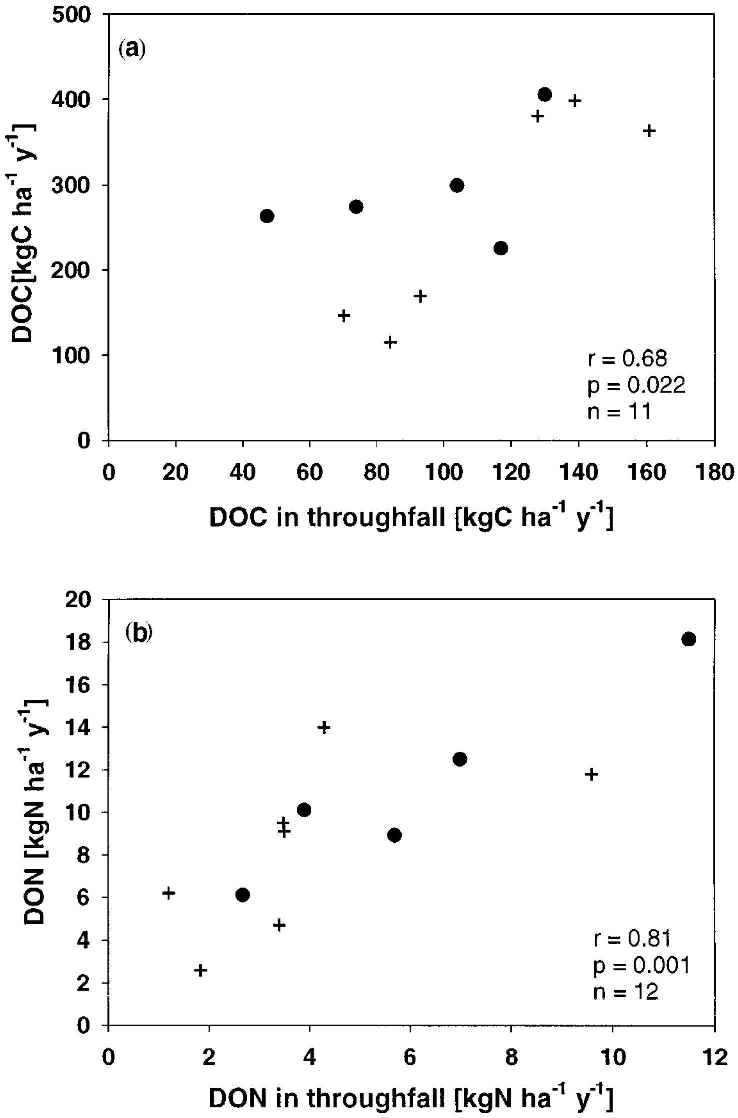


Figure 4. Mean annual fluxes of (a) DOC from the Oa versus mean annual fluxes of DOC in throughfall and (b) DON from the Oa versus mean annual fluxes of DON in throughfall. (•) indicate hardwood (✚) coniferous forest ecosystems.

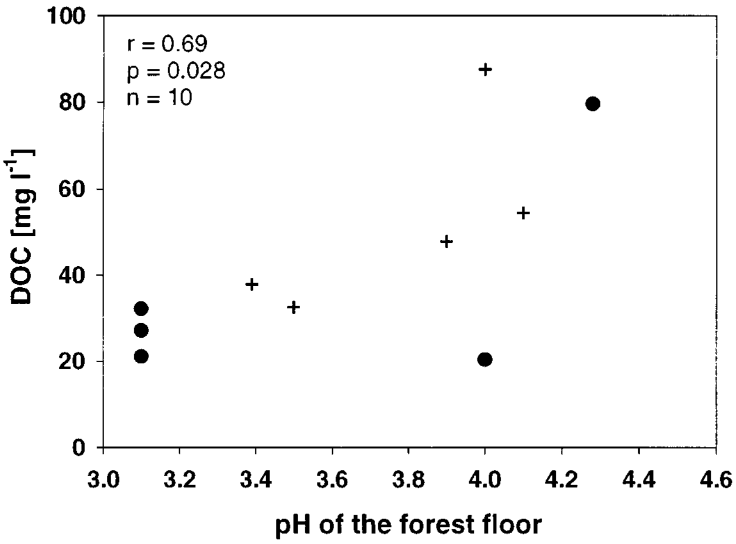


Figure 5. Mean concentrations of DOC from leachates of the Oa versus the pH of the forest floor. (•) indicate hardwood (✚) coniferous forest ecosystems.

ation in DOC and DON fluxes from the forest floor, respectively (Figure 4). Throughfall fluxes of NH_4-N and NO_3-N (range: 0.3 to 46 kg ha^{-1} y^{-1} and 0.5 to 16.8 kg ha^{-1} y^{-1}, respectively) do not correlate with DOC and DON fluxes from the forest floor.

The concentrations of DOC in the forest floor leachates of coniferous and hardwood sites are not statistically different with average concentrations of 46.5 mg l^{-1} (standard deviation of 19.6 mg l^{-1}) and 33.8 mg l^{-1} (standard deviation of 18 mg l^{-1}), respectively (Figure 1(a)). A statistical comparison of the concentrations of DON in leachates between coniferous and hardwood forests and of the DOC and DON fluxes is not possible because the number of studies from hardwood vegetation was too small (n = 5). However, the reported annual fluxes of DOC and DON in hardwood forests are within the range of those from coniferous sites in all compartments (Figure 1(b) and 2(a) and (b)).

The C and N input by annual above-ground litter varying between 900 and 2600 kg C ha^{-1} y^{-1}and between 20 and 55 kg N ha^{-1} y^{-1}, is not related to the DOC (n = 10) and DON (n = 11) fluxes from the forest floor. The fluxes of DOC and DON in the forest floor leachates show no relationship to the storage of C and N in the forest floor, soil C/N, dissolved inorganic N, temperature and altitude. Concentrations of DOC in forest floor leachates are positively correlated to the pH of the forest floor ($r = 0.69$, $p = 0.028$ and $n = 10$) (Figure 5). Concerning effects of soil solution pH and soil pH (H_2O)

on fluxes and concentrations of DON and fluxes of DOC not enough cases (maximum of n = 6) were available for statistical analysis.

Controls of DOC and DON concentrations and fluxes in the mineral soil

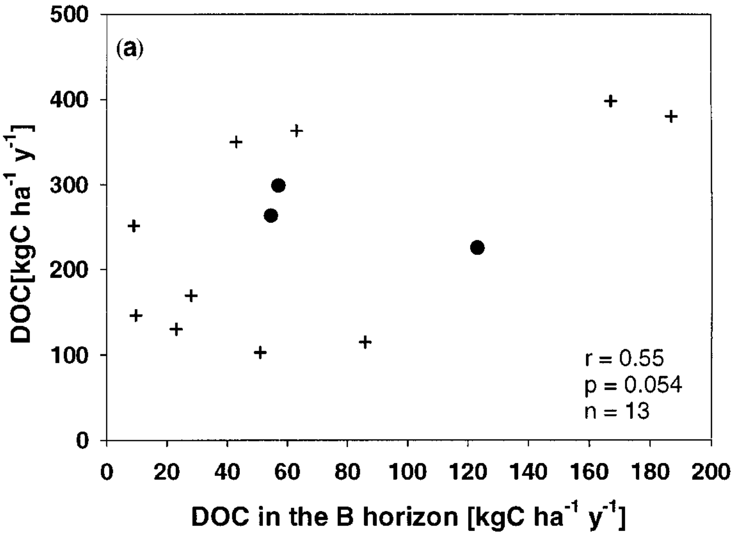
The results of the correlation analysis indicate that in the mineral soil DOC and DON concentrations and fluxes are independent from precipitation, storage of C and N in the mineral soil, C/N ratio of the mineral soil, dissolved inorganic N (concerning only fluxes) in the mineral soil and mean annual temperature. Though covering a wide range of soil solution pH (3.5 and 6.5) and soil pH (3.7 to 5.2), the pH is not related to the concentrations and fluxes of DOC. Because the number of observations was too small (n = 5) no statistical analysis can be made for pH and DON concentrations.

The fluxes of DON with forest floor leachates are positively related to the fluxes of DON in the B horizon (r = 0.65, p = 0.017 and n = 13). Whereas, a significant correlation between DOC fluxes of the forest floor and the B horizon is not observed (Figure 6). For fluxes of DOC and DON in the B horizon no correlation to the amount of precipitation is found.

Relation of DOC to DON

If all soil compartments are analyzed together, the fluxes of DON are generally highly correlated with DOC (r = 0.74; p = 0.000; n = 26) (Figure 7). In the B and C horizons with DOC fluxes from 20 to 100 kg ha^{-1} y^{-1} the fluxes of DON are less than 2 kg ha^{-1} y^{-1} and do not show a clear relation to DOC. With DOC fluxes larger 100 kg ha^{-1} y^{-1} a positive relationship between DOC and DON is observed.

Ratios of DOC to DON in different soil compartments calculated from annual fluxes are about 8 to 42 with 3 values larger than 100 (343 in the Oa and 429 and 102 in the B horizon, which all occurred in coniferous sites), which are due to low fluxes of DON ($<$ 0.5 kg ha^{-1} y^{-1}) and therefore probably connected with a high analytical error (Figure 8). Apart from the three values, the average DOC to DON ratio in the soil horizons is about 25.7 with a standard deviation of 9.8. The ratio of DOC to DON in throughfall calculated from annual fluxes (n = 6) is similar to those from soil horizons with an average of 28.2 and a standard deviation of 14.2. On a regional scale the ratios of DOC to DON do not change with soil depth, whereas within two study sites ratios from the O, A and B horizon showed a decrease in ratios with increasing soil depth (Figure 8).



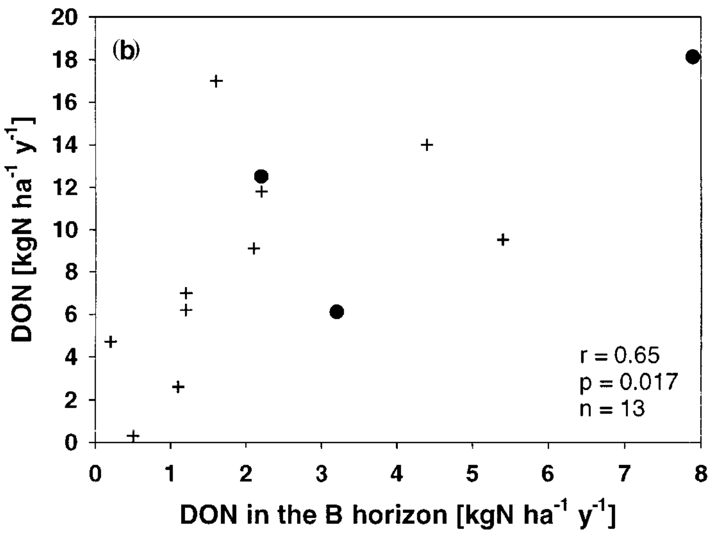


Figure 6. Mean annual fluxes of (a) DOC from the Oa versus mean annual fluxes of DOC in the B horizon and (b) DON from the Oa versus mean annual fluxes of DON in the B horizon. (•) indicate hardwood (✚) coniferous forest ecosystems.

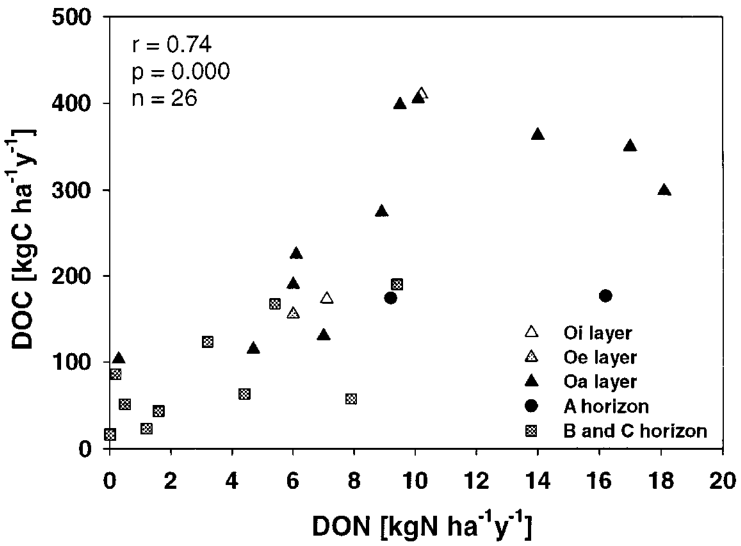


Figure 7. Annual fluxes of DOC versus DON in the ecosystem.

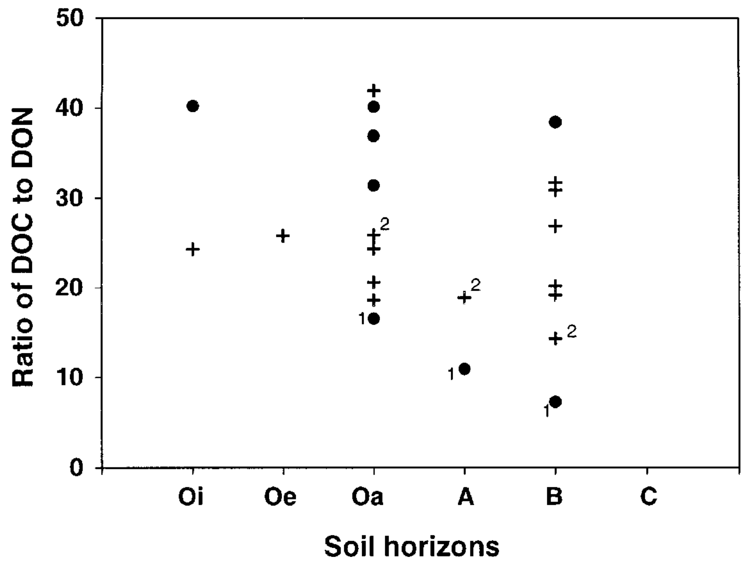


Figure 8. Ratios of DOC to DON in the ecosystem calculated from annual fluxes. (•) indicate hardwood (✚) coniferous forest ecosystems; same numbers indicate values from one study site.

Discussion

The mean annual concentrations and fluxes of DOC and DON in the forest floor as reported in the evaluated studies showed a high variability between the sites. In relation to the input of C and N to soil by annual above-ground litter fall, the annual transport of DOC and DON from the forest floor into the mineral soil amounted to an average of 17% (range: 6 to 30%) of the annual litter input of C and to 26% (range: 1 to 53%) of the litter N input. Though a significant portion of the C and N input by above-ground litter can be translocated by DOC and DON, the degradability of DOC and its role as a substrate for microbial metabolism is still unclear. Some authors (Qualls & Haines 1992; Dai et al. 1996) found microbial degradation rates of DOM in soil solution to be rather low. Thus, DOM is considered to play a central role for the pool of SOM and as precursor substance for refractory SOM (Vance & David 1995) in mineral soils. Jandl and Sollins (1997) observed that part of the water extractable carbon from forest floor litter was degraded rapidly by micro-organisms pointing to the potential importance of DOC fluxes from the forest floor for short term biogeochemical dynamics. On the other hand a significant proportion of the high-molecular-weight acid fractions was much less degradable. In the mineral soil, DOM from the forest floor might be stabilized by sorption on mineral surfaces or by complexation with aluminium (Boudot et al. 1995).

Controls on the DOC and DON release from the forest floor

We found the mean annual precipitation as one factor on a regional scale, which affected the annual fluxes of DOC and DON from the forest floor in a positive way. This observation is confirmed by a plot scale experiment by Tipping et al. (1999), who reported increased DOC fluxes with increasing amounts of water passing through the soil. In laboratory studies, the amounts of DOM released are enhanced by increasing leaching rates and water fluxes (Christ & David 1996b; Kalbitz & Knappe 1997). Thus, the partitioning of litter C input into SOM, DOC and CO_2 seems to be influenced by precipitation. The ecological effects of high water fluxes in connection with high amounts of translocated DOM are reflected by the genesis of spodosols: podsolization characterized by an accumulation of SOM in the mineral soil is much more pronounced under high precipitation conditions. However, we cannot evaluate whether DOM fluxes from the forest floor are directly controlled by precipitation or whether precipitation effects the conditions for an enhanced DOM productivity in the forest floor.

On a regional scale, there was no dilution effect of precipitation for both DOC and DON concentrations. Since ratios of DOC to DON calculated from annual fluxes appeared to be independent from precipitation, a similar response of DOC and DON to the amount of precipitation is assumed. The latter is confirmed by Michalzik and Matzner (1999), who found a dilution effect on both DOC and DON concentrations in forest floor leachates of a spruce forest site under conditions of high daily throughfall intensity.

Annual fluxes of DOC and DON in the forest floor were positively related to the fluxes of DOC and DON in throughfall (Figure 4). Variation in throughfall fluxes could explain about 46% and 65% of the variation in DOC and DON fluxes from the forest floor, respectively. This result supply evidence for the hypothesis that DOM fluxes in throughfall positively affect the fluxes of DOM in the forest floor. It is not likely that the DOM in throughfall solution just simply passes the forest floor without changes in chemical composition. As reported by Qualls and Haines (1992) the decomposition of DOM in throughfall solution reaches up to 60% with highest rates of decomposition within the first 3 weeks. Guggenberger and Zech (1994) found that about 50% (35 to 50 kg C ha^{-1} y^{-1}) of the DOC fluxes in throughfall consists of carbohydrates, which are dominated by microbial metabolites washed from the canopy. About 80% of those carbohydrates were assigned to hydrophilic neutrals, occurring in free form and thus being easily decomposable. In contrast, carbohydrates leaving the forest floor are mainly composed of plant-derived pentoses, which are water-soluble products from the degradation of lignocellulose and are covalently bound to hydrophobic acids. For an oak stand Carlisle et al. (1966) reported an annual carbohydrate input by throughfall of 89.2 kg ha^{-1} with highest amounts of glucose, fructose and melizitose during August. Thus, the throughfall provides easily decomposable C and N compounds, which probably act as co-substrates or promoters for decomposition and mineralization processes of organic matter in the forest floor, leading to increased fluxes of DOC and DON with forest floor leachates. It also appears possible that the interaction of certain environmental factors, such as high temperatures and optimal moisture conditions, cause an enhanced production of DOC and DON in both ecosystem compartments the canopy and the forest floor.

Concentrations of DOC in forest floor leachates were positively correlated to the pH of the forest floor. Since this relationship could not be attributed to an effect of the vegetation type (Figure 5), this result might reflect more favorable degradation conditions for decomposer communities in the forest floor at higher pH values (Chang & Alexander 1984; Andersson et al. 2000) or an increased deprotonation of functional groups resulting in an increased solubility of DOC (Tipping & Hurley 1988).

The annual fluxes of DOC and DON in the forest floor were not statistically related to throughfall fluxes of mineral N. In a manipulation experiment on a plot scale, Currie et al. (1996) found a significant positive correlation between annual DON fluxes in Oa leachates of a pine stand and the level of N amendments after 5 years of treatment. No correlations were observed for DON fluxes from the forest floor in the hardwood stand and for DOC fluxes under both hardwood and coniferous vegetation. In contrast, Gundersen et al. (1998) reported no consistent long-term responses in DON leaching to N addition at 5 coniferous sites. The same held true for DOC. The influence of the dominant vegetation on DOC and DON fluxes from the forest floor might have been overestimated (Cronan & Aiken 1985; Currie et al. 1996) since hardwood and coniferous forests had similar DOC concentrations and fluxes on a regional scale. The influence of vegetation can be surpassed by the dominance of regional different environmental conditions, but even under similar environmental conditions contradictory findings occurred. Currie et al. (1996), who investigated DOC and DON fluxes in coniferous and hardwood forests, found higher fluxes of both from the forest floor under coniferous vegetation, whereas Matzner (1988) found no differences in DON fluxes from the forest floor of a beech and spruce stand.

Annual fluxes of DOC and DON from the forest floor were not related to C and N input with above-ground litter fall. This contradicts findings from field and manipulation studies, where the seasonality of DOC and DON concentrations in forest floor leachates was related to the amount of litter fall (Casals et al. 1995; Currie et al. 1996). Furthermore, in manipulation studies DOC fluxes in the forest floor leachates were correlated to the amount of litter fall (Gundersen et al. 1998).

Additionally, other factors such as the storage of C and N, soil C/N, temperature, fluxes of dissolved inorganic N were not related to DOM fluxes and concentrations in the forest floor. These contrasting findings on controls of DOC and DON fluxes and concentrations in forest floor leachates on a regional scale as compared to a plot scale or lab experiments might be due to synergistic or antagonistic effects of several controls or the dominance of a new control when changing temporal and spatial scales. Like that, the independence of DOC fluxes from storage of C at the regional scale contradicted findings from the field studies of Currie and Aber (1997). They reported a positive correlation between DOC leaching and the stock of organic matter (OM) in the forest floor. In a field manipulation study, Tipping et al. (1999) observed higher DOC fluxes from a peaty gley in comparison to a brown earth and a micropodzol due to the higher content of organic matter.

One parameter to describe the quality of substrate for potential decomposition is the C/N ratio of soils. We found no relation of DOC and DON fluxes in the forest floor and the C/N ratio of the organic matter. Findings on the role of C/N ratios from laboratory experiments are inconsistent. In laboratory incubation studies, Michel and Matzner (1999) observed no correlation between rates of DOC and DON release and the C/N ratios of forest floor material from different Norway spruce stands. This is in contrast to the findings by Gödde et al. (1996), who reported a positive relationship between the C/N ratios and the respiration rates and DOC release.

On a regional scale we could not observe a temperature effect on the fluxes and concentrations of DOM in the forest floor. Though a positive temperature dependence on the DOM release is proved under laboratory conditions (Clark & Gilmour 1983; Christ & David 1996; Gödde et al. 1996) and also a negative relationship is given between the temperature and stocks of organic C and N (valid for reviewed data in this paper; Post et al. 1982), no general relationship between DOM and temperature can be derived from published field data. In individual field studies a seasonality or a temperature dependence of DOC and DON concentrations in forest floor leachates were observed (Cronan & Aiken 1985; Guggenberger 1992; Michalzik & Matzner 1999). However, the positive temperature dependence was not found when fluxes were considered (Michalzik & Matzner 1999). Based on the limited information about climatic conditions in the analyzed literature, it was not possible to test if for example the growing season degree-days instead of mean annual temperatures function as main driver for processes (Ågren et al. 1991). Thus, a temperature dependence of DOM dynamics could not be excluded. It also appears likely that under field conditions competing processes like DOC mobilization and the mineralization of DOC and SOC, respectively, are both affected by temperature and thus cancel each other out. The net outcome of those processes can additionally be affected by site specific properties such as nutrient status, litter quality and microbiology. According to changes in microbiology, Wardle (1998) reported that temporal variability of soil microbial biomas C increases with increasing latitude due to higher interseasonal variations in temperature which is reflected by greater interseasonal flux of the biomass.

Controls on the concentrations and fluxes of DOC and DON in the mineral soil

In the mineral soil, no statistically significant relationship between DOC and DON fluxes and environmental conditions (altitude a.s.l., mean annual temperature, annual precipitation) was found. Fluxes of DOC were also not correlated with soil and solution parameters (storage of C, solution and soil pH (H_2O), soil C/N, dissolved inorganic N). The sharp decrease of DOC concentrations with depth of mineral soil indicates strong retention in the mineral soil either by decomposition or adsorption. Qualls and Haines (1992) investigated the importance of decomposition in the removal of dissolved organic N and C. They reported rather low rates of decomposition of C and N in laboratory studies. For DOC the adsorption in the mineral soil is an effective retention mechanism (Qualls & Haines 1992; Kaiser & Zech 1997). Assuming a similar behaviour for nitrogen, adsorption rather than decomposition is the most likely mechanism for the retention of DON in the mineral soil. Under laboratory conditions, adsorption of DOC on mineral surfaces was found to be pH dependent, but on a regional scale concentrations of DOC in the subsoil showed no relation to soil solution pH in a wide range between 3.5 and 6.5. The same is true for DOC and the soil pH indicating no relation within a range of 3.7 to 5.2. These observations contradict laboratory findings, which assume a reduction of the adsorption capacity with increasing pH and therefore an increase in DOM mobilization (Tipping & Hurley 1988; Tipping & Woof 1990). On the other hand, Kaiser (1996) observed no effects on DOM sorption within the pH range of most natural soils between 3.5 and 6.0, which is also confirmed by field observations (McDowell & Likens 1988; Michalzik & Matzner 1999). The effect of pH on DOM dynamics could be hidden by other soil properties such as the content of organic matter and sesquioxides in the mineral soil, which strongly influences the DOM adsorption in the subsoil (McCarthy et al. 1996; Moore et al. 1992). Due to a lack of information, we could not take into account the broad range of soil types and thus individual sorption capacities for DOM on each site.

Relation of DOC to DON

On a regional scale, the mean annual concentrations and fluxes of DOC and DON in different soil compartments were highly correlated. This result is only partly confirmed by observations on a plot scale in fortnightly sampling intervals, where correlations within distinct compartments were highly significant but correlations coefficients surprisingly low, pointing to different release rates or consumption mechanisms (Michalzik & Matzner 1999). Reasons for the different findings from regional and individual sites might be the different spatial and temporal resolution of observation or a scale depending relevance of environmental conditions.

Qualls and Haines (1991) found hydrophilic acids and neutrals as main fractions of DON and hydrophobic and hydrophilic acids as main fractions of DOC. During adsorption DOM is fractionated due to its different surface charge properties. In general, hydrophobic compounds are selectively sorbed in the mineral soil, which causes a relative enrichment of hydrophilic substances in solutions with increasing soil depth (Jardine et al. 1989; Kaiser & Zech 1998). Because of the allocation of DOC and DON on different fractions, differences concerning sorption behaviour or degradability in different compartments can be expected. For two studies (Mulder & Clarke 2000;

Gallardo & Vicente Esteban 2000), a decrease in the DOC to DON ratio with increasing soil depth was observed on a plot-level scale, whereas this was not confirmed on a regional scale, where ratios remained constant with soil depth (Figure 8). Differences in results between small and large scales might be due to the range of varying site specific soil properties which could affect preferential sorption or decomposition of DOM due to nutrient availability. Pastor and Post (1986) found that N availability and leaf litter N in several mixed old growth forest stands depended on the soil texture showing an increase of both parameters with finer soil texture. Fahey and Yavitt (1988) emphasized the importance of the soil clay content which can affect soil solution chemistry by increases in soil water-holding capacity, cation exchange capacity and DOM adsorption. Thus, in view of the numerous possibilities of DOM response to soil properties and the sparse information on DON dynamics (Kalbitz et al. 2000), we can only suggest that a wide range of site specific soil properties in different forest sites caused a high variability of DOC to DON ratios which might obscured differences on a regional scale.

Conclusions

The published data on average concentrations and annual fluxes of DOC and DON in different ecosystem compartments revealed a high variation between ecosystems on a regional scale. Highest concentrations and fluxes were generally observed in the forest floor leachates. Overall, DOM represents a substantial part of the C and N cycle in forest ecosystems and especially in forest soils as indicated by high rates of input from the forest floor and strong retention of DOM in mineral soils. Furthermore, the observations made in hardwood forests were well within the range of those in coniferous ones indicating that differences between both forest types are smaller than previously assumed.

Fluxes of both DOC and DON from the forest floor were generally high and positively related to the amount of precipitation and – surprisingly – to DOC and DON fluxes with throughfall. No relation of DOC and DON fluxes could be detected to NH_4^+ and NO_3^- fluxes in throughfall and in forest floor leachates, to litterfall, storage of C and N in the forest floor, C/N-ratio of the forest floor and temperature as was postulated from studies on smaller temporal and spatial scales. Thus, controls on DOM dynamics observed on a plot scale and in laboratory experiments on shorter time scales are in many cases not confirmed on a regional scale when considering annual fluxes.

The fluxes and concentrations of DOC and DON were highly correlated. Fluxes and concentrations of DON and DOC appeared to have a similar response to precipitation. On a plot scale, data from two studies gave indication for selective sorption or decomposition of DOC in the mineral soil in comparison to DON as the ratio of DOC to DON decreased with soil depth. This was not confirmed when analyzing data on a large scale, where ratios remained constant. The results show that our predictive capabilities for DOM fluxes on regional scales and in response to changing environmental conditions are still quite poor. Future research on controls on DOM dynamics in ecosystems should be focussed on field studies, including field scale manipulation experiments, and the development of integrative simulation models of DOM dynamics, designed for field situations on larger temporal and spatial scales.

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