Tree species effects on the release of dissolved organic carbon and nitrogen from decomposing logs

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„Es ist keine Schande nichts zu wissen,

wohl aber, nichts lernen zu wollen."

PLATON

FÜR MEINE ELTERN

EVA-ANNETTE & SIEGFRIED BANTLE.

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Keywords

CWD, coarse woody debris, DOC, dissolved organic carbon, dissolved organic nitrogen, DON, tree species effect, forest management, net release, mass loss.

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ANOVA	analysis of variance
a.s.l.	above sea level
BayCEER	Bayreuth Center of Ecology and Environmental Research
BE	*Biodiversity Exploratories*
C	carbon
CH	hydrolysable carbohydrate carbon
CO_2	carbondioxide
CON	forest management type: age class conifers
CWD	coarse woody debris
DFG	German Science Foundation
DOC	dissolved organic carbon
DOM	dissolved organic matter
DON	dissolved organic nitrogen
EC	electric conductivity
F	forest management type: age class *Fagus*
HDPE	high density polyethylene
HIX_{em}	humification index deduced from fluorescence emission spectra
H_2SO_4	sulfuric acid
M	molar
MRT	mean residence time
n	sample size

N	nitrogen
n.d.	not detected
NH_4	ammonia
NO_3	nitrate
n.s.	not significant
p	significance
PHE	phenolic carbon
PVC	poly vinyl chloride
r^2	adjusted coefficient of determination
SD	standard deviation
SFF	forest management type: selection forest *Fagus*
SOM	soil organic matter
sp.	species
$SUVA_{280nm}$	specific ultraviolet light absorption at 280 nm
TF	throughfall
UF	forest management type: unmanaged *Fagus*
UV	ultraviolet light

Summary

Besides carbon dioxide emissions, the leaching of dissolved organic carbon (DOC) and nitrogen (DON) is the most important process contributing to the mass loss of coarse woody debris (CWD comprising all dead woody material with at least >7 cm in diameter). Increased DOC and nitrogen (N) inputs into the forest floor can be expected from CWD. Since the fate of leached DOC depends on its biodegradability, the latter might play a substantial role for carbon sequestration in forest soils.

The general goal of this study was the investigation of tree species effects, forest management type and site conditions on the release and quality of dissolved organic C and N from CWD.

Within the *Biodiversity Exploratories*, a long-term and large scale biodiversity project funded by the DFG, logs of 13 different coniferous and deciduous European tree species were exposed to decomposition on the soil under natural environmental conditions in winter 2008/2009. Logs were exposed at three geographically distinct *Exploratory* sites in Germany (*Schorfheide/Brandenburg*, *Hainich/Thuringia*, *Swabian Alb/Baden-Württemberg*) underneath different forest management types. From June 2011 until November 2012, CWD runoff from 120 logs was collected periodically at the three *Exploratories*. After filtration (0.45 µm) the amount of DOC, DON, NO_3 and NH was measured to calculate C and N budgets. Quality of DOC was measured in runoff and in incubation solutions, namely the content of phenols, hydrolysable carbohydrates, spectroscopic properties as $SUVA_{280nm}$, HIX_{em} and FTIR. Furthermore initial parameters of wood and bark were determined. In order to quantify DOC biodegradation an incubation experiment lasting 64 days was carried out. As proxy for biodegradation the CO_2 production was adapted to a 2-phase first order kinetic model.

DOC concentrations in CWD log runoff were 3-10 times higher than in throughfall for all 13 tree species. The highest concentrations and accordingly the largest net release were found for *Prunus* and *Quercus* (56 resp. 60 g DOC m^{-2} yr^{-1}), the lowest for *Fraxinus* (14.8 g m^{-2} yr^{-1}). On monthly to annual scale, the amount of precipitation had only minor influence on DOC net release, but a clear seasonality resulted in a higher net release during the growing season. Carbohydrate concentrations in CWD runoff ranged from 2.5-9.4 mg L^{-1} and phenols from 2.7-9.5 mg L^{-1}. The spectroscopic measurements indicated microbial modification of the leached DOC compared to DOC extracted initially from

CWD. The most dominant N form in runoff from CWD was DON and a net release of N was found for all tree species, even though there was a high variation. The net N release was not related to the initial C/N ratio of bark and sapwood. The NH_4-N net release was larger in the dormant than in the growing season. For NO_3-N the seasonality was opposite to NH_4-N. No seasonality was found for DON net release. Throughfall amount as well as temperature had only minor influence on the total release of N from CWD pointing to other key drivers.

The linear mixed effect model based on single sampling dates revealed management effects on DOC and DON net release, whereas effects of *Exploratory* were only observed for DON. However these factors were not identified for the cumulative net release of C and N.

The biodegradation of DOC was quite similar for all tree species, ranging from 14 to 29% of the initial DOC in 64 days and no significant differences in the mean residence times (MRT) were found between coniferous and deciduous species.

As a conclusion, CWD-derived DOC is tree species specific and causes large C inputs to the soil underneath CWD. Depending on time scales, DOC derived from CWD has the potential to increase soil organic matter (SOM) pools beneath CWD. Furthermore it was shown, that CWD provides a source for solute N, even in the early phase of decomposition.

Zusammenfassung

Neben der Freisetzung von Kohlenstoffdioxid (CO_2) leistet die Auswaschung von gelöstem organischem Kohlenstoff (DOC) und Stickstoff (DON) aus Totholz den wichtigsten Beitrag zum Massenverlust von grobem Totholz. Hierzu zählt Totholz mit einem Durchmesser von >7cm. Die Zersetzung von Totholz kann zu einem erhöhten Eintrag von C und N in den Auflagehumus von Waldböden führen. Da der Verbleib des DOC aus Totholz direkt von seiner Abbaubarkeit abhängt, ist die Kinetik des Abbaus eine wichtige Größe für die Kohlenstoffbindung in Waldböden.

Das übergeordnete Ziel dieser Studie war es, Baumarteneffekte, den Einfluss des Managementtyps eines Bestandes, und die Auswirkungen von klimatischen Bedingungen auf die Freisetzung und Qualität von DOC und DON aus Totholz zu ermitteln.

Im Rahmen der *Biodiversitäts-Exploratorien*, einem DFG-finanzierten Langzeitexperiment zur großräumigen Erforschung von Biodiversität, wurden im Winter 2008/2009 Stämme von 13 europäischen Baumarten in Wäldern ausgebracht und unter natürlichen Umweltbedingungen ihrer Zersetzung überlassen. Die Stämme wurden in drei geographisch separaten *Exploratorien* (*Schorfheide/Brandenburg*, *Hainich/Thüringen*, *Schwäbische Alb/Baden-Württemberg*) unter verschiedenen Bestandesmanagementtypen ausgebracht. Von Juni 2011 bis November 2012 wurde in allen drei *Exploratorien* der Abfluss von 120 Stämmen in etwa monatlichem Turnus beprobt. In den filtrierten Proben (0.45 µm) wurde der Gehalt an DOC, gelöstem Gesamt-N sowie Nitrat (NO_3) und Ammonium (NH_4) gemessen, um den Haushalt von gelöstem Kohlenstoff (C) und Stickstoff (N) zu bilanzieren. Die Qualität des DOC wurde sowohl in den Stammabfluss-Proben als auch in den Inkubationslösungen anhand ihres Gehaltes an Phenolen und hydrolysierbaren Kohlenhydraten, sowie ihrer spektroskopischen Eigenschaften (HIX_{em}, FTIR und $SUVA_{280nm}$) bestimmt. Des Weiteren wurden initiale Holz- und Rindeneigenschaften erhoben. Zur Charakterisierung der DOC-Stabilität wurde ein Inkubationsversuch für die Dauer von 64 Tagen angesetzt. Als Maß für den Abbau des DOC aus Totholz wurde die CO_2-Produktion herangezogen und eine zwei-termige Exponentialfunktion an die Daten angepasst.

Die DOC Konzentrationen im Totholzabfluss waren drei- bis zehnfach höher verglichen mit jenen im Bestandesniederschlag. Die höchsten DOC Konzentrationen und die größten Nettofreisetzungen wurden für Totholz von *Prunus* und *Quercus* (56 bzw.

60 g DOC m^{-2} yr^{-1}) bestimmt. Die geringsten DOC -Freisetzungen lagen hingegen für *Fraxinus* (14.8 g m^{-2} yr^{-1}) vor. Auf einer Zeitskala von Monaten bis Jahren konnte nur ein geringfügiger Zusammenhang zwischen der DOC-Nettofreisetzung und dem Bestandesniederschlag nachgewiesen werden. Allerdings führte eine deutliche Saisonalität zu höheren DOC Freisetzungen aus Totholz während der Vegetationsperiode.

Die Kohlenhydratkonzentrationen im Totholz-Abfluss lagen im Bereich von 2,5-9,4 mg C L^{-1} und die Phenolkonzentrationen reichten von 2,7-9,5 mg C L^{-1}. Die spektroskopische Charakterisierung des DOC ließ auf eine mikrobielle Umsetzung des aus dem Totholz stammenden DOCs im Vergleich zu den initialen Extrakten schließen. Den größten Anteil am gelösten Gesamtstickstoff bildete DON und trotz großer Variabilität wurde für alle Stickstoffkomponenten eine netto-Freisetzung aus Totholz gefunden. Diese stand jedoch in keinem Zusammenhang zu den initialen C/N-Verhältnissen der Rinde oder des Splintholzes. Die saisonale Freisetzung von NH_4-N war während des Winters größer als während der Vegetationsperiode und traf umgekehrt für NO_3-N zu. Die Freisetzung von DON unterlag hingegen keiner signifikanten Saisonalität. Der Bestandesniederschlag wie auch die Temperatur schien nur einen geringen Einfluss auf die Gesamtstickstoff-Freisetzung zu haben. Dies deutet auf andere abbau-relevante Schlüsselfaktoren hin.

Während der Managementtyp des Bestandes die DOC- und DON-Freisetzung nach dem Ergebnis eines linearen Modells für alle Probenahmetermine („lme“ in R) signifikant beeinflusste, konnte ein Effekt des *Exploratoriums* nur für die DON Freisetzung nachgewiesen werden. Dies traf jedoch aufgrund der Daten-Aggregation nicht für die kumulierten Jahresflüsse zu.

Der DOC-Abbau verhielt sich für alle Baumarten ähnlich (14-29% des initialen DOC-Gehaltes) und es wurden keine signifikanten Unterschiede für die mittleren Verweilzeiten (MRT) zwischen Koniferen und Laubbäumen gefunden.

Zusammenfassend konnte gezeigt werden, dass die DOC Freisetzung aus Totholz baumartenspezifisch ist und zu einem substanziellen C-Eintrag in den Boden unter Totholz führt. Ferner konnte gezeigt werden, dass DOC aus Totholz das Potential zur Anreicherung der organischen Bodensubstanz in Böden unter Totholz hat. Darüber hinaus stellt Totholz auch während der frühen Zersetzungsphase eine Quelle für gelöste Stickstoffkomponenten dar.

1. Synthesis: Tree species effects on the release of dissolved organic carbon and nitrogen from decomposing logs

1.1 Introduction

1.1.1 Motivation

Since forests store about 50% of the global terrestrial C stocks (Jandl et al. 2007), they are of major interest for the global C balance (IPCC 2000). Coarse woody debris (CWD) comprising dead woody material >7 cm, in diameter (e.g.: Müller-Using and Bartsch 2009) today is in the focus of forest management , as CWD provides habitats for a large number of species (Freedman et al. 1996), and CWD represents a short to middle term C sink (Laiho and Prescott 2004; Lorenz and Lal 2010). Being influenced by forest management type, CWD provides hotspots of C (McClain et al. 2003) and nutrient supply in forests since CWD in un-managed forests can account for huge C stocks (e.g.: Harmon et al. 1986; Mund 2004).

Dissolved organic C and N, as leaching products from CWD, are in the focus of this thesis, since a lack of knowledge exists concerning the amount and quality of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) derived from CWD of different tree species. Only few data on management or tree species effects on DOC and DON exports from CWD into the soil are available from the literature. Furthermore, only little information is available on the N turnover in CWD, answering the question if logs of CWD are sources or sinks for N. In order to predict the effect of CWD on C and N pools in forests, it is indispensable to identify the key drivers of DOC and DON release from CWD. With respect to the soil C accumulation potential, there is a research need to identify the biodegradability of DOC derived from CWD.

1.1.2 CWD in forest ecosystems

In forest ecosystems, CWD is known to be an important nutrient stock and fulfils long-term ecological functions by providing structural and habitat elements (e.g.: Sollins

1982; Harmon et al 1986; Keenan et al 1993; Zhou et al 2007). Low stocks of CWD are identified as an important factor for a decrease in biodiversity of European forests (Schuck et al. 2004; Christensen et al. 2005; von Oheimb et al. 2007). CWD needs to be considered for C sequestration in forest ecosystems due to its influence on C retention (Yatskov et al. 2003). Standing as well as downed CWD is a long-term nutrient storage and important C sink for many decades (Harmon et al. 1986; Keenan et al. 1993). As an example, in European beech forests and the stocks of CWD range from nil up to 550 m^3 ha^{-1} (mean 130 m^3 ha^{-1}). CWD stocks are larger in un-managed than in managed forests (Christensen et al. 2005). Thus during its degradation, CWD represents a large C and also potentially a N source and provides “hot spots” of C and N turnover (McClain et al. 2003).

Three main processes are influencing the mass loss of CWD: (i) the mineralization to CO_2, (ii) leaching and (iii) fragmentation (physically and chemically, mostly in later stages of decomposition) (Harmon et al. 1986). Besides CO_2 emissions due to respiration of the microbial and fungal biomass in wood and bark tissue, the mass loss of CWD by leaching of DOC is the second important pathway of C loss (Mattson et al. 1987), as highlighted in figure 1.1 (blue).

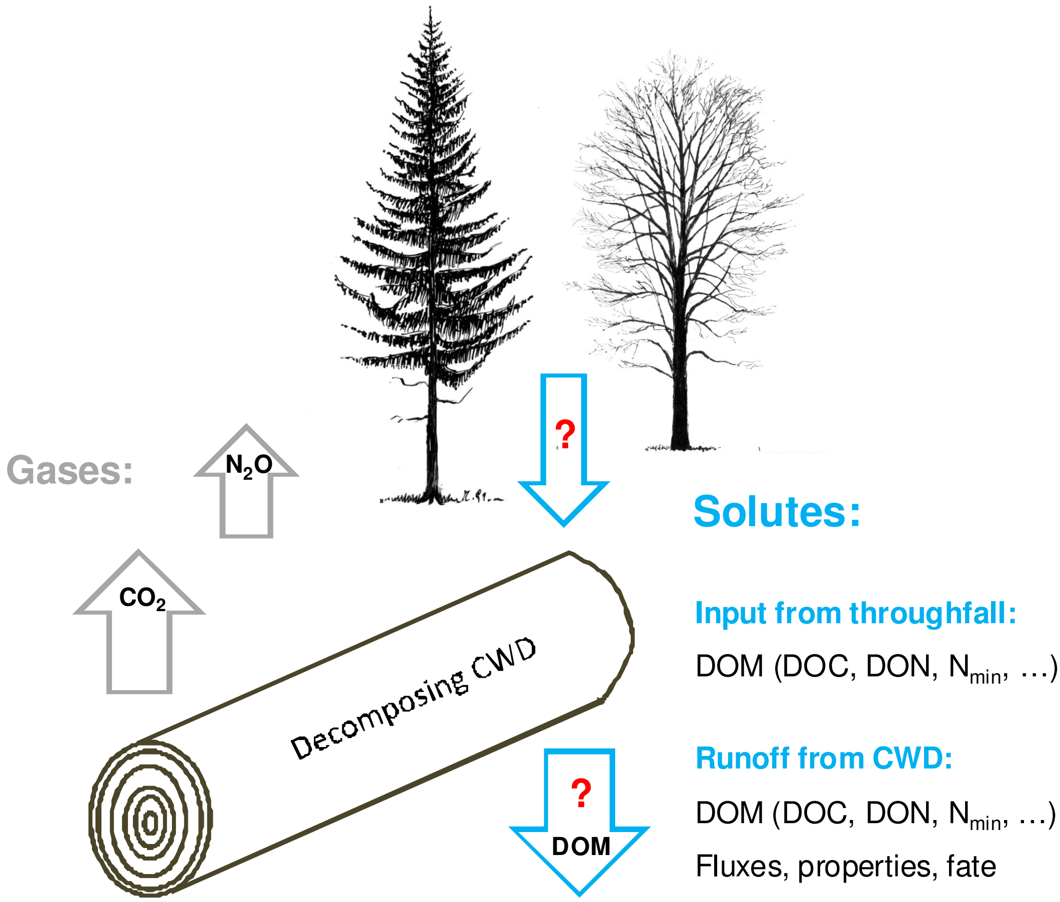

Figure 1.1: Pathways of carbon and nitrogen release from CWD.

The graphics of *Fagus* and *Picea* were used with the kindly permission of Manfred Müller-Berg (www.baumkunde.de, March 2015).

1.1.3 Concentrations of C and N in runoff from CWD

In leachates from forest floor beneath CWD of *Pseudotsuga*, DOC concentrations up to 250 mg L^{-1} were found (Spears and Lajtha 2004). In log runoff DOC concentrations up to 300 mg L^{-1} were reported (Hafner et al. 2005), exceeding those measured in throughfall (TF) by far. Under *Fagus* CWD log runoff DOC concentrations ranged from 28 to 118 mg L^{-1} and increased with proceeding decomposition stage (Kuehne et al. 2008). Kahl et al. (2012) found peak concentrations of >500 mg L^{-1} in solutions beneath *Fagus* logs. In the early phase of CWD decomposition, the average DOC concentrations in runoff from logs of different tree species were between 30 and 120 mg L^{-1} (see manuscript chapter 2, Figure 2.1).

Information on solute fluxes of N from CWD is very limited and the controlling factors as well as the drivers for N export from CWD are widely unknown. With ongoing decomposition, the concentration of DON and mineral N from CWD exceeded those of throughfall by far, as it was reported for CWD of *Fagus* (Kuehne et al. 2008), indicating a N net release during decomposition. In runoff from CWD of various decomposition states, DON was the major form of N (Hafner et al 2005). No significant relation of precipitation and solute N concentrations in CWD runoff were published by Hafner et al. (2005), questioning the implication of environmental factors on solute N release from CWD. According to the findings from Schmidt et al. (2010) for forest floors, the net N release from CWD should be positively related to precipitation amount.

1.1.4 Factors influencing DOC and solute N release from CWD

Decomposition state: While drivers of CWD decomposition have been intensively studied (e.g.: Harmon et al 1986; Harmon et al 2000; Weedon et al 2009; Herrmann and Bauhus 2013), only few information on DOC release derived from CWD is available from the literature. DOC release from CWD is estimated to increase with decomposition state (Hafner et al. 2005; Kuehne et al. 2008) which is in contrast to DOC release from leaf litter (Don and Kalbitz 2005). A higher DOC release from fresh than from decomposed leaf litter has been reported. The C/N ratio of CWD decreases with time of decomposition (Yang et al. 2010) pointing to an increase of the total N pool in CWD especially during the early decomposition phase. This is due to the high N demand of the decomposer community, while N net release mainly occurred at later states of decomposition (Creed et al. 2004a; Laiho and Prescott 2004; Palviainen et al. 2008; Preston et al. 2012). Several processes might be responsible for an increase of the N stock in CWD and thereby for the N leaching: (i) microbial immobilization of mineral N yield from throughfall of canopy, (ii) the translocation of N from the soil beneath and surrounding environment by funghi (Boddy and Watkinson 1995) and (iii) asymbiontic N_2 fixation (Brunner and Kimmins 2003).

Quality of CWD: The DOC released from CWD of different tree species might differ in its amount and quality, since the lignin quality also varies among tree species. Lignin of coniferous wood is built up primarily by guaiacyl-units combined with small amounts of *p*-hydroxyphenyl-units. In contrast, lignin of deciduous wood consists of guaiacyl and syringyl units and to a minor proportion of *p*-hydroxyphenyl-units (Wong 2009). Furthermore it is widely accepted, that deciduous CWD generally decomposes faster than coniferous due to the narrower C/N ratio (Weedon et al. 2009). Lignin decomposition is expected to be the source of the aromatic DOC compounds released from leaf and needle litter (Kalbitz et al. 2006). Therefore, CWD decomposition is assumed to release large amounts of DOC during its decomposition due to the high lignin content of wood and bark tissue and the wide C/N ratio. The DOC release from forest floors of different tree species increased with C/N of the forest floor (Michel and Matzner 2002; Kindler et al. 2011; Borken et al. 2011). Additionally, the C and N release from CWD likely will be influenced by inhibition of decomposers by phenols in wood and bark (Benoit and Starkey 1968). Contrary, the decomposition of CWD is enhanced by the availability of carbohydrates. During CWD decomposition, dynamics of C and N were reported to be tree species specific, since the C/N ratio decreased faster for birch logs compared to those in conifers (Palviainen et al. 2008). Substantial differences of C/N ratios were published for coniferous species during decomposition (Laiho and Prescott 2004) promising tree species effects on N release.

Environmental conditions: Precipitation amount increased the DOC fluxes in forest floors on monthly to annual scale (Park and Matzner 2003; Schmidt et al. 2011; Gielen et al. 2011; Borken et al. 2011) suggesting precipitation amount also as a major driver of DOC release from CWD. As the respiration of CO_2 from CWD and the decomposition rates were related to temperature (Herrmann and Bauhus 2013), DOC release in the growing season is expected to exceed the release during the dormant season. Up to now, no information on the relation of seasonality and precipitation on the DOC release from CWD is available.

1.1.5 Fate of DOC from CWD: Degradability versus sequestration?

Large DOC inputs to the soil beneath CWD can be expected, even though the distribution of CWD is spatially “clumped”. The DOC input to the soil underneath CWD might influence the soil microbial community (Brant et al. 2006; Crow et al. 2009) and soil organic matter pools (Kalbitz and Kaiser 2008) as well as the rates of soil respiration (van Hees et al. 2008; Iqbal et al. 2010).

In several studies, biodegradability of DOC was shown to be affected by its quality, the latter being dependent of the DOC source (Boyer and Groffman 1996; Marschner and Kalbitz 2003; Fellman et al. 2008) and microbial community composition (Young et al.

2005). DOC biodegradation was examined in laboratory incubation experiments using various incubation times from several weeks up to one year. The degradable portions of DOC were found to be about 70-90% for DOC in extracts of fresh litter and 40% for extracts of decomposed litter extracts (Kalbitz et al. 2003b; Don and Kalbitz 2005), whereas only 7% of the total DOC from Oa leachates beneath spruce canopy was decomposed. In another study, 12-17% of the DOC have been found to be biodegradable after 7 weeks of incubation (Kiikkilä et al. 2005).

Mineralization rate constants for the biodegradation of DOC from O layers ranged from 0.02 to 0.05 d^{-1} for labile fractions of degradable DOC and from 0.00009 to 0.0008 d^{-1} for stable fractions (Kalbitz et al. 2005). Corresponding mean residence times ranged from 21 to 46 days for the labile and from 3 to 28 years for the stable fraction of biodegradable DOC.

Numerous studies on leachate from litter of different ages (Don and Kalbitz 2005) and on forest floor percolates (Strobel et al. 2001; Kaiser et al. 2001; Kalbitz et al. 2007; Kiikkilä et al. 2014) highlighted the influence of tree species on DOC quality and biodegradability. The DOC biodegradability derived from O layers was negatively related to the humification index of the DOC deduced from spectroscopic measurements (Kalbitz et al. 2003b). DOC derived from birch leaves and birch forest floor degraded faster than DOC derived from spruce needles and spruce forest floor (Kiikkilä et al. 2011).

Coarse woody debris differs largely in chemical properties (e.g.: wider C/N ratio, higher lignin content) from leaf litter or forest floor organic matter. These differences are expected to result in specific properties of the DOC leached from CWD. In addition, differences in DOC quality between coniferous and deciduous species will cause variations in biodegradability, since coniferous CWD usually has a wider C/N ratio resulting in lower degradability than deciduous CWD (Weedon et al. 2009). As mentioned before, differences in lignin structure between coniferous and deciduous CWD promise varying mineralization rates for different tree species.

Up to now, biodegradability of CWD derived DOC has not been investigated. Hence, in chapter 4 of this thesis, the biodegradability of DOC from CWD of 13 different tree species in the early state of decomposition and its implication on soil carbon is introduced.

1.2 Aims and hypothesis

The overall goal of this thesis was the investigation of the effects of tree species, climatic conditions and forest management type on the production and quality of DOC and DON from CWD during the early phase of decomposition. Being linked to other working groups of the *BELongDead* initiative within the *Biodiversity Exploratories*, the results of the present work will lead to an improved understanding of the processes driving and controlling the solute budget of the CWD as well as the potential of CWD derived C and/or N to accumulate in the soil beneath. Furthermore, an estimation of the contribution of leaching on total mass loss will be given.

The following hypotheses were tested using a combined design of laboratory and field measurements. The hypotheses are blocked and numbered according to the chapters 1-4.

(H 1) DOC and DON net release from CWD is affected by forest management type and *Exploratory*.

(H 2.1) The amount and composition of DOC released from CWD is tree species specific and affected by the initial chemical properties of bark and sapwood.

(H 2.2) The net release of DOC from CWD increases with precipitation.

(H 2.3) The net release of DOC from CWD is larger in the growing than in the dormant season.

(H 3.1) In the early phase of decomposition, CWD will act as a sink for mineral N from throughfall.

(H 3.2) The N budget of the CWD is related to initial C/N of bark and sapwood.

(H 3.3) The release of solute N from CWD is larger in the growing than in the dormant season and depends on the precipitation amount.

(H 4.1) The mineralization rates of DOC from CWD differ between coniferous and deciduous tree species.

(H 4.2) The mineralization rates of DOC from CWD are related to spectroscopic properties and carbohydrate content of DOC.

(H 5) The DOC and DON released from CWD increases significantly the DOC and DON concentrations in soil solution underneath CWD.

1.3 Material and methods

1.3.1 The *Biodiversity Exploratories*: field sites, experimental design

Developing a research platform for functional biodiversity research, the *Biodiversity Exploratories* project (www.biodiversity-exploratories.de) was set up in the year 2008, funded by the Deutsche Forschungsgemeinschaft (DFG) priority program 1374 in order to elucidate interactions of land-use, biodiversity and ecosystem processes (Fischer et al. 2010). The *Biodiversity Exploratory* sites (in the following called *Exploratories*) were installed at three different areas in Germany. Located in *Brandenburg* (*Schorfheide-Chorin* biosphere reserve, 3-140 m a.s.l.), *Thuringia* (*Hainich-Dün* national park, 285-550 m a.s.l.) and *Baden-Württemberg* (*Swabian Alb* biosphere reserve, 460-860 m a.s.l.) more than 1100 plots in grass land and forests were implemented.

As a sub-project under the umbrella of the ***B**iodiversity **E**xploratories*, the ***BE**LongDead* initiative was initiated comprising several research groups working on the following research questions:

(i) How does CWD impact on ecosystem processes,
(ii) what is the influence of the surrounding habitat on colonization and decomposition of CWD,
(iii) how does CWD degradation influence the carbon cycle and microbial communities on the forest soil surface?

Within *BELongDead*, at each forest plot of the three *Exploratories* a set of freshly cut logs of 13 tree species of the temperate forest zone (*Acer sp.*, *Betula sp.*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Populus sp.*, *Prunus avium*, *Pseudotsuga menziesii*, *Quercus sp.*, *Tilia sp.*) was exposed to decomposition under natural environmental conditions amounting to 1140 logs in total. The CWD logs had a length of 4 m and 0.30-0.40 m in diameter. All logs were obtained from the forest authority of the Federal State of *Thuringia*, Germany.

The distribution of the plots among one *Exploratory* was set up in three spatially separated forest sites with a different management type respectively: “age class conifers” (CON), “age class *Fagus*” (F) and “unmanaged *Fagus*” (UF) forests. Each management type and plot was represented by three replicates at *Swabian Alb* and *Hainich*, whereas at the *Schorfheide* only 2 plots with “age class *Fagus*” and 4 plots with “age class conifers” were available.

For this thesis, a subset of 120 logs within the *BELongDead* project was sampled following two different goals: (i) To determine management and site effects on the release of DOC and DON. For this purpose, at all three *Exploratories*, runoff from logs of *Fagus sylvatica*, *Picea abies* and *Quercus sp.* was sampled at 9 plots per *Exploratory* representing the 3 management types. (ii) To determine tree species effects in more detail, additionally 3 plots of “selection forest *Fagus*” (SFF, see chapter 2) were installed at the *Hainich Exploratory* and runoff was sampled from all 13 tree species as described below.

To detect the DOC signal from CWD into the soil, in total 60 suction cups (SK20, UMS, Munich, Germany) were installed at five plots at the *Schorfheide Exploratory*. The installation was carried out at one plot with “age class *Fagus*”, two plots with “unmanaged *Fagus*” and two plots with “age class coniferous” canopy, in 10 cm depth beneath CWD of *Fagus*, *Picea* and *Quercus* with n = 3 per log, and three controls per plot. The soil at the *Schorfheide* was chosen due to its sandy texture and low organic matter content of the mineral soil in order to avoid sorption of DOC.

Schorfheide forest soils are sandy Dystric Cambisols from glacial deposits. The soil at the *Hainich Exploratory* has developed from loess deposits over calcareous bedrock and is classified as Luvisol. At the *Swabian Alb* also calcareous bedrock was predominant and the soil developed on Jurassic shell limestone, being rich in clay and classified as Eutric Cambisol and Leptosol.

1.3.2 CWD runoff and throughfall sampling, sample treatment, log runoff

Leaching from CWD (logs with >30 cm in diameter) was investigated in the early phase of decomposition. Sampling of CWD runoff solution was conducted from June 2011 until November 2012 after about 2-3 years of exposure of the logs. Small PVC gutters (10 × 30 cm) were installed beneath the CWD logs and runoff was sampled periodically at about monthly intervals using 2.0 L HDPE bottles located in buckets, dug in the soil next to the logs thereby avoiding exposition to direct sun light and high temperatures. Additionally, throughfall samples (sampler type: RS200, UMS, Munich, Germany) were collected (1 sampler at each plot) in order to determine precipitation amount and concentration of DOM in throughfall.

All runoff, throughfall and soil solution samples were stored at 2 °C in a climate chamber at the BayCEER department until filtration using Millipore water pre-washed cellulose acetate filters (0.45 µm, Whatman OE 67, GE Health Care Europe, Freiburg, D). The filtrates were stored frozen until measurement. The DOC concentration in the samples was measured using a total N/C analyzer (N/C 2100 Analyzer, Analytik Jena, D). Furthermore, NO_3 and NH_4 concentrations were detected using flow injection analysis (FIA-LAB, MLE, Dresden, D). Subsequently, DON concentration was calculated by subtracting NH_4-N and NO_3-N from the total N concentration and negative concentrations of DON were set to zero.

1.3.3 Flux calculations, DOC and DON net release, statistics

Fluxes of DOC and DON from each log were calculated by multiplication of throughfall volumes of every single sampling date with the respective DOC or DON concentration and were referred to the unit “square meter projected CWD log area”. The water loss due to evaporation from the logs was considered to be negligible on annual scale. The net fluxes were calculated by subtracting fluxes in throughfall from the fluxes of the logs.

In order to determine tree species and management effects and temporal patterns a linear mixed model (“lme” in R) was adapted comprising the total set of DOC and DON runoff data for 17 months for three tree species and three management types.

All data management and calculations were performed using the Microsoft Excel 2007 package and all statistical analyses were conducted using the open source statistical software R 3.0.1 (R Core Team 2013). Significances were tested using a one way ANOVA and subsequently a Tukey’s post-hoc test in case of normal distribution of tested data. Few data sets were $\log_{10}$-transformed being conform to the acquirements for using an ANOVA. Alternatively, non-parametric tests were conducted using a pairwise Wilcoxon rank sum test.

1.3.4 Measurements on DOC quality

In all CWD runoff samples pH-value and electric conductivity (EC) were measured immediately after filtration.

Carbohydrates: Hydrolysable carbohydrates were analyzed in log runoff samples of four sampling dates as well as in initial bark and sapwood extracts according to the procedure published by Johnson and Sieburth (1977) and Johnson et al. (1981). In short: freeze dried DOC samples were hydrolyzed using 12 molar H_2SO_4. The resulting carbohydrate monomers were reduced to alditols using potassium borohydride (10%) and were measured spectrophotometrically at 635 nm (UV 1800, Shimadzu) after complexation using 3-methylbenz-thiazaolinon-2-hydrazon (MBTH reagent).

Phenols: The content of water soluble phenols in log runoff samples was determined for three sampling dates following the method of Folin-Ciocalteu (Box 1983). The samples were diluted to 10 mg C L^{-1} and Folin-Ciocalteu reagent was applied to the samples in the ratio 5:0.75:0.25 (sample : sodium carbonate solution : Folin-Ciocalteu reagent, Box 1983). After dark incubation for one hour, phenols were detected spectrophotometrically at 730 nm (UV 1800, Shimadzu, Duisburg, D).

Humification index and specific UV absorbance at 280 nm wavelength ($SUVA_{280nm}$): At 4 sampling dates distributed along the sampling period, fluorescence emission spectra of DOM were recorded (SFM 25, BIO-TEK Instruments, Bad Friedrichshall, D) and a humification index (HIX) was calculated based on the method of Zsolnay (1999). In short: a quotient is calculated by dividing the proportion of the upper area of the emission spectra (435-480 nm) by the lower area (300-445 nm), resulting in a positive value about approximately between 1 and 15. The index specifies a dimension of humification of the molecules in sample solutions. Increasing humification is associated with decreasing ratios of H/C (Lüttig 1986; Stevenson 1994). The specific UV absorbance at 280 nm was detected to estimate the aromaticity of the dissolved compounds (Kalbitz et al. 2003b; McKnight et al. 1997).

1.3.5 DOC biodegradation

Logs of 13 tree species were irrigated in June 2013 using an artificial precipitation solution. The irrigation was applied drop-wise within several hours using glass burettes being installed above the logs. The total amount of irrigation was 2.5 L per log representing a precipitation amount of 10 mm.

The runoff sampled beneath the logs was filtered (0.45 µm cellulose acetate, Whatman OE 67, GE Health Care Europe, Freiburg, D) and samples were kept frozen until further analysis. DOC concentrations were analyzed by combustion using a C-Analyzer (N/C 2100 Analyzer, Analytik Jena, D).

Prior to incubation, 3 samples per tree species were merged due to the small sample volumes obtaining one pooled sample per tree species. After merging, three pseudo replicates of 40 mL volume per tree species were incubated. To each incubation flask (Müller-Krempel, 120 mL, Bülach, CH) a glass fibre filter (Ø 55 mm, 47.5 cm^2, Schleicher & Schuell, GF 55, München, D) was added providing surface for the establishment of biofilms (Qualls and Haines 1992).

Nitrogen supply of microbial inoculum (extracted with 0.01 molar $CaCl_2$ from Oi + Oe horizons mixed from spruce and beech sites) was ensured by adding 50 µL of a 0.5 molar NH_4NO_3 solution to each sample and after sealing an overpressure of 80 hPa was applied. During the 64 days of incubation CO_2 emission was measured periodically at 10 occasions in the flask headspace using a gas capillary chromatography equipped with a flame ionization detector (SRI 8610C, SRI Instruments Europe GmbH, D). Subsequently, the amount of CO_2 was calculated in the headspace using the general gas equation and the physically dissolved CO_2 in the solution phase was calculated by Henry's law. The kinetic of total CO_2 production (CO_2 in headspace + physically dissolved CO_2 + HCO_3^-) was adapted to a 2-phase exponential model using a least square optimization.

1.4 Synopsis and discussion of key findings

1.4.1 Basic environmental factors: throughfall amount, DOC and DON in throughfall as influenced by *Exploratory* and management type

As shown in Figure 1.1, the solutes in throughfall give an imprint on solutes in CWD runoff and throughfall might provide an initial supply of nutrients to the microbial community associated with CWD. Therefore, throughfall is one of the key factors influencing the decomposition of CWD under field conditions and thus the release of solutes from CWD.

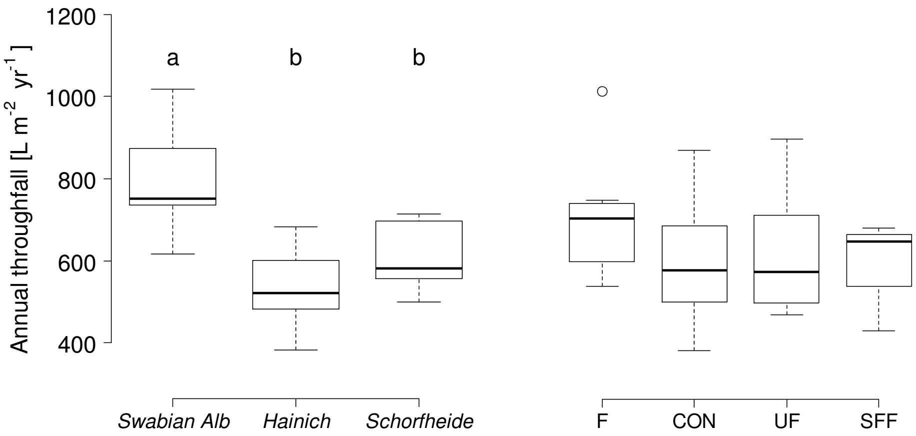

Figure 1.2: Annual throughfall amount in the *Exploratories* and forest management types.

Calculated for one year with median and quartiles for each *Exploratory* (n = 9), "age class *Fagus*" (F), "age class conifers" (CON), "unmanaged *Fagus*" (UF) forest and "selection forest *Fagus*" (SFF) (n = 3). Significance is indicated by the characters a, b ($p < 0.01$) obtained by an ANOVA.

The annual throughfall was significantly larger at the *Swabian Alb Exploratory* than at *Hainich* or *Schorfheide* (Figure 1.2). In contrast to the expectation, the throughfall at *Schorfheide* was larger than at *Hainich*, even though not statistically significant.

The amount of throughfall might be influenced furthermore by the management type of the forest due to different age and structure of branches and leaves (e.g.: Harmon et al 1986). But as it is shown in Figure 1.2, no significant influence of forest management type on the annual throughfall was found. In this case, the effect of management type was potentially hidden by the fact, that only one throughfall sampling device per plot was installed to investigate the amount of throughfall, and as it is known from the literature, that throughfall amounts in forests can largely vary at short distances (Stout and McMahon 1961; Parker 1983; Seiler and Matzner 1995; Levia and Frost 2006).

All throughfall data were tested for differences in throughfall amounts between the growing and the dormant season (Figure 1.3) using $\log_{10}$-transformed data to ensure normal distribution.

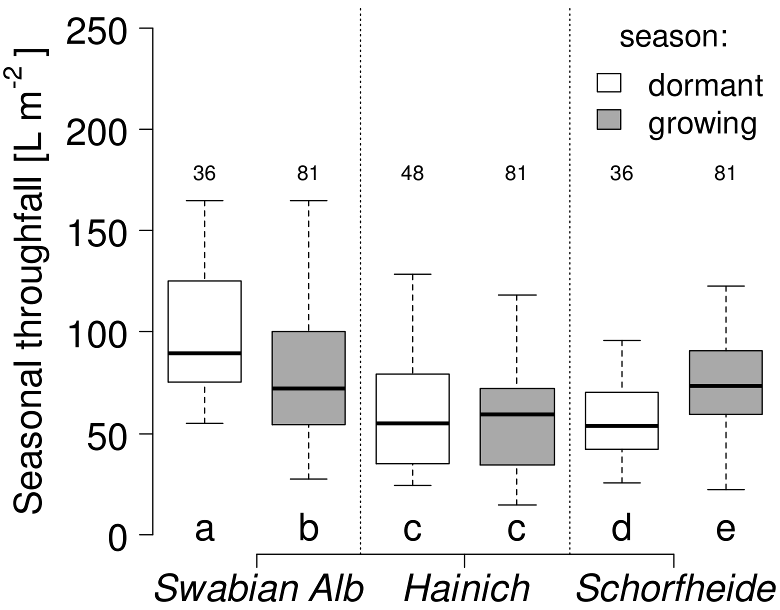

Figure 1.3: Average througfall amounts in the growing (May-October) and dormant (November – April) season.

The number of samples is given above the boxes and represent sampling dates and the 9 species replicates. Significance is indicated by the characters a-e separately for every *Exploratory* ($p < 0.05$) using $\log_{10}$-transformed data in an ANOVA.

Seasonality was pronounced for the *Swabian Alb* with larger throughfall amounts during the dormant season and for the *Schorfheide Exploratory* with larger throughfall amounts during the growing season.(Figure 1.3). At the *Hainich Exploratory*, throughfall amounts of dormant and growing season were similar.

The DOC concentrations in throughfall were significantly higher at plots with “age class conifers” canopy (Figure 1.4) compared to “age class *Fagus*”, “unmanaged *Fagus*” forest or “selection forest *Fagus*”. Hence, significant effects of throughfall might be expected on the DOC net release from CWD of different forest management types.

No significant seasonality in DOC concentration of throughfall was found in the three

Exploratories (data not shown), but DOC concentrations in *Schorfheide* throughfall were significantly higher than at *Hainich* or *Swabian Alb* plots ($p < 0.01$) (Figure 1.4).

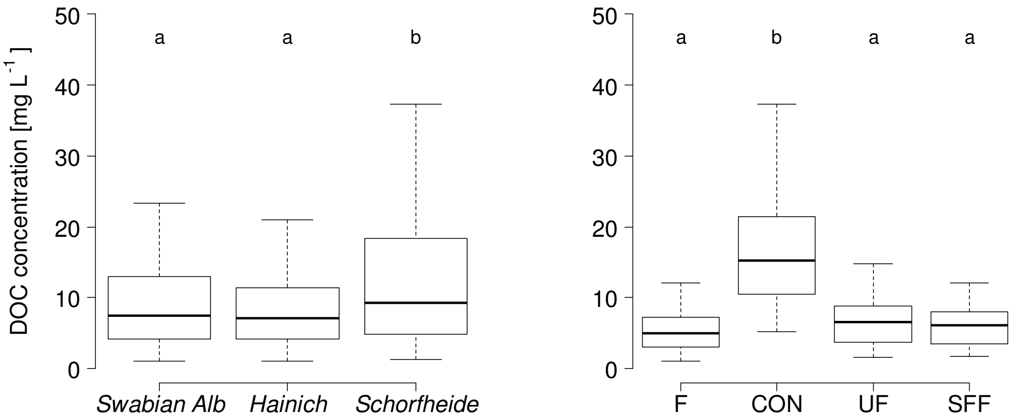

Figure 1.4: Boxplot of DOC concentrations in throughfall beneath different forest management types and in the different *Exploratories*.

"Age class *Fagus*" (F, n = 102), "age class conifers" (CON, n = 126), "unmanaged *Fagus*" forest (UF, n = 114) and "selection forest *Fagus*" (SFF, n = 39) for the single sampling events including all three *Exploratories* with median and quartiles. Differences of $\log_{10}$-transformed DOC concentration data obtained by an ANOVA are indicated by the characters a, b ($p < 0.001$).

DON concentrations in throughfall ranged from 0-1.25 mg DON L^{-1} and were significantly higher in coniferous sites compared to "age class *Fagus*" and "unmanaged *Fagus*" ($p < 0.001$) and also significantly higher than DON in throughfall of "selection forest *Fagus*" ($p < 0.05$) (Figure 1.5). These findings are supported by the results of Michalzik and Matzner (1999), who reported high DON concentrations in throughfall of coniferous sites. No significant influence of *Exploratory* on DON concentration was observed (Figure 1.5).

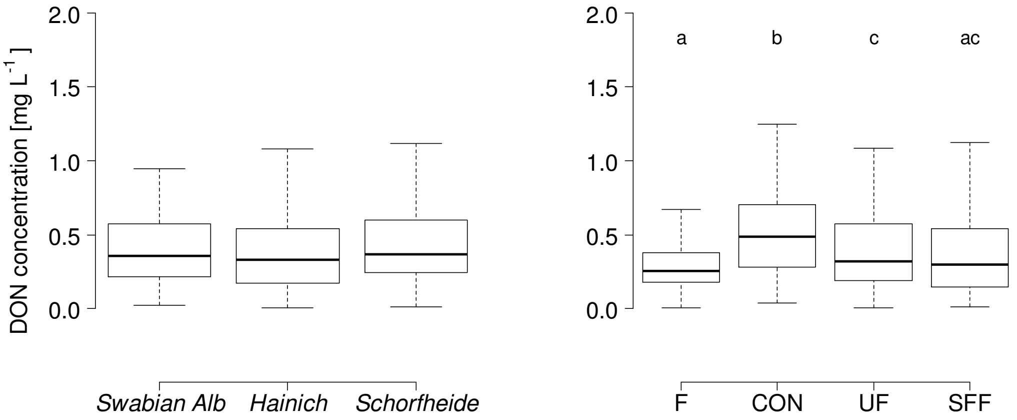

Figure 1.5: Boxplot of DON concentrations in throughfall for all sampling events for the different forest management types and *Exploratories*.

“Age class *Fagus*” (F, n = 102), “age class conifers” (CON, n = 126), “unmanaged *Fagus*” forest (UF, n = 114) and “selection forest *Fagus*” (SFF, n = 39) for all three *Exploratories* with median and quartiles. Significant differences are indicated by the characters a, b, c ($p < 0.01$) obtained by a pairwise Wilcoxon rank sum test.

1.4.2 Quality of throughfall: HIX_{em} , $SUVA_{280nm}$

The HIX_{em} in throughfall was significantly lower in “age class *Fagus*” (Figure 1.6) (average: 3.62) than in “age class conifers”. No significant differences were found compared to “unmanaged *Fagus*” or “selection forest *Fagus*”. Likewise no significant differences were found for HIX_{em} between throughfall in the three *Exploratories*, hence data were merged for Figure 1.6. The $SUVA_{280nm}$ ranged from 0.029 up to 0.323 L 10 mg DOC^{-1} cm^{-1} and no significant differences between *Exploratories* or management types were found.

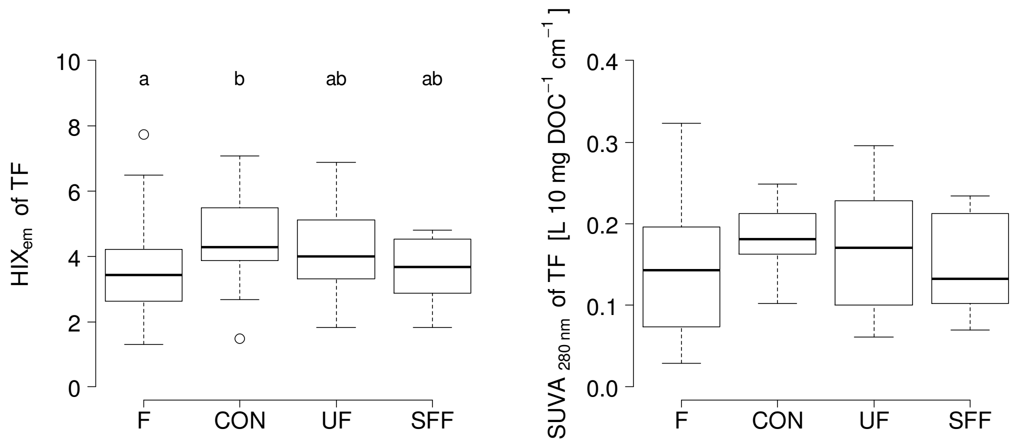

Figure 1.6: Boxplot of humification index and $SUVA_{280nm}$ of throughfall for four sampling dates in different forest management types.

"Age class *Fagus*" (F, n = 30), "age class conifers" (CON, n = 36), "unmanaged *Fagus*" forest (UF, n = 33) and "selection forest *Fagus*" (SFF, n = 12) including all three *Exploratories* with median and quartiles. Significant differences determined by ANOVA are indicated by the characters a, b ($p < 0.05$)

1.4.3 Quality change of CWD runoff during the observation period

To determine the changing DOC properties in runoff from CWD during the early phase of CWD degradation, quality properties were measured at 4 dates during the observation period of 17 months.

The increasing HIX_{em} in CWD runoff of 3 tree species *Fagus*, *Picea* and *Quercus* (Figure 1.7, significant for *Picea* and *Quercus*) indicates an increasing recalcitrance of DOC compounds released from CWD with proceeding degradation of CWD. Increasing HIX_{em} quotients points to an increasing humification of DOC molecules. The HIX_{em} of soil derived DOM showed significant correlation to C mineralization (Kalbitz et al. 2005) and an inverse correlation with carbohydrate content (Kalbitz et al. 2003b).

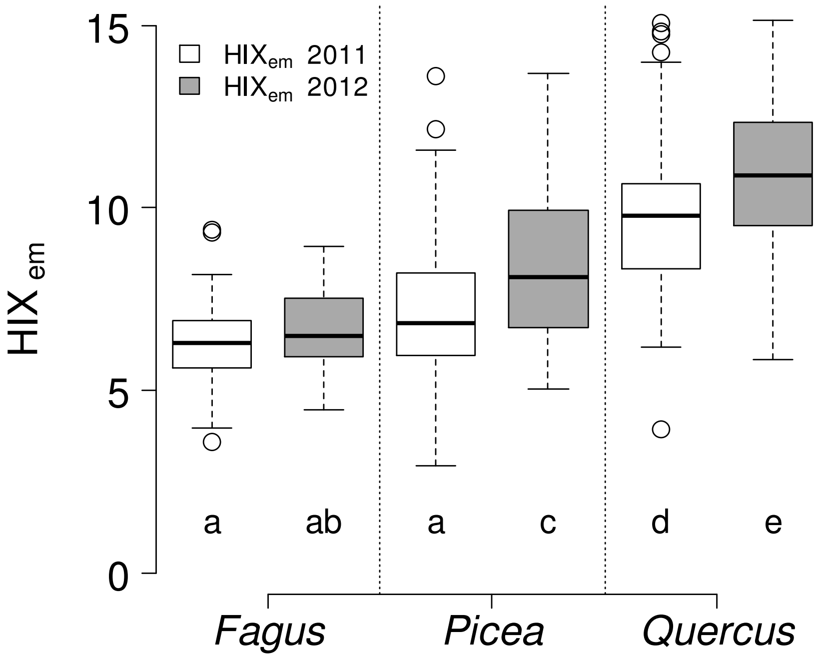

Figure 1.7: Boxplot of humification index for runoff samples of *Fagus*, *Picea* and *Quercus* in the year 2011 and 2012.

Significance is indicated by the characters a-e obtained by a pairwise Wilcoxon rank sum test ($p < 0.05$; n per species 2011: 63, n per species 2012: 36).

No significant change of $SUVA_{280nm}$ in CWD runoff was observed during the observation period.

1.4.4 Flux weighted DOC/DON ratios of CWD runoff samples

No significant influence of management type was found for the flux weighted DOC/DON ratios (Figure 1.8).

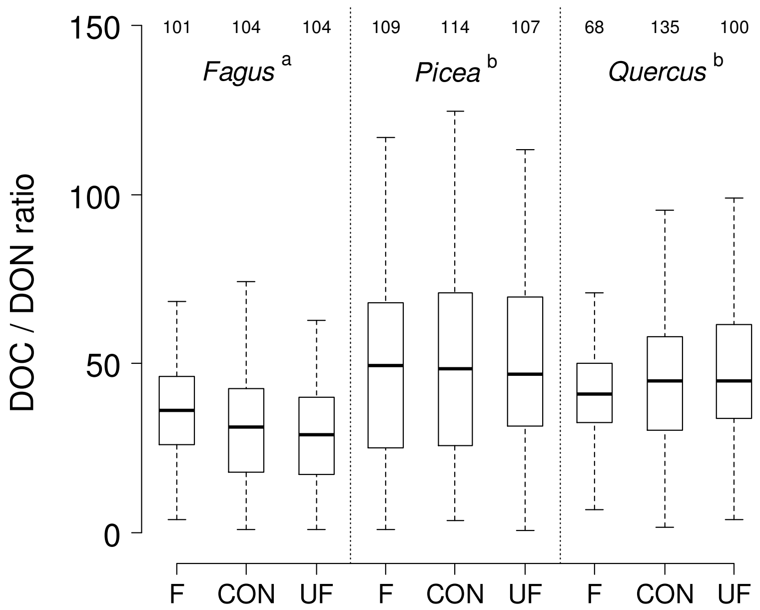

Figure 1.8: Boxplot of flux weighted DOC/DON ratios in CWD runoff averaged for all sampling events and stratified according to forest management type.

With n = 9 logs per tree species and forest management type (F = "age class *Fagus*", CON = "age class conifers", UF = "unmanaged *Fagus*"). Characters a, b indicate significances of log_{10}-transformed DOC/DON ratios tested using an ANOVA ($p < 0.001$) The total number of samples is givenb above the boxes.

The DOC/DON ratios ranged from 1-246 and increased in the order *Fagus* < *Quercus* < *Picea*. The order corresponds to results from chapter 3 (Figure 3.5), where the highest DOC/DON ratios were found for the coniferous species. This can be referred to the generally lower C/N ratios in deciduous than in coniferous CWD.

The DOC/DON ratios were nearly twice (Figure 1.8) thus reported for leachates from A horizons beneath coniferous stands and one order of magnitude higher than in leachates from B horizons (Fröberg et al. 2011). DOC/DON ratios in CWD runoff were declining with time for *Fagus* and *Picea* (data not shown), contradicting Kuehne et al. (2008) who reported increasing C/N ratios in solutes from CWD with increasing decomposition. The significant decline of DOC/DON ratios during the preceeding decomposition of CWD points to a preferential C mineralization in comparison to N in CWD.

1.4.5 DOC and DON net release from CWD is affected by forest management type and *Exploratory* (H 1)

The cumulative DOC net release for the three tree species *Fagus*, *Picea* and *Quercus* ranged from 3.5-98 g m^{-2} yr^{-1} (Figure 1.9). No significant differences in DOC net release were found between the three *Exploratories*. At the *Swabian Alb Exploratory*, no significant difference was found for DOC net release between the three tree species. At *Hainich* and *Schorfheide* DOC net release of *Fagus* and *Picea* was quite similar but significantly lower than from *Quercus*.

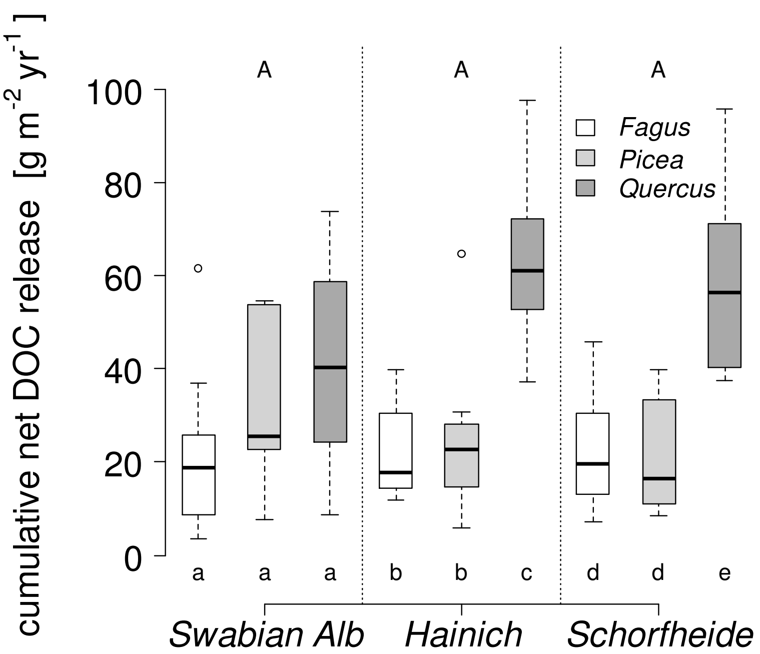

Figure 1.9: Cumulative DOC net release from CWD in the three *Exploratories*.

Referred to projected CWD log area in g m^{-2} with n = 9 logs per tree species. Significance is indicated by characters a-e for tree species and A for *Exploratory* obtained by an ANOVA using $\log_{10}$-transformed data.

The cumulative annual net DOC release was significantly higher for *Quercus* compared to *Fagus* and *Picea* (Figure 1.10).

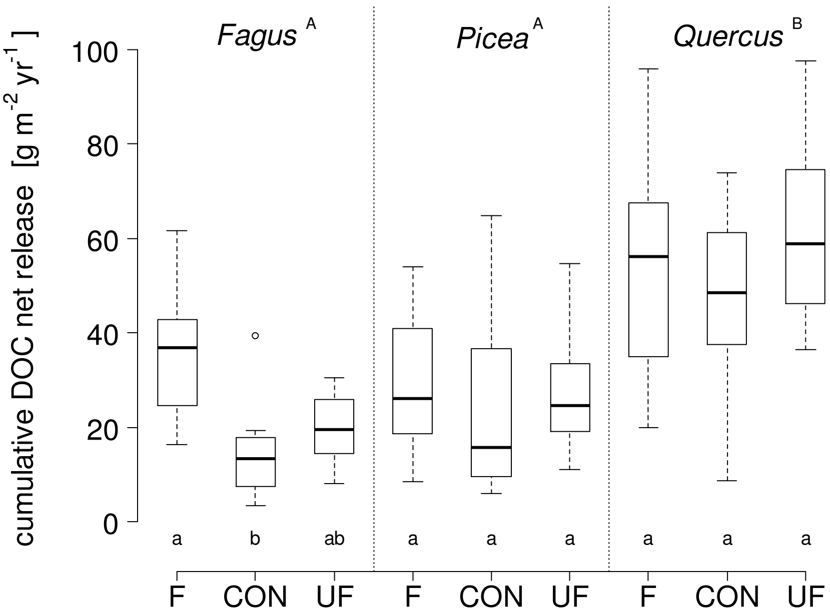

Figure 1.10: Cumulative DOC net release from CWD in different management types.

Referred to the projected CWD log area in g m^{-2} yr^{-1} with n = 9 logs per tree species and forest management type (F = "age class *Fagus*", CON = "age class conifers", UF = "unmanaged *Fagus*") including data for all three *Exploratories*. Significance is indicated by the characters a, b and A, B obtained by an ANOVA using log_{10}-transformed cumulative net release data.
Management type within one tree species: a, b ($p < 0.05$),
tree species: A, B ($p < 0.001$).

The influence of the management type on the cumulative DOC net release from CWD was only significant for "age class *Fagus*" (Figure 1.10) providing a higher DOC flux in runoff from *Fagus* CWD. Runoff from *Fagus* CWD in "unmanaged *Fagus*" plots was not statistically different from the other forest management types (F, CON).

The results for HIX_{em} of throughfall (Figure 1.6) indicated a higher availability of low molecular weight compounds (e.g.: carbohydrates) in throughfall of "age class *Fagus*" potentially influencing the decomposer community and the decomposition rate in CWD.

In general, the cumulative DON net release from CWD was similar in the 3 *Exploratories* amounting to 0-3.4 g DON m^{-2} yr^{-1} for single logs (Figure 1.11).

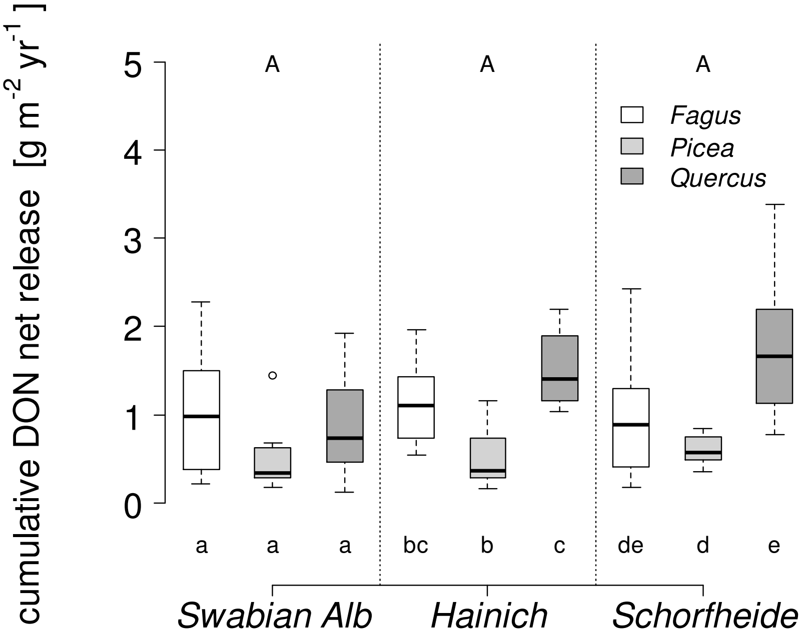

Figure 1.11: Cumulative DON net release from CWD in the three *Exploratories*.

Referred to the projected CWD log area in g m^{-2} with n = 9 logs per tree species. Significance is indicated by characters a-e for tree species and A for *Exploratory* obtained by an ANOVA ($p < 0.05$) using $\log_{10}$-transformed data.

Largest DON net release occurred beneath CWD of *Quercus* at *Hainich* and *Schorfheide*. At the *Swabian Alb Exploratory* DON net release from CWD was similar for all tree species. Since no significant effect of *Exploratories* (Figure 1.11) on the cumulative DON net release was found, only minor influence of the environmental conditions on the DON net release is indicated. The high DON net release in general was an unexpected finding, as a total increase of N stocks in CWD were reported with proceeding decay class (Holub et al. 2001) for coniferous species. This total increase of N stock in CWD however might be referred to other factors, like fungal translocation of N.

Only in case of *Fagus* CWD the cumulative DON net release was affected by forest management type (Figure 1.12). In “age class *Fagus*” significantly larger DON release resulted compared to “age class conifer” or “unmanaged *Fagus*” forest (Figure 1.12). The cumulative DON net release was found significantly lower for *Picea* than for *Fagus* and *Quercus*.

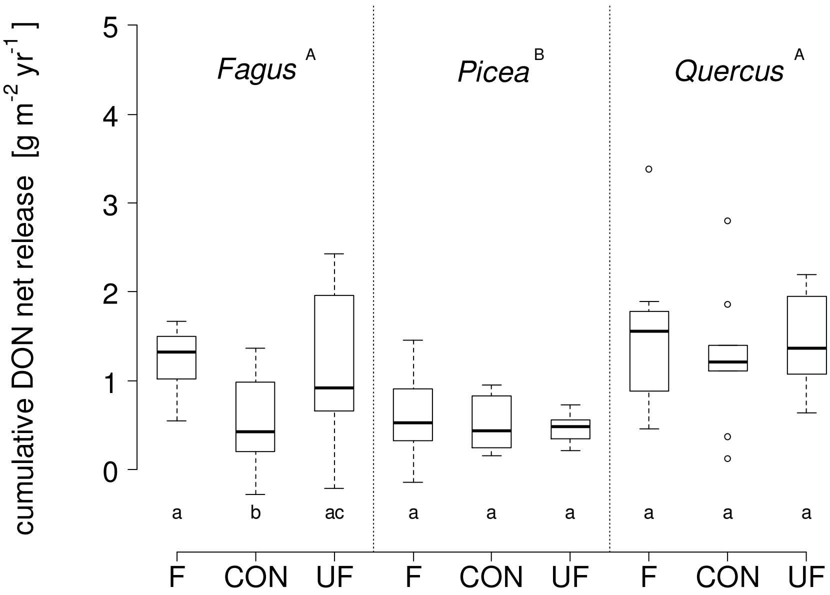

Figure 1.12: Cumulative DON net release from CWD in different forest management types.

Referred to the projected CWD log area in g m^{-2} yr^{-1} with n = 3 per tree species and forest management type (F = age class *Fagus*, CON = age class conifers, UF = unmanaged *Fagus*).
Significance is indicated by characters a, b, c ($p < 0.05$) for the management type within one tree species and A, B ($p < 0.05$) for tree species including all three *Exploratories* obtained by an ANOVA using log_{10}-transformed data of cumulative net DON release.

The effect of forest management type on the DOC and DON net release might be caused by the higher inputs of low molecular weight compounds in throughfall under *Fagus* (as mentioned before), but differences in the decomposer community in CWD might be also involved. While no information on species diversity of the CWD decomposer community is available from the literature, it seem likely that the decomposition process of *Fagus* CWD in *Fagus* forests is enhanced by the presence of a specific *Fagus*-associated fungal community.

Another explanation for the lower DOC and DON net release from *Fagus* CWD beneath coniferous canopy might be the lower solubility of DOC and DON from CWD due to significantly lower pH in throughfall, as the pH value was reported to be a more important factor influencing the solubility of DOC and DON than microbial activity (Andersson et al. 2000).

The effect of *Exploratory* and forest management type on the cumulative DOC and DON release was only found for *Fagus*. However, when considering single sampling dates in a linear mixed effect model ("*lme*" using the "*nlme*" and "*multcomp*" package in R), significant effects of management type ($p < 0.01$) on DOC and DON net release became obvious. In case of DOC, "age class *Fagus*" had a significantly higher net release compared to "age class conifers" for all three tree species. Furthermore, the net release under "age class *Fagus*" also tended to be higher compared to "unmanaged *Fagus*". No significant influence of *Exploratory* was found.

DON net release beneath "age class *Fagus*" and "unmanaged *Fagus*" was significantly higher compared to "age class conifers". In contrast to DOC, the model yielded a significant effect of *Exploratory* ($p < 0.01$) on the DON net release increasing in the order *Swabian Alb*, *Hainich* and *Schorfheide*. Significant higher DON net release occurred at *Hainich* and *Schorfheide* compared to *Swabian Alb* respectively.

One reason for the significant but contrasting effects resulting from the model with respect to the cumulative annual net release data was the increased number of replicates for sampling dates (even though included to the model as random factor representing repeated measurements) and the influence of seasonal dynamics that were excluded in the cumulative fluxes.

In conclusion, the hypothesis on the effects of management and *Exploratory* influencing the DOC and DON net release was supported.

1.4.6 The amount and composition of DOC released from CWD is tree species specific and affected by the initial chemical properties of bark and sapwood (H 2.1)

Due to large intraspecific variation no significant differences in DOC net release from CWD of deciduous and coniferous became obvious, but among the deciduous tree species substantial variation emerged (see manuscript chapter 2, Figure 2.1). Average DOC concentrations in runoff were largest under *Quercus* and *Prunus* and lowest under *Tilia* and *Fraxinus*. Accordingly, the net release of DOC from the logs was largest under *Prunus* and *Quercus* amounting to 56 and 60 g C m^{-2} projected log area yr^{-1}, respectively.

DOC net release was affected by the initial properties of wood and bark, as supported by the positive relation of soluble phenols in sapwood to DOC net release (see manuscript chapter 2, Table 2.4), but the DOC net release was not related to the C/N ratios in bark and sapwood. Thus, other factors seems to be responsible for the large interspecific variation of DOC net release, as species specific bark morphology, hydrophobicity, invasion of CWD decomposing arthropods and fungi (Stokland 2012). The HIX_{em} of DOC in runoff was also positively related to water soluble phenol content of the bark.

As other correlations were weak and not significant, the hypothesis 2.1 on the influence of initial chemical properties of bark and sapwood on DOC and DON release was only partly supported in case of phenols and the cumulative net DOC release in runoff.

1.4.7 The net release of DOC from CWD increases with precipitation (H 2.2)

Since the varying throughfall amounts at single sampling dates (range: 15-165 L m^{-2}) may affect DOC net release from CWD, the relation of throughfall to DOC net release in runoff was investigated (Figure 1.13).

The positive correlation between throughfall amount and DOC net release (Figure 1.13) was highly significant for all three tree species, but as indicated by the coefficients of determination, the relation is only weak, (more data are shown in manuscript chapter 2, table 2.2). Though the relation was weak, the hypothesis 2.2 was supported. The weak relation suggests that the DOC net release in runoff from CWD is likely more influenced by the previous precipitation events influencing wettability of bark and wood surfaces than by the throughfall amount at a single event. Furthermore, DOC net release might be limited kinetically by short contact times of throughfall solution with CWD and/or the temporal and spatial kinetics of throughfall infiltration in bark and sapwood tissue.

As studies on the relation of solute C and N fluxes from CWD to throughfall are scarce, the results were interpreted using forest floor publications. This study on CWD leachates confirmed to some extend the findings for DOC fluxes from forest floors (Park and Matzner 2003; Schmidt et al. 2011; Gielen et al. 2011; Borken et al. 2011), the latter being highly correlated to water fluxes. However, the poor correlation for CWD indicated generally different processes being active in CWD leaching as compared to forest floors.

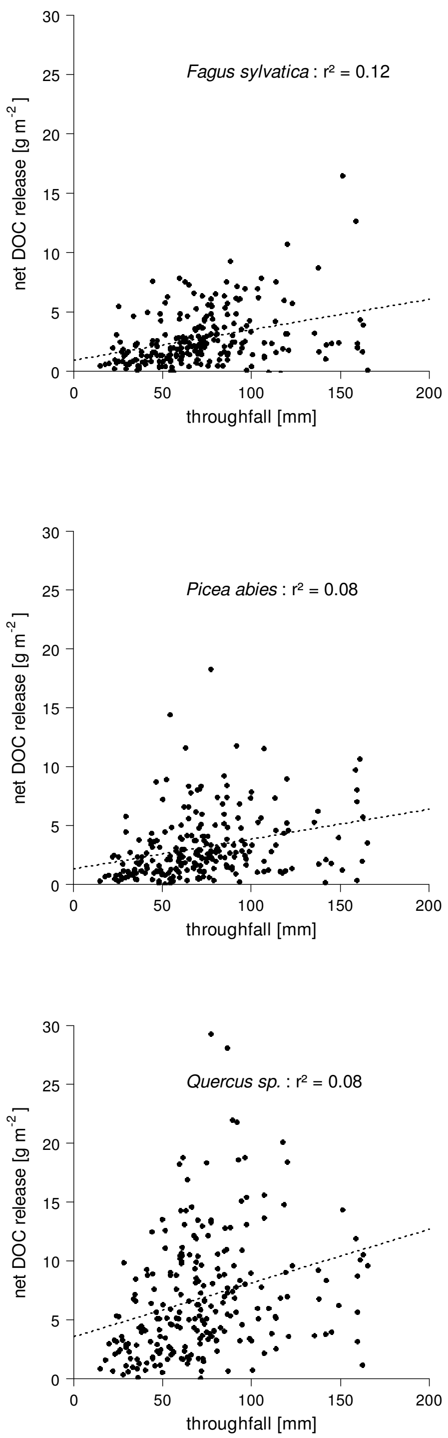

Figure 1.13: Relation of net DOC release from CWD of *Fagus*, *Picea* and *Quercus* at single sampling dates to throughfall amount in the growing season.

The data include all sampling dates, management types and *Exploratories* with $n = 234$ per species. The dotted lines represent a linear regression ($p < 0.001$) and the Spearman's coefficient of determination is given for every species.

1.4.8 The net release of DOC from CWD is larger in the growing than in the dormant season (H 2.3)

DOC net release from CWD log runoff had a tendency for larger release in the growing than in dormant season (see manuscript chapter 2, Figure 2.2). This was true for all tree species except *Pseudotsuga* thereby supporting the hypothesis 2.3. However, the differences in DOC net release were only significant for *Tilia*. The larger DOC net release during the growing season points to the temperature dependence of the processes involved in the DOC net release. The DOC release from soils was found temperature dependent (Gödde et al. 1996; Kalbitz et al. 2000) which might be due to the higher biological activity at higher temperatures. This dependency might be also true for DOC net release from CWD, since a strong correlation of CO_2 emissions from CWD to temperature exists (Wu et al. 2010; Herrmann and Bauhus 2013).

1.4.9 In the early phase of decomposition, CWD will act as a sink for mineral N from throughfall (H 3.1)

During the period of observation, the CWD of 13 tree species acted as a source of solute N, except for *Fagus* and *Pseudotsuga*. Dominant N form in CWD runoff was DON (manuscript chapter 3, Figure 3.2) with concentrations exceeding those in throughfall by far. Similarly, the cumulative annual N fluxes in runoff exceeded those of throughfall mostly more than twofold (manuscript chapter 3, Figure 3.3).

Hence the hypothesis 3.1 was not supported. In contrast to the expectation, that mineral N from throughfall might be immobilized by microorganisms, the opposite effect was observed. The release of N with DON as the dominating form was also reported in previous studies (Yavitt and Fahey 1982; Hafner et al. 2005). The source of mineral N in runoff from CWD remains unclear. Either, it was a product of microbial mineralization of DON in the sampling devices and thereby an artefact, or mineral N was leached after net mineralization of organic N in CWD. In addition to the mineralization of organic N in bark and sapwood, other sources for N in runoff might be the fungal translocation of N from the surrounding soil into the CWD or N_2 fixation (Schimel and Hättenschwiler 2007; Chigineva et al. 2011). The finding that CWD represents a source of solute N in the early phase of decomposition is contradictory to results published for decomposing stumps of pine, spruce and birch being a sink of N for a long time (Palviainen et al. 2010).

1.4.10 The N budget of the CWD is related to initial C/N ratio of bark and sapwood (H 3.2)

The net release of DON, NH_4-N and NO_3-N was not significantly related to the initial contents of soluble phenols and carbohydrates or the initial C/N ratios of bark and sapwood when comparing the 13 tree species and the hypothesis 3.2 was rejected. This is potentially caused by the large variation of these parameters, while only 3 replicates for each tree species were investigated and the sampling area for runoff was small in relation to the total CWD size.

Furthermore, other factors might be relevant for the observed variability in N budgets of CWD like the morphology of bark and wood tissue, infiltration time during precipitation events, hydrophobicity of surfaces, canopy structure and shade of the particular plot, or varying colonization by decomposers. The large variation of DOC/DON ratios might be influenced by these factors as no significant correlation of throughfall and temperature was observed (manuscript chapter 3).

1.4.11 The release of solute N from CWD is larger in the growing than in the dormant season and depends on the precipitation amount (H 3.3)

In contrast to the results for the seasonality of DOC net release discussed before in chapter 1.4.7, the DON net release was similar in the growing and the dormant season (manuscript chapter 3, Figure 3.4). The fact, that no significant relation of DON net release to temperature was found, points to other factors being mainly responsible for DON net release. No data on DON net release from CWD are available from the literature, but DON concentration in CWD leachate was reported to be rather independent from temperature (Hafner et al. 2005). The lack of seasonality in DON net release from CWD is contradicting with findings for DON net release in forest floor leachates (Morris 2009) being closely related to soil temperature and moisture. Furthermore, as DON concentrations in forest floor leachates were reported to be seasonally influenced (Cronan and Aiken 1985; Guggenberger 1992; Michalzik and Matzner 1999), solute N dynamics in CWD runoff seems to be driven by other factors compared to forest floor leachates. For mineral N the picture was opposite as the release of mineral N was larger during the growing season than during dormant season indicating the temperature dependency N net mineralization.

The negative budget of NH_4-N was often found for deciduous species in the growing season and subsequently NO_3-N release was increased during the growing season likely due to the preceeding nitrification. Hence the hypothesis on seasonality of the N release was only confirmed for NO_3-N and needs to be rejected for NH_4-N and DON.

During the period of observation only weak relation of throughfall amount and DON net release became obvious. This is supported by the results from Hafner et al. (2005) who reported DON concentrations beneath CWD being widely independent from precipitation amount.

The relation of throughfall amount in the snow free period (≈ growing season) to DON net release from CWD was quite weak, indicated by the low coefficients of determination ranging from -0.04 up to 0.54 (*Fagus*), but however significant for *Acer*, *Betula*, *Fagus*, *Picea* and *Pinus* ($p < 0.05$) (see manuscript chapter 3, table 3.1). No data on the relation of CWD N release to precipitation were available from the literature, but DON concentration in CWD leachate was unrelated to throughfall (Hafner et al. 2005).

Hence, the hypothesis on the N release being influenced by throughfall needs to be rejected, as solute N net release was only weakly related to throughfall amount. Summing up, other key drivers seem to be involved into the processes driving the DON net release like previous precipitation regime, throughfall infiltration in bark and sapwood, and the particular state of decomposition of CWD.

1.4.12 The mineralization rates of DOC from CWD differ between coniferous and deciduous tree species (H 4.1)

In case of the labile proportion of biodegradable DOC from CWD, mineralization rates k_1 ranged from 0.051-0.088 d^{-1} (manuscript chapter 4, table 4.2) and were not statistically different between coniferous and deciduous DOC. As different incubation times were applied in studies on DOC biodegradation ranging from only a few days (Marschner and Bredow 2002) to 365 day (Marschner and Kalbitz 2003; Qualls 2005;

Kalbitz et al. 2005), it is complicated to compare results from different studies. Since no other study on DOC from CWD is available, comparisons can only be made to DOC derived from forest floor percolates.

The mineralization rates found is this study corresponded well with results for DOC derived from Oe and Oa layers (Qualls and Haines 1992; Kalbitz et al. 2005; Kalbitz et al. 2005), whereas mineralization rates calculated for DOC in Oa layer leachates of spruce and beech were one magnitude order lower than those of CWD derived DOC (Kalbitz et al. 2003b).

The mineralization rates of the stable proportion of biodegradable DOC (k_2) were significantly larger for the coniferous DOC, even though the incubation time of the experiment was rather short. The observed DOC losses during incubation were consistently larger than the CO_2 production for all tree species, indicating the C assimilation into microbial biomass. Furthermore it can be assumed that an unknown proportion of DOC might be precipitated (Bowen et al. 2009).

Microbial assimilation might result in an overestimation of the stable proportion of biodegradable DOC due to the shorter turnover time of microbial biomass compared to the determined k_2 values. When the DOC loss would be attributed completely to microbial growth, the y_{stable} fraction of DOC would be diminished to 45-81% of the total DOC compared to 68-93% (see manuscript chapter 4, table 4.2). However, although the absolute mineralization rates of DOC can be challenged, the results of DOC mineralization suggest a rather recalcitrant proportion of DOC in CWD leachate with long mean residence times.

In conclusion, the hypothesis 4.1 was partly confirmed, since significant differences between coniferous and deciduous CWD derived DOC mineralization rates were found for the stabile proportion of DOC (k_2).

1.4.13 The mineralization rates of DOC from CWD are related to spectroscopic properties and carbohydrate content of DOC (H 4.2)

No significant effect of initial $SUVA_{280nm}$ was found on the biodegradability of DOC, even though it was significantly higher for the coniferous species ($p < 0.01$) indicating a larger aromaticity of coniferous DOC. The $SUVA_{280nm}$ and the HIX_{em} both increased significantly during the incubation pointing to an accumulation of aromatic recalcitrant DOC compounds (see chapter 4, Table 4.1, Figure 4.1).

Furthermore, the HIX_{em} did also not influence the mineralization rate, even though HIX_{em} was significantly lower for deciduous than for coniferous tree species ($p < 0.05$). In contrast the HIX_{em} and $SUVA_{280nm}$ were reported to correlate with the biodegradability of DOC derived from agricultural top soils and forest floors (Kalbitz et al. 2003b).

As the mineralization rates were also not related to the loss of carbohydrates (chapter 4, Table 4.1) the hypothesis 4.2 needs to be rejected. The largest proportion of CO_2 was produced by the mineralization of unknown DOC compounds. One reason for the low proportion of carbohydrates in the initial DOC prior to incubation might be that soluble carbohydrates has already been mineralized during the exposition of CWD to field conditions. Moreover, other unspecified compounds like tannins or proteins may influence the DOC mineralization.

Furthermore, the determination of DOC biodegradability was critically influenced by the pH value of the incubated solutions. Already small changes in pH around 6.4 led to large variation in the calculation of HCO_3^- and resulted thereby in uncertainties regarding the total mineralization rates. This is supposed to be considered in future experiments on the DOC biodegradability.

1.4.14 The DOC and DON released from CWD increases significantly the DOC and DON concentrations in soil solution underneath CWD (H 5)

The DOC concentrations in soil solution from mineral soil in 10 cm depth beneath CWD at five plots of the *Schorfheide Exploratory* were significantly higher beneath CWD compared to the control without CWD. This holds for all three tree species (Figure 1.14).

The DOC concentration in soil solution beneath CWD reflected the DOC concentration pattern in CWD runoff, as *Fagus* and *Picea*, had similar average concentrations in runoff (about 50 mg DOC L^{-1}) whereas the DOC concentrations in *Quercus* CWD runoff were about twofold higher (115 mg DOC L^{-1}). Accordingly the DOC concentration in soil solution beneath *Quercus* CWD was significantly higher than those beneath *Fagus* and *Picea* ($p < 0.05$, Figure 1.14).

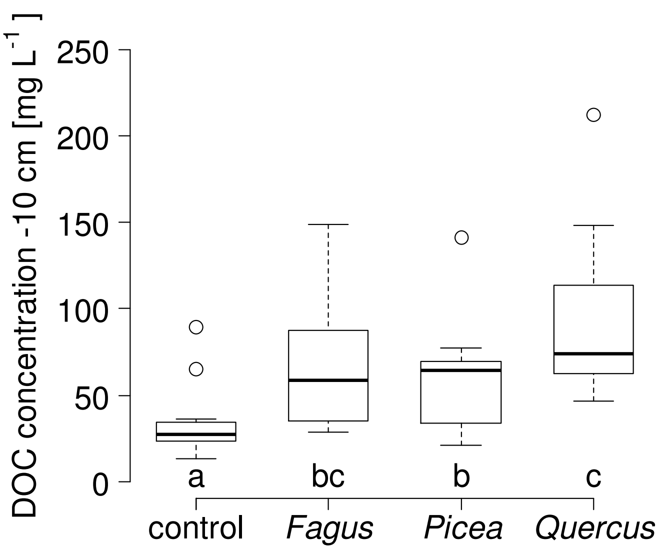

Figure 1.14: Boxplot of DOC concentration in 10 cm depth beneath CWD of *Fagus*, *Picea* and *Quercus* versus control.

With n = 12 for control and *Fagus*, n = 11 for *Picea* and n = 13 for *Quercus* with median and quartiles. Significance is indicated by the characters a-c ($p < 0.05$) obtained by an ANOVA.

The similar DOC concentration in soil solution beneath CWD and in runoff from CWD implied that only a minor amount of DOC was lost by retention or mineralization during the infiltration into the top soil. Only for *Quercus* CWD derived DOC the signal in soil solution was reduced noticeably compared to the averaged DOC concentration in runoff.

The sandy soil of the *Schorfheide* plots has a low capacity to sorb DOC especially in the podsolic A horizon. It seems likely that much of the DOC released from CWD and transported through the A horizon is sorbed in the B horizon comprising less organic matter and a higher content of Fe-oxides.

The incubation experiment on the biodegradation of DOC (chapter 4) showed that the proportion of recalcitrant DOC (y_{stable} as stable fraction of biodegradable DOC) was quite large (see manuscript chapter 4, Figure 4.2, Table 4.2) ranging from 68-93% of the initial DOC. Hence, the large DOC fluxes into the soil underneath CWD might contribute to increasing soil organic carbon pool through the sorption of DOC in to soil minerals (Kalbitz and Kaiser 2008). This is supported by findings of an increase of soil organic carbon stocks beneath *Fagus sylvatica* CWD in an andic soil (Pichler et al. 2013) and underneath *Eucalyptus* CWD (Goldin and Hutchinson 2013). In constrast, Kahl (2008) reported no significant increase of soil organic carbon beneath CWD of different age, although high DOC concentrations were present in the corresponding soil solution. The labile compounds of DOC might – however –also cause priming effects on recalcitrant proportions of soil organic matter (Kuzyakov 2010) and the net effect of DOC from CWD on soil organic matter remains to be determined in future studies.

As it was shown in figure 1.14, a significant C input from CWD into the mineral soil beneath was observed due to the DOC net release from CWD ranging from 15 up to 60 g m^{-2} yr^{-1}. Depending on the time scale and CWD decomposition dynamics, the DOC from CWD might increase the stock of C in the mineral soil. The stock of soil organic C in *Hainich* was reported at about 12 kg m^{-2} (Kindler et al. 2011) down to 60 cm depth. Assuming that about 70% (y_{stable}, see manuscript chapter 4) of the annual DOC input from CWD might be stabilized in the mineral soil by sorption to minerals or precipitation by metals (Scheel et al. 2007), it could contribute to a soil organic C accumulation ranging from 0.36-5.2 kg m^{-2} during 34-123 years (range of CWD decomposition time used for calculation, see chapter 1.4.15) underneath CWD. Compared to the total soil C stock of 12 kg m^{-2} at *Hainich* this might be a significant increase.

In order to extrapolate these potential accumulation rates to the ecosystem scale, the CWD coverage needs to be considered. The percentage of CWD coverage of the forest soil is rather low ranging from <1% in managed up to 10% in unmanaged forests (Krüger

2013). Hence the overall contribution of CWD to soil C stocks will be rather slow on a hectar base. For the *Hainich Exploratory* an average CWD carbon stock was calculated at 7.8 t C ha^{-1} (Mund 2004)˙ The estimation of soil C accumulation by CWD based on net release via leaching may account for 14-63 kg C t^{-1} CWD^{-1} ha^{-1}, assuming the total mass loss via leaching as described below in chapter 1.4.15 and 70% of the leached DOC proportion to be stable.

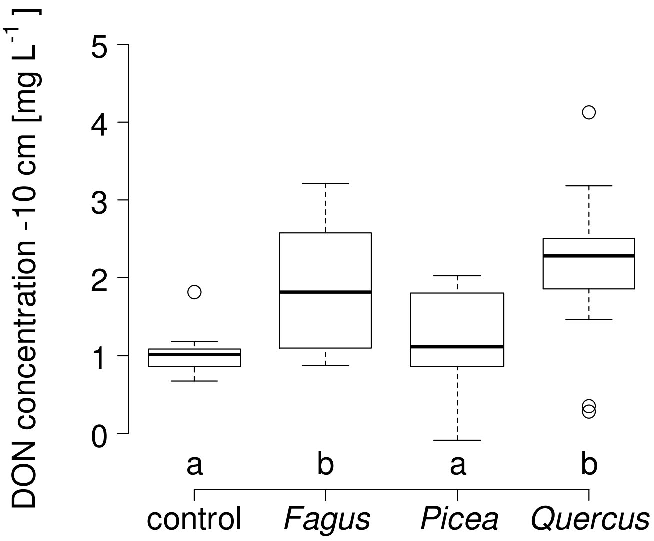

Figure 1.15: Boxplot of DON concentration in 10 cm depth beneath CWD of *Fagus*, *Picea* and *Quercus* versus control.

With n = 12 for control and *Fagus*, n = 11 for *Picea* and n = 13 for *Quercus* with median and quartiles. Significance is indicated by the characters a-b ($p < 0.05$) obtained by an ANOVA.

In case of DON, significantly higher DON concentrations were found in soil solutions beneath *Fagus* and *Quercus* CWD compared to the control without CWD (Figure 1.15).

The DON concentrations in soil solution collected beneath *Picea* CWD were not significantly higher than those of the control. The DON concentration found in mineral soil beneath CWD was in the same magnitude order as the flux weighted DON concentrations in CWD runoff ranging from 1.1-3.6 mg DON L^{-1} for all three tree species (see manuscript chapter 3, Figure 3.4) indicating only minor DON mineralization or retention after infiltration into the mineral soil beneath CWD.

The DON concentrations in mineral soil beneath CWD confirm the findings for DON concentrations derived from mineral horizons beneath CWD of birch, spruce and pine stands (Suominen et al. 2003) and northern hardwood stands (Fisk et al. 2002) but were one magnitude order higher than reported DON concentration in mineral soil beneath CWD in 30 cm of depth (Spears et al. 2003).

In conclusion, the hypothesis 5 of an imprint of DOC and DON inputs underneath CWD on soil solution DOC and DON can be confirmed at least for acid sandy soils. The DOC input into the soil beneath CWD might play a substantial role for C accumulation in soils underneath CWD since a substantial proportion of DOC derived from CWD is rather recalcitrant.

1.4.15 Relevance of DOC and DON release for CWD mass loss

During the early phase of decomposition, the C net release from CWD provides an annual C flux of 15 to 60 g m^{-2} yr^{-1} (manuscript chapter 2, Figure 2.1), representing a large and spatially distinct C flux infiltrating into the soil beneath CWD. This is in accordance with findings reported for a flux of DOC leached from CWD on a clear-cut area in North Carolina (Mattson et al. 1987) amounting up to 14.7 g C m^{-2} yr^{-1}.

While data on the mass loss of bark and sapwood were currently not available for the CWD investigated in this study, the quantification of the leaching contribution to mass loss of CWD is hampered. Combining average data for wood density from the literature with results from this thesis (see manuscript chapter 2), the total annual mass loss of CWD logs in form of leached DOC was tree species specific and accounted for 0.02-0.09% (range for the 13 tree species) of the total initial C mass. This is supported by findings for coniferous logs being exposed to decomposition in temperate rainforests. The contribution of mass loss of those logs by leaching amounted 0.02% yr^{-1} during the initial phase of decomposition (Schowalter et al. 1992).

Extrapolated for a total duration of the CWD decomposition of 100 years, the contribution of leaching to total mass loss may account for 2-9%. As *Fagus* CWD is reported to degrade to 95% within 34 years (Müller-Using and Bartsch 2009) the contribution to mass loss by DOC leaching would be 1.1%. If for *Picea* and *Pinus* CWD decay times to 95% of 123 and 42 years are assumed (Herrmann and Prescott 2008) the predicted contribution of DOC release to mass loss would be 6.7 (*Picea*) and 1.9% (*Pinus*). These estimates are supported by Spears et al. (2003), who estimated a leaching contribution to total C mass loss of CWD at 5% of the total C mass during 87 years of decomposition.

In case of DON, 0.2-2.2% (range of 13 tree species) of the initial N content of the logs was lost during one year in the early phase of decomposition. Extrapolated to the similar decay time as described above, the contribution of DON leaching to 95% of initial N mass loss in CWD amounted from 10% (*Fagus*) to 90% (*Pinus*) and 92% (*Picea*).

This is contradicting to findings published by Laiho and Prescott (1999), who published increasing N pools in CWD of pine logs after 14 years of decomposition. But no change in spruce logs and a loss of 30% of initial N content for fir logs was also observed. CWD of decay class 1-3 of red spruce, Fraser fir and yellow birch represented a net source of N during decomposition (Creed et al. 2004b), supporting the results of this thesis. An explanation for the varying N budgets of CWD might be the different state of decomposition of the logs or differences in fungal translocation of N into CWD from the soil or different N_2 fixation rates.

However, for the estimation of the contribution of DOC and DON to the initial CWD mass loss the increasing leaching amounts with continuing decomposition as reported by Harmon et al. (1986) was not considered due to the rather short period of observation compared to the total time of CWD decay. Hence, this limitation may lead to a rather conservative estimation of the leaching contribution to CWD mass loss.

1.4.16 Shortcomings of instrumentation and methods

Regarding the large variation of the initially measured parameters of wood and bark tissue of the CWD, it should be considered that the sampling method for runoff in this study has a shortcoming due to the fact, that runoff solution was collected only at a relatively small section of the logs (10 cm of the PVC gutters) causing strong variation of the findings for single tree species. From other studies it is known, that intra-specific wood density variations can occur depending on the environmental conditions during growth, distance from the crown and cambial age (Lei et al. 1996; Gartner et al. 2002; Swenson and Enquist 2007). This variability in wood properties potentially affects also the degradation processes and thereby DOC and DON release dynamics.

Furthermore, throughfall amounts can vary largely on small scale beneath the canopy cover, being influenced by phenology, diversity and age of the canopy as well as microclimatic factors (e.g.: Levia and Frost 2006). Throughfall was only sampled at one position per plot during this project. This does not reflect the variation of throughfall amount and solutes at single logs. On an annual scale, the absolute variation in throughfall amount was from 433 to 684 mm for the 8 comparable *Fagus* sites at *Hainich*. The corresponding DOC input by throughfall varied from 3.8-5.5 g m^{-2} yr^{-1}. Although those throughfall inputs were rather low with respect to the high net release from CWD of *Quercus* or *Prunus*, they may cause an potential error of the DOC net release from CWD of about 20-25% concerning tree species with low DOC net release (<20 g m^{-2} yr^{-1} like for *Fraxinus*, *Populus* and *Tilia,* see manuscript chapter 2, Figure 2.1).

In this study, the CWD degradation was in early phase. Decomposition and break down of wood and bark tissue likely does not follow similar kinetics for the 13 investigated tree species (Mattson et al. 1987; Herrmann and Prescott 2008; Müller-Using and Bartsch 2009; Zell et al. 2009). Hence, varying degree of decomposition can be expected for single species although the CWD was exposed at the same time. Therefore it can be assumed, that inter-specific differences may occur due to different colonization stages of microbial and fungal community. This is also supported by the observation of different fruit bodies of fungi (personal observation of the author) and furthermore by the variable fungal colonization (Dickie et al. 2012; Ottosson 2013).

1.5 Conclusions and outlook

This study highlighted the significant imprint of CWD on forest soils influencing the spatial patterns of soil C accumulation and soil C turnover. Already in the early phase of decomposition, CWD of different tree species represents a “hotspot” of DOC and N net release providing substantial C and N inputs into the soil beneath CWD.

Only weakly related to initial chemical properties of wood and bark tissue, DOC net release was tree species specific and - surprisingly - only little affected by throughfall amount. The quality of CWD derived DOC was tree species specific and potentially influencing the soil beneath CWD in different ways.

The variation of DOC net release was only insufficiently explained by the determined wood properties and environmental factors. Since the biodegradability of CWD derived DOC was generally low due to a high proportion of rather recalcitrant DOC attributed to the field exposition of CWD for several years, CWD derived DOC may contribute to a substantial C sequestration beneath CWD depending on time scale.

The forest management type influenced DOC and DON net release from CWD significantly and an effect of *Exploratory* was only found for DON net release.

Similarly to the DOC net release, the DON net release was not significantly related to the initial C/N ratio of sapwood. Opposite to DOC, no significant seasonality was found for DON net release. As the relations of DON net release to temperature and throughfall were weak, the drivers inducing the large intra- and interspecific variation and temporal patterns deserve future research.

For future experiments, the influence of fungal and arthropod invasion should be considered and analyzed in combination with DOC net release as well as the relative contribution of bark and sapwood to the DOC net release should be taken into account. Furthermore, a combined sampling of CWD runoff and soil solution beneath CWD is suggested in order to determine the fate and soil imprint of CWD derived dissolved organic C and N. The use of larger CWD runoff sampling devices as they were used for this thesis is recommended promising lower intra specific standard deviations. Future research might also consider structure of forest canopy in relation to DOM release from CWD, to study the influence of forest management type on DOC and DON release in more detail.

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MANUSCRIPTS

2. Quantity and quality of dissolved organic carbon released from coarse woody debris of different tree species in the early phase of decomposition

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2.1 Abstract

The release of dissolved organic carbon (DOC) from decomposing coarse woody debris (CWD) may result in large DOC inputs to the forest soil. Here we investigated the influence of tree species on the amounts and quality of DOC from CWD in the early phase of decomposition.

Logs from 13 tree species were exposed in winter 2008/2009 on the soil in a temperate *Fagus sylvatica* L. forest in Germany. Runoff solutions were periodically collected for 17 months from June 2011- November 2012 underneath logs and the net release of DOC was calculated for each log on an annual scale. The quality of DOC was assessed by its contents of soluble phenols, hydrolysable carbohydrates and by spectroscopic properties. Prior to field exposure of CWD, bark and sapwood were analyzed for their initial element content and water extractable DOC.

Concentrations of DOC in log runoff were much (3 to 10 times) higher than in throughfall for all tree species. Average concentrations in runoff were largest under *Quercus* and *Prunus* and lowest under *Tilia* and *Fraxinus*. Accordingly, the net release of DOC from the logs was largest under *Quercus* and *Prunus* amounting to 60 and 56 g C m^{-2} projected log area yr^{-1}, respectively. The DOC net release for the tree species was positively related to the initial phenol content of sapwood, but not to C/N ratios in bark and sapwood. On a monthly to annual scale, the amount of precipitation had only a small influence on the net release of DOC, but the DOC net release was larger in the growing than in the dormant season. The concentrations of hydrolysable carbohydrates in log runoff were largest for *Prunus* and *Quercus* and lowest for *Fraxinus* and *Tilia*. Average concentrations of total phenols in runoff ranged from about 2 to 7 mg L^{-1} with *Quercus*, *Fraxinus*, *Betula*, *Picea* and *Larix* representing the upper range. Spectroscopic properties indicate that the DOC leached from logs is microbially modified and oxidized in comparison to DOC in initial bark and wood extracts.

Our results suggest that the DOC release from CWD is tree species specific in terms of quantity and quality and causes huge DOC fluxes to the soil underneath CWD.

2.2 Introduction

The mass loss through decomposition of coarse woody debris (CWD) is driven by respiration, fragmentation and leaching of substances (Harmon et al. 1986). In forest floor leachates underneath *Pseudotsuga* logs, concentrations of dissolved organic carbon (DOC) up to 250 mg L^{-1} were found (Spears and Lajtha 2004) and up to 300 mg L^{-1} in log runoff (Hafner et al. 2005), exceeding the DOC concentrations in the throughfall by far. Kuehne et al. (2008) found DOC concentrations in runoff from *Fagus* logs increasing with decomposition stage from 28 to 118 mg L^{-1}. DOC concentrations in forest floor leachates also doubled after addition of shredded wood to the soil surface. (Lajtha et al. 2005). Large DOC inputs into the soil underneath CWD might cause accumulation of soil organic matter (Kalbitz and Kaiser 2008; Kahl et al. 2012; Goldin and Hutchinson 2013) as well as changes in soil microbial communities (Brant et al. 2006; Yurkov et al. 2012).

While drivers of CWD decomposition have been intensively studied (Harmon et al. 1986; Harmon et al. 2000; Weedon et al 2009; Herrmann and Bauhus 2013), those for DOC release from CWD have not been investigated in detail. The release of DOC from CWD under field conditions seems to increase with decomposition stage of CWD (Hafner et al. 2005; Kuehne et al. 2008) which is different to the DOC release from leaf and needle litter being much larger from fresh than from decomposed litter (Don and Kalbitz 2005). In the case of forest floor percolates under different tree species, DOC release from the forest floor increased with C/N (Michel and Matzner 2002; Kindler et al. 2011; Borken et al. 2011). Based on the large amount of aromatic moieties in DOC, the decomposition of lignin is seen as a major source for DOC from leaf and needle litter (Kalbitz et al. 2006). Hence, the wide C/N ratio and the high lignin content of CWD suggest large rates of DOC release during CWD decomposition.

The amount and composition of DOC from CWD may differ with tree species since the lignin of coniferous wood is primarily formed by guaiacyl-units combined with low amounts of p-hydroxy-phenyl-units, whereas deciduous wood is formed by syringyl and guaiacyl units in a 1:1 ratio with traces of p-hydroxyphenyl-units (Wong 2009). Moreover, coniferous wood generally decomposes slower than deciduous and wood of narrow C/N decomposes faster than wood of wide C/N (Weedon et al. 2009). Tree species specific decomposition rates likely also influence the DOC release.

Besides decomposition stage and wood properties, the environmental conditions should also be important for the DOC release from CWD. DOC fluxes in forest floors were generally shown to increase with precipitation at the monthly to annual scale (Park and Matzner 2003; Schmidt et al. 2011; Gielen et al. 2011; Borken et al. 2011). The respiration of CO_2 from CWD and hence the decomposition rate was correlated to temperature (Herrmann and Bauhus 2013) suggesting also a larger DOC release in the growing season than in the dormant season. However, relations of DOC release from CWD to precipitation and seasonality have not been reported so far.

Here, we investigated the release of DOC from CWD of 13 temperate forest tree species in the early stage of decomposition. We hypothesized that (i) the amount and composition of DOC released from CWD is tree species specific and affected by the initial chemical properties of bark and sapwood, (ii) the net release of DOC increases with precipitation and iii) the net release of DOC is larger in the growing than in the dormant season.

2.3 Materials and methods

2.3.1 Study site and sampling

Freshly cut logs of 30-40 cm diameter and 4 m length from 13 tree species of the temperate forest zone (*Acer sp., Betula sp., Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, Larix decidua, Picea abies, Pinus sylvestris, Populus nigra, Prunus avium, Pseudotsuga menziesii, Quercus sp., Tilia sp.*) were obtained from the forest authority of the Federal State of Thuringia, Germany.

Logs were exposed to the forest soil in late 2008 until beginning of 2009 in the *Hainich* forest area (Central Germany, 51°38’N, 10°78’E), in the frame of the so-called *Biodiversity Exploratories*, a priority program of the Deutsche Forschungsgemeinschaft (DFG) (Fischer et al. 2010). A set of 13 logs (1 per species) was exposed each in 3 spatially separated beech (*Fagus sylvatica* L.) forest sites of a “selection forest” management type with wide age distribution of beech trees. In total we collected runoff from 39 logs. The experimental plots are located between 420 and 520 m a.s.l. and the average annual temperature is 6.5-8.0 °C.

The soil has developed from loess deposits over calcareous bedrock and is classified as Luvisol (WRB 2006). The forest floor is mull type with an Oi layer and a shallow

(< 1 cm) Oe layer. The averaged cumulative throughfall during the 17 months observation period was 536 mm.

2.3.2 Initial bark and wood properties

A disc of 5 cm was cut from each log before exposure to the soil. After drying, sapwood chips were obtained by drilling across several year rings starting from the youngest year ring towards the center. Subsamples of bark and the sapwood chips were milled by ball mill (MM2, Retsch GmbH, Haan, D). The C and N content was analyzed using a CN analyzer (Vario MAX, Elementar, Hanau, D). To investigate the water soluble fractions, subsamples of bark and sapwood were chopped by a cutting mill (SM200, Retsch GmbH, Haan, D) to small pieces of < 3 mm in diameter. Those were extracted with water (ratio of wood chips to water: 1:15) at 20 °C for 24 hours under continuous overhead shaking and concentrations of hydrolysable carbohydrates, water soluble phenols and spectroscopic properties of DOC (Fourier-transform infrared spectra, FTIR) were determined in the extracts.

2.3.3 Runoff from logs and throughfall

Runoff from logs was collected about 2 years after the exposure of the logs and lasted from July 2011 through November 2012. Small gutters (10 × 30 cm) were installed beneath the logs. Solutions were sampled in 2.0 L bottles which were located in buckets in the mineral soil next to the logs, avoiding exposition to high temperatures and light. All runoff and throughfall samples were stored in the laboratory at 2 °C and filtered using Millipore water prewashed cellulose acetate filters (0.45 µm, Whatman OE 67, GE Health Care Europe, Freiburg, D). The filtrates were kept frozen until DOC concentrations were analyzed by elemental analysis (N/C 2100 Analyzer, Analytik Jena, D). Furthermore, the pH and conductivity of the solutions were determined.

At each plot, throughfall amount (sampler type: RS200, UMS, Munich, Germany) and concentrations of DOC in throughfall were determined at the same intervals as for the runoff. Depending on the amount of throughfall, runoff samples were taken periodically within 1 to 2 weeks after major precipitation events. The sampling period was composed of 13 sampling dates.

2.3.4 Flux calculations and net release

Fluxes of DOC with runoff from each log were calculated by multiplying the DOC concentration in runoff at a single sampling date with the respective throughfall amount and referred to m^{-2} projected log area. Evaporation from logs under the forest canopy is considered negligible at the annual scale. Net release of DOC from logs results from the difference of DOC flux in runoff minus DOC flux in throughfall.

2.3.5 Hydrolysable carbohydrates

Carbohydrates in log runoff and in the initial wood extracts were analyzed following the procedure of Johnson and Sieburth (1977) and Johnson et al. (1981). In short, freeze dried DOC samples were hydrolyzed with 12M H_2SO_4. The resulting carbohydrate monomers were reduced to sugar alcohols (alditols) using potassium borohydride (10%). After complexation by 3-methylbenzthiazolinon-2-hydrazon (MBTH reagent), the carbohydrate content was detected spectrophotometrically at 635 nm (UV 1800, Shimadzu).

2.3.6 Soluble phenols

The content of water soluble phenols was determined using the Folin-Ciocalteu-method (Box 1983). Samples of log runoff and initial water extracts from bark and wood were prepared after dilution to 10 mg C L^{-1}. For the detection of phenols, Folin-Ciocalteu-reagent was applied at a ratio of 5:0.75:0.25 (sample:sodium carbonate:Folin-Ciocalteu reagent, Box 1983). After 60 minutes of incubation in the dark the phenols were detected at a wavelength of 730 nm (UV 1800, Shimadzu, Duisburg, D).

2.3.7 Humification index, specific UV absorption and FTIR spectra

Fluorescence emission spectra were recorded (SFM 25, BIO-TEK Instruments, Bad Friedrichshall, D) for runoff samples at 4 sampling dates and a humification index (HIX) of DOC was calculated according to Zsolnay (1999). Furthermore, the specific UV absorbance (UVIKON 930, BIO-TEK Instruments, Bad Friedrichshall, D) at 280 nm was determined in runoff samples for 4 sampling dates. UV absorbance at 280 nm is an estimate of aromaticity of DOC (McKnight et al. 1997; Kalbitz et al. 2003).

FTIR spectroscopy is a widespread method to analyze organic matter composition. In FTIR spectra, absorption bands at distinct wave numbers indicate the presence of functional groups with known chemical compositions and properties. The intensity of the absorption bands depends on the amount of absorbing groups (Günzler & Böck, 1990). The intensity of the aliphatic (CH) absorption band in FTIR spectra was used to estimate the content of hydrophobic while that of the carbonylic (C=O) absorption band can be used to estimate the content of hydrophilic groups within OM. The ratio between the CH and C=O band (CH/C=O) could be used to estimate the potential wettability of OM (Ellerbrock et al. 2005). The hydrophobic CH groups show absorption bands at 2920 cm^{-1} (asymmetric stretch) and at 2860 cm^{-1} (symmetric stretch) (Capriel et al. 1995). Here, both bands were combined and denoted as absorption band CH. For the hydrophilic C=O-groups, absorption bands at 1640-1615 cm^{-1} and at 1740-1720 cm^{-1} were combined (Günzler and Böck 1990; Celi et al. 1997), here denoted as absorption band C=O. The most intense band at 1100 to 1050 cm^{-1} was used to consider the amount of C-O-C groups. The heights of the absorption bands were computed using BioRad® software.

For FTIR analysis, the filtrates were freeze dried. Spectra of log runoff samples and of initial water extracts of wood and bark were recorded with a BioRad FTS 135, Munich, D. The potassium bromide (KBr) technique (Celi et al. 1997) was applied to obtain absorption spectra of organic matter in a range of wave numbers between 4000 and 400 cm^{-1}. Here, 0.5 mg of freeze dried DOC was mixed with 80 mg KBr and finely ground in an agate mortar. The resulting mixture was dried for 12 hours over silica gel in a desiccator to standardize the water content. For all spectra, 16 scans were carried out at a resolution of 1 cm^{-1} (Ellerbrock et al. 1999).

2.3.8 Statistics

All statistical analysis was conducted using R 3.0.1 (R Core Team 2013). For testing significances, DOC net release was log-transformed ensuring normal distribution. After an ANOVA, significances were tested using the Tukey post-hoc test. Seasonality of net release was tested using a t-test. Homogeneity of variances was tested using the Levene's test.

2.4 Results

2.4.1 Initial bark and sapwood properties

The C/N ratios in sapwood were generally higher than in bark (Table 2.1). There was a huge variation in initial wood and bark parameters among the 13 tree species, but also within species as indicated by the standard deviations. The average C/N ratio of sapwood ranged between 242 (*Larix*) and 1569 (*Pinus*) and for bark from 38 (*Carpinus*) to 197 (*Pinus*). C/N ratios were generally larger in coniferous species than in deciduous species. Contents of water soluble phenols in sapwood ranged from 0.03 (*Fagus*) to 0.49 (*Quercus*) mg g^{-1} and from 0.31 (*Fagus*) to 1.76 (*Fraxinus*) mg g^{-1} in bark. Sapwood from ring porous deciduous trees had the highest phenol contents. The content of hydrolysable carbohydrates in sapwood ranged between 0.14 (*Quercus*) to 1.28 (*Tilia*) and in bark from 0.11 (*Quercus*) to 0.77 (*Larix*) mg g^{-1}. The ring porous tree species had the lowest content of hydrolysable carbohydrates in sapwood.

2.4.2 DOC concentrations and net release

The DOC concentrations in the runoff from the logs were always much larger than in throughfall (Fig. 2.1). The average DOC concentration in runoff ranged between 30 (*Fraxinus*) and 130 mg C L^{-1} (*Quercus*). There were no general differences in the concentrations and net release of DOC between coniferous and deciduous tree species. However, concentrations and net release for the coniferous species were rather similar, while large differences were found for deciduous species. For net release, significant differences ($p < 0.05$) were found for the following couples of tree species: *Betula-Quercus*, *Fagus-Quercus*, *Fraxinus-Prunus*, *Fraxinus-Quercus*, *Larix-Quercus*, *Picea-Quercus*, *Populus-Quercus*, *Tilia-Quercus*.

The largest cumulative net release of DOC was found for *Prunus* and *Quercus* logs, the lowest net release for *Fraxinus, Tilia* and *Populus* (Fig. 2.1).

The throughfall amount throughout the single sampling intervals of the snow free period ranged from 10 to 170 mm. This large range had only a minor effect on the net release of DOC. The coefficients of determination for periodic DOC release and throughfall amount ranged from 0.02 to 0.33 indicating only weak relations (Table 2.2).

Those were however significant ($p < 0.05$) for *Betula*, *Fagus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga* and *Quercus*.

When normalized by the amount of precipitation, the DOC net release per mm throughfall was 14-189% larger during the growing than during the dormant season (Fig. 2.2). This pattern was obvious for all tree species (except *Pseudotsuga*), however the seasonal differences were statistically significant ($p < 0.05$) only for *Tilia*.

2.4.3 DOC quality

The concentrations of hydrolysable carbohydrates was largest in runoff samples from *Prunus* and *Quercus* (9.4 and 7.4 mg L^{-1}, respectively) and lowest under *Fraxinus* and *Tilia* logs (<3 mg L^{-1}) (Table 2.3). While the absolute concentrations of carbohydrates was rather variable, the contribution of carbohydrates to total DOC was similar for all tree species in the range of 7 to 11%.

Average concentrations of total water soluble phenols in the runoff samples ranged from 3 to 10 mg L^{-1} with those from *Prunus*, *Tilia*, *Fraxinus*, *Quercus*, *Betula*, *Larix* and *Picea* in the upper range, and those from *Fagus*, *Pseudotsuga*, *Pinus* and *Acer* in the lower range (Table 2.4). The contribution of phenols to total DOC ranged from 6% (*Fagus*) to 27% (*Fraxinus*).

The humification index (HIX) of DOC in runoff was for all species larger than in throughfall, but also differed with tree species (Table 4). Most humified DOC (largest HIX) was observed under logs of *Quercus*, *Carpinus* and *Larix* whereas those from *Pinus* logs had the lowest HIX. The aromaticity of DOC as indicated by SUVA 280 nm was larger in runoff than in throughfall for all species. Differences between tree species were small and not significant.

The intensity of the FTIR absorption bands indicates the relative amount of the corresponding functional groups. For most tree species the C=O/COC ratio was larger in the runoff samples than in the initial bark and sapwood extracts (Fig. 2.3). However, for *Fraxinus*, *Quercus sp.* and *Acer* the ratios were similar to those in extracts from the corresponding barks. For all tree species the CH/C=O ratio was lower in the runoff samples than in bark and sapwood extracts. The differentiation of both ratios between bark/wood extracts and runoff samples was largest for coniferous tree species.

The cumulative DOC release from CWD of the 13 tree species was positively related to the initial sapwood content of water soluble phenols (Table 2.4). Furthermore, the HIX of DOC in runoff was positively related to the water soluble phenol content of the bark while phenols in runoff were not. All other relations of DOC in runoff to initial wood and bark properties were weak and non significant.

2.5 Discussion

2.5.1 DOC release from CWD

The concentration range of DOC in runoff from the logs observed in our study corresponds to the range observed in past studies (Hafner et al. 2005; Kahl 2008; Kuehne et al. 2008). The average DOC concentrations were 5 to 10 times higher than in throughfall, emphasizing CWD as hotspot for DOC inputs to forest soils, even in the early stage of decomposition. DOC release from CWD is supposed to increase with decomposition stage (Kuehne et al. 2008).

There was no significant difference in net DOC release between coniferous and deciduous logs while the differences between single deciduous tree species were substantial. The initial properties of wood and bark affect the net DOC release, as the DOC release was positively related to initial content of soluble phenols in sapwood, but not to C/N ratios being generally larger in coniferous than in deciduous species. These differences in C/N ratios between coniferous and deciduous species were also found for leaf litter in a set of similar tree species (Hobbie et al. 2006). However, the observed relation of DOC release to initial soluble phenols was poor and other factors seem to contribute to interspecies variation, like species specific bark morphology and hydrophobicity, invasion of wood decomposing arthropods and fungi (Stokland 2012).

The intra-species variation of DOC release from the 3 species replicates was also large as indicated by standard deviations. The reasons for intra-specific variations remain speculative. The invasion of decomposers as well as variations of chemical composition of bark and wood between single logs of one species and small scale heterogeneity of throughfall inputs at the sites might be involved. In this field study we also cannot quantify for single logs how much of the runoff solution was in contact with bark and/or sapwood. Differences in flow paths of water on the logs might add to the variability of

DOC release within single species. The intraspecific variation might partly be caused by the small collectors. For future studies we recommend samplers covering a larger area of the logs.

The contribution of DOC net release to the C loss of CWD in our study can only roughly be calculated, since data of mass loss for bark and the outer part of the sapwood are not available. In case of *Fagus*, *Picea* and *Quercus*, the DOC net release amounted to about 0.7 (*Fagus*) 0.9 *(Picea)* and 1.6 (*Quercus*) % yr^{-1} of the total initial C stock in the outer 5 cm sapwood as a standardized volume. The C stock was estimated based on species specific density and C content of the sapwood. If the total log is considered, the contribution of DOC to mass loss will be smaller. However, we consider our estimate of DOC contribution to mass loss rather conservative, since an unknown proportion of DOC leached from the logs might have been mineralized to CO_2 in the samplers prior to filtration and analysis. We are not aware of a published study on the kinetics of microbial use of DOC leached from CWD and thus cannot estimate the proportion of labile DOC being not accounted for. In the case of forest floor extracts from Oa horizon the proportion of DOC mineralized in solution during in the first few days of an laboratory incubation at 20 °C was around 15% but this proportion was much higher for extracts from Oi horizons (Kalbitz et al. 2005).

The large amounts of DOC infiltrating the soil for many years might cause the accumulation of soil organic matter underneath CWD (Kalbitz and Kaiser 2008). The quality of DOC, especially its stability against microbial decay prior and after sorption to mineral surfaces is decisive and differences between tree species can be expected: The humification index (HIX) was shown to be a predictor for DOC stability against decomposition (Kalbitz et al. 2005). Hence, DOC with a high HIX, like DOC from *Quercus*, *Carpinus* and *Larix* should have a higher potential for accumulation in the soil organic matter pool than DOC from other tree species. Studies on soil organic matter changes under CWD are rare and this aspect warrants future research. Kahl et al. (2012) did not find an increase of soil organic matter content in the upper mineral soil underneath *Fagus* logs exposed for 8 to 16 years. In contrast, larger content of C and N as well as lower pH in the upper mineral soil were found underneath *Eucalyptus* CWD (Goldin and Hutchinson 2013). After experimental addition of shredded wood to the soil surface, Laitha et al. (2005) also suggested increased retention of wood derived DOC in forest soils.

The rates of net DOC release from the logs were only weakly related to precipitation amounts at a monthly to annual time scale. This is in contrast to findings for DOC fluxes in forest floor percolates (Park and Matzner 2003; Schmidt et al. 2011; Gielen et al. 2011; Borken et al. 2011), those fluxes being tightly correlated to water fluxes. The conditions preceding the precipitation events (previous leaching rates, water content of the bark/sapwood, temperature, wettability of surfaces) seem to be more important for the DOC net release than the actual precipitation. On top, the net DOC release might be kinetically restricted by the short contact time of throughfall water with CWD and by slow diffusion of DOC in the bark and sapwood tissue into the runoff solution.

The DOC net release was larger in the growing than in the dormant season, which points to the temperature dependence of the biological and physical processes involved. Temperature dependency of DOC release from soils is a well known phenomenon (Gödde et al. 1996; Kalbitz et al. 2000) and mostly attributed to dynamics of microbial activity. This is likely also true for DOC release from CWD as the CO_2 respiration from CWD is tightly correlated to temperature (Herrmann and Bauhus 2013).

2.5.2 DOC quality

The DOC quality in runoff from CWD was found tree species specific with huge variation of spectroscopic properties, phenol and carbohydrate contents. The carbohydrate and phenol concentration in runoff from logs of different tree species were not related to the initial carbohydrate and phenol content of bark and sapwood, indicating that the DOC in runoff from CWD logs does not primarily result from soluble compounds leached out of sapwood or bark, but result from metabolic processes. The collection of runoff started about 2 years after exposure of the logs and an unknown proportion of the initial carbohydrates and phenols in bark and sapwood might have been leached already. This is to be expected for soluble carbohydrates which are easily mineralized, but not for phenols being more recalcitrant. Hence, DOM in runoff from the logs seems to be largely modified by microbial processes towards the formation of humic substances which integrates phenols into macromolecules (Stevenson 1994). This is supported by the humification index of runoff being positively related to the phenol content of bark while phenol content of runoff was not. The higher C=O/COC and lower CH/C=O ratios in runoff samples than in the initial wood/bark extracts further supports the microbial modification by re-synthesis and decomposition of the initial water soluble compounds before leaching. While this is likely, the changing ratios can also be caused by selective leaching of specific compounds before the start of runoff measurements. The change in C=O/COC and CH/C=O ratios between runoff and initial wood/bark extracts seems to be most relevant for coniferous species as the differences of the ratios were larger than for deciduous tree species. The uniformity of the FTIR spectra of the runoff samples from *Larix*, *Picea*, *Pinus*, and *Pseudotsuga* logs (data not shown) also suggested a higher similarity in functional groups in DOC from coniferous as compared to deciduous species. The colonization of logs by tree species specific fungi (Stokland 2012) might be involved in the production of different DOC qualities as shown for leaf litter incubated with different fungal species (Moller et al. 1999).

2.6 Conclusions

In temperate forests, the release from CWD is a hotspot of DOC input to the soil in the early phase of decomposition. Net DOC release is tree species specific and only weakly related to the measured initial chemical wood and bark properties. The amount of precipitation only has a minor relevance for DOC net release, but the release is larger in the growing than in the dormant season. The quality of DOC from CWD differs among tree species, which might cause differing effects on soil properties underneath CWD.

Since DOC release was insufficiently explained by the measured wood properties and environmental conditions, the influence of fungal and arthropod invasion of CWD on DOC release and the relative contribution of bark versus wood as sources for DOC from logs should to be addressed in future studies.

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Tables chapter 2

Table 2.1: Average initial properties of bark and sapwood extracts (n = 3).

		sapwood						bark					
	tree species	C/N		phenols		carbohydrates		C/N		phenols		carbohydrates	
			±SD	[mg/g DW]	±SD	[mg/g DW]	±SD		±SD	[mg/g DW]	±SD	[mg/g DW]	±SD
coniferous	*Larix decidua*	242	131	0.10	0.02	1.11	0.75	144	20	1.65	0.004	0.77	0.31
	Picea abies	661	73	0.05	0.03	0.57	0.51	109	19	0.60	0.005	0.23	0.03
	Pinus sylvestris	1569	121	0.05	0.01	0.92	0.75	197	16	0.38	0.004	0.15	0.04
	Pseudotsuga m.	1019	65	0.10	0.01	0.83	0.63	141	13	1.02	0.004	0.23	0.02
deciduous	*Acer sp.*	328	86	0.05	0.002	0.94	0.51	52	13	0.38	0.003	0.12	0.02
diffuse porous	*Betula sp.*	711	229	0.04	0.02	0.75	0.43	106	16	0.65	0.029	0.15	0.06
	Carpinus betulus	244	77	0.10	0.02	0.71	0.39	38	19	1.76	0.050	0.45	0.03
	Fagus sylvatica	373	99	0.03	0.02	0.90	0.66	81	15	0.31	0.004	0.15	0.02
	Populus sp.	547	298	0.03	0.01	1.06	0.72	68	14	0.59	0.010	0.13	0.05
	Prunus avium	351	110	0.12	0.04	0.74	0.53	63	7	0.40	0.006	0.49	0.04
	Tilia sp.	364	86	0.04	0.02	1.28	0.81	75	3	1.38	0.020	0.38	0.09
deciduous	*Fraxinus excelsior*	398	44	0.17	0.02	0.40	0.19	66	6	1.37	0.028	0.37	0.08
ring porous	*Quercus sp.*	363	103	0.49	0.07	0.14	0.15	72	8	0.98	0.010	0.11	0.03

Table 2.2: Relation of DOC net release on single sampling dates to throughfall amount in the snow free period. Coefficients of determination (r^2) and p-values.

	tree species	r^2	p
coniferous	*Larix decidua*	0.25	<0.01
	Picea abies	0.17	<0.01
	Pinus sylvestris	0.21	<0.01
	Pseudotsuga m.	0.18	0.04
deciduous	*Acer sp.*	0.04	0.79
diffuse porous	*Betula sp.*	0.11	0.05
	Carpinus betulus	0.05	0.13
	Fagus sylvatica	0.23	<0.01
	Populus sp.	0.03	0.69
	Prunus avium	0.02	0.51
	Tilia sp.	0.04	0.96
deciduous	*Fraxinus excelsior*	0.01	0.30
ring porous	*Quercus sp.*	0.33	<0.01

Table 2.3: Average quality of DOC in runoff from CWD and in throughfall.

HIX_{em} and $SUVA_{280nm}$ were detected for 4 sampling dates, phenols and carbohydrates for 3 sampling dates (±SD for n = 3 logs per species).

	tree species	HIX_{em}		$SUVA_{280nm}$		phenols			carbohydrates		
			± SD	[µg $C^{-1}cm^{-1}$]	± SD	[mg L^{-1}]	± SD	[% DOC]	[mg L^{-1}]	± SD	[% DOC]
coniferous	*Larix decidua*	8.4	1.0	24.3	8.1	6.5	5.5	21.6	2.5	1.8	7.0
	Picea abies	7.5	1.2	25.8	5.7	6.4	5.2	10.0	4.9	4.9	8.6
	Pinus sylvestris	5.0	1.5	21.5	3.0	3.9	2.0	9.6	4.5	2.9	10.5
	Pseudotsuga m.	7.3	0.7	27.2	4.7	2.8	1.1	11.1	4.5	3.7	10.6
deciduous	*Acer sp.*	6.6	1.7	23.4	3.8	4.0	2.6	10.2	2.6	1.0	8.6
diffuse porous	*Betula sp.*	7.2	0.5	20.8	7.1	6.6	7.1	14.8	3.4	2.0	10.4
	Carpinus betulus	9.0	1.3	26.5	5.9	4.8	2.4	8.7	5.9	3.2	9.2
	Fagus sylvatica	6.6	0.6	24.6	4.3	2.7	1.3	6.2	3.8	2.3	9.4
	Populus sp.	6.2	0.6	28.8	4.9	4.4	2.6	14.0	2.5	1.3	8.8
	Prunus avium	6.6	0.9	22.0	6.5	9.5	12.3	10.7	9.4	5.3	10.1
	Tilia sp.	8.1	0.5	21.1	3.1	8.8	10.5	10.7	2.5	0.9	7.5
deciduous	*Fraxinus excelsior*	6.4	0.2	21.3	6.6	7.6	5.3	26.8	2.4	1.4	9.8
ring porous	*Quercus sp.*	9.3	1.3	26.8	9.9	6.6	3.2	11.3	7.4	7.3	8.4
throughfall		3.8	0.8	16.7	5.9	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

n.d.: not detected.

Table 2.4: Relation of average initial sapwood and bark properties to average DOC release from CWD of the 13 tree species (r^2; n = 13).

Log runoff	Initial properties			FTIR spectra		
	phenols	carbohydrates	C/N	CH/C=O	CH/COC	C=O/COC
	sapwood					
Cum. DOC net release	0.30*	0.23 (-)	0.01 (-)	0.12 (-)	0.21 (-)	0.07
Carbohydrates	0.24	0.26 (-)	0.00 (-)	0.16 (-)	0.18 (-)	0.09
Phenols	0.05	0.02 (-)	0.15 (-)	0.00	0.00	0.00
HIX_{em}	0.27	0.07 (-)	0.34* (-)	0.00	0.15 (-)	0.01
	bark					
Cum. DOC net release	0.03 (-)	0.00	0.03 (-)	0.00 (-)	0.11 (-)	0.00 (-)
Carbohydrates	0.03 (-)	0.00	0.03 (-)	0.00	0.09 (-)	0.01 (-)
Phenols	0.07	0.23	0.09 (-)	0.14	0.00	0.08 (-)
HIX_{em}	0.46*	0.13	0.13	0.16 (-)	0.14	0.03

*: $p < 0.05$.

(-): negative correlation.

Figures chapter 2

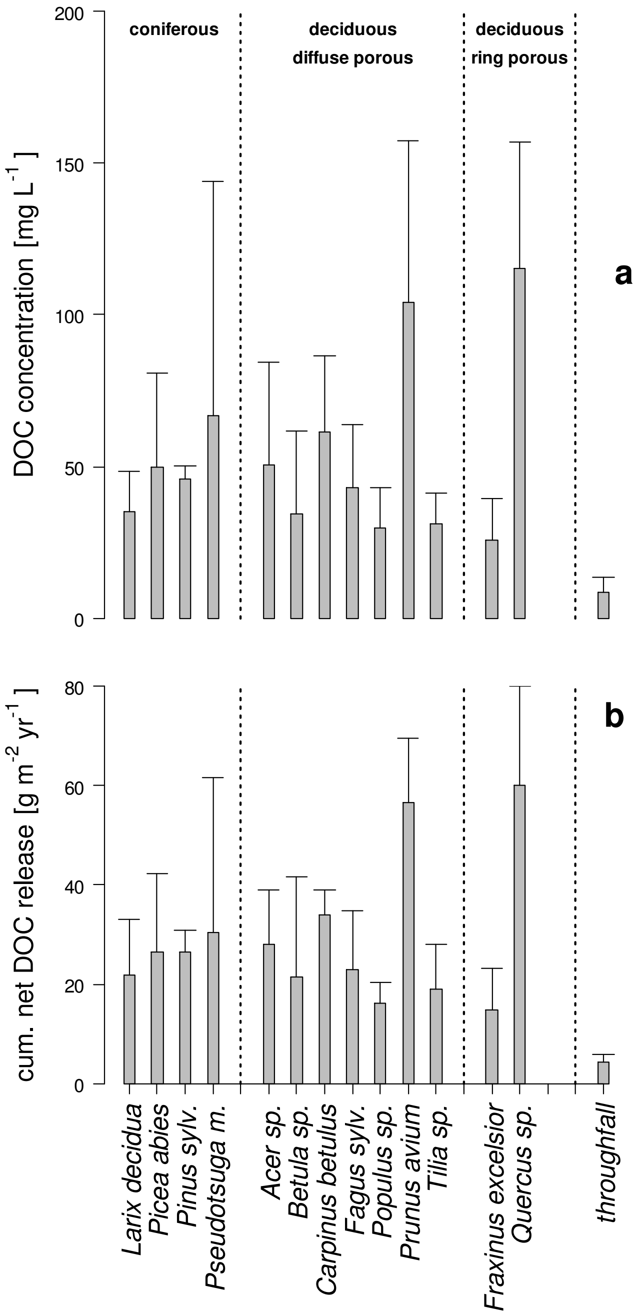

Figure 2.1: Flux weighted average DOC concentrations (a), cumulative net DOC release per projected log area (b) and DOC fluxes with throughfall.

With n = 3 for tree species, ±SD.

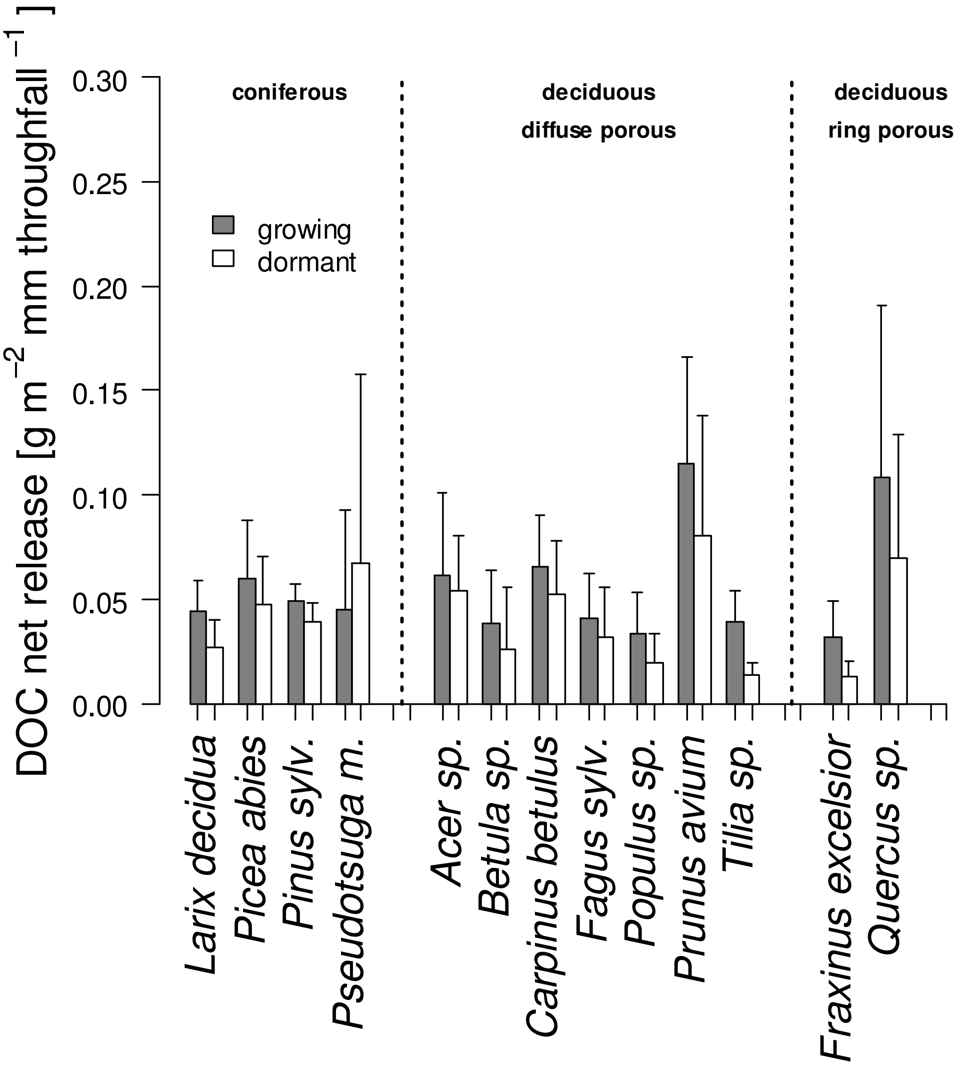

Figure 2.2: Seasonal DOC net release per projected log area normalized by throughfall.
With n = 3 for tree species, ±SD.

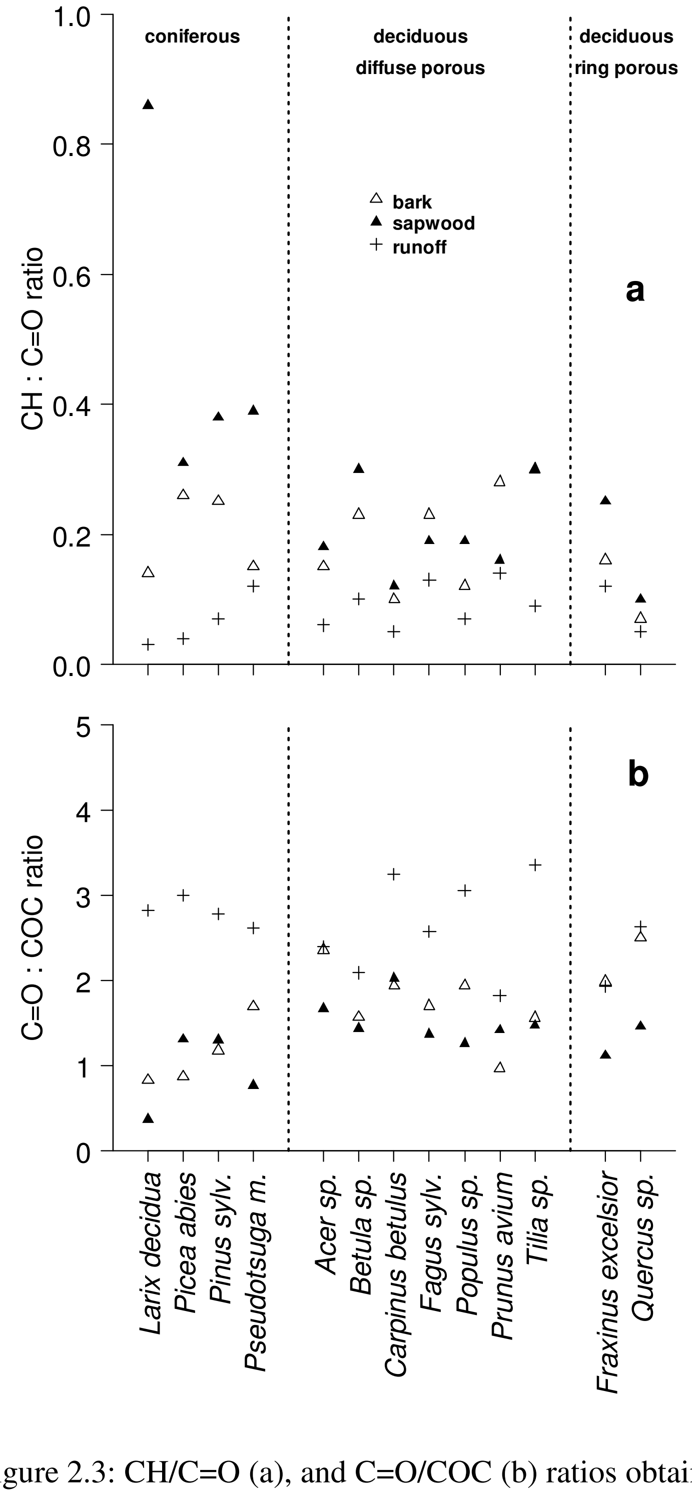

Figure 2.3: CH/C=O (a), and C=O/COC (b) ratios obtained from FTIR spectra.

Water extracts from bark and sapwood (initial contents prior to field exposition) and of runoff samples (n = 3 per species).

3. Dissolved nitrogen release from coarse woody debris of different tree species in the early phase of decomposition

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3.1 Abstract

In forest ecosystems, coarse woody debris (CWD) can represent a large stock of organic matter that contributes to the C and N cycling in forest ecosystems. Here we investigated the net release of dissolved organic N (DON), NH_4 and NO_3 from CWD of different tree species in the early phase of decomposition. Logs of 13 tree species were exposed in the winter 2008/2009 on the soil in a temperate *Fagus sylvatica* L. forest in Germany. Runoff solutions were periodically collected underneath logs for 17 months from June 2011-November 2012 in the third to fourth year of decomposition. The net release of N was calculated for each log on an annual scale as difference of N fluxes in runoff and throughfall.

Nitrogen was net released from CWD of all tree species with DON as the dominant N form, but leaching of NH_4 and NO_3 was also observed. Differences in total N release between tree species were not statistically significant due to high intra-specific variation. The net release of N ranged from 0.42 (*Pseudotsuga*) to 1.39 (*Carpinus*) g N m^{-2} log projection area yr^{-1} The variation in net release of N was not related to the initial C/N ratio of bark and sapwood of the different species. The DOC/DON ratios in runoff were positively related to the initial C/N ratio of bark and sapwood. Net release of NH_4 was larger in the dormant than in the growing season, opposite to the release of NO_3, but no seasonality was found for DON release. Average ratios of NH_4/NO_3 in runoff from CWD did not significantly differ between species. Precipitation amount and temperature had only minor effect on the total N release, suggesting other dominating drivers.

Our results demonstrate that CWD is a source of solute N, even in the early phase of decomposition.

3.2 Introduction

In forest ecosystems, coarse woody debris (CWD comprising twigs and logs of trees with >7 cm diameter) may represent a major component of above- and belowground litter contributing to C and N cycling (Harmon et al. 1986; Currie and Nadelhoffer 2002; Spears et al. 2003; Hafner and Groffman 2005). The stock of CWD in forests strongly depends on the management (Christensen et al. 2005; Stevenson et al. 2006), stand age and disturbing events (Harmon et al. 1986).

During decomposition of CWD, the C/N ratio decreases with time (Yang et al. 2010). While the decrease in the C/N ratio in CWD can occur under a net loss of N from the initial N stock, in other cases, the decrease in C/N might be associated with an absolute increase in the total N stock. An increase in the total N pool in CWD seems to dominate in early states of decomposition with high demand of N for the growing decomposer biomass, while N net release seems to dominate in later states of decomposition (Creed et al. 2004; Laiho and Prescott 2004; Palviainen et al. 2008; Preston et al. 2012).

A net increase in the N stock in CWD during decomposition can result from microbial immobilization of mineral N in throughfall, non-symbiotic N_2 fixation (Brunner and Kimmins 2003) and fungal translocation of N from the soil into the CWD (Boddy and Watkinson 1995). Nitrogen losses from CWD occur in solute forms of N either as dissolved organic N (DON), NO_3 or NH_4. Gaseous losses of N from decomposing logs have not been reported so far, but are likely rather low, given the low availability of NO_3 for denitrification.

Studies on solute fluxes of N from CWD leachate are scarce and information on controls and drivers of solute N fluxes from CWD is very limited. In late states of decomposition, concentrations of DON and mineral N in runoff from beech logs were about 2-3 times higher than in throughfall, indicating net release of N from the decomposing logs (Kuehne et al. 2008). Hafner et al. (2005) found the DON and NO_3 concentrations in runoff from CWD of various decomposition stages higher and NH_4 concentrations lower than in throughfall. DON was the most dominant N form in runoff from CWD. In contrast, NO_3 concentrations were lower in runoff from logs than in throughfall in a study on highly decomposed CWD from lodgepole pine (Yavitt and Fahey 1985).

The C and N dynamics in decomposing CWD are tree species specific: The C/N ratios of decomposing birch logs decreased faster than in conifers (Palviainen et al. 2008). Differences between coniferous tree species in the dynamics of C/N ratios during CWD decomposition were also substantial (Laiho and Prescott 2004), suggesting tree species effects on the N leaching of CWD. Tree species specific differences in the N leaching from CWD might be related to different decomposition rates (Yang et al. 2010) and bark morphology. Furthermore, a wide C/N ratio of bark and wood should cause a higher demand of N for decomposers and less leaching of N than from bark and wood of narrow C/N ratios. Phenols in wood and bark inhibit decomposers (Benoit and Starkey 1968) while decomposers might benefit from the availability of soluble carbohydrates. Hence, both parameters might influence the N leaching.

Beside tree species and CWD properties, environmental factors should also influence the release of solute N from CWD. In the study of Fahey et al. (1985) on highly decomposed lodgepole pine CWD, concentrations of total N in runoff from CWD decreased with water flux during snow melt, but an increase with precipitation was observed by Hafner et al. (2005). However, net release of N was not calculated in both studies. A positive relation of net N release to the precipitation amount is expected, as was shown for the fluxes of dissolved organic carbon from forest floors (Schmidt et al. 2010). Microbial processes like enzymatic de-polymerization, mineralization and immobilization will largely determine the N leaching from CWD and these processes are temperature dependent (Hafner et al. 2005; Koch et al. 2007; Herrmann and Bauhus 2013), suggesting seasonal patterns of N release. Moreover the solubility of dissolved organic matter increases with temperature (Gödde et al. 1996).

In this field study, we established solute N budgets for CWD of 13 temperate forest tree species during a 17 months period, thereby testing the following hypotheses: (i) In the initial phase of decomposition, CWD will act as a sink for mineral N from throughfall. (ii) The N budget of the CWD related to initial C/N of bark and sapwood. (iii) The release of solute N from CWD is larger in the growing than in the dormant season and (iv) depends on the precipitation amount.

3.3 Material and Methods

Logs from 13 tree species of the temperate forest zone (*Acer sp., Betula sp., Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, Larix decidua, Picea abies, Pinus sylvestris, Populus sp., Prunus avium, Pseudotsuga menziesii, Quercus sp., Tilia sp.*) were obtained from the forest authority of the Federal State of Thuringia, Germany. The logs were freshly cut and had a diameter of 30-40 cm and 4 m length.

Logs were exposed to the forest soil in late 2008 until beginning of 2009 in the *Hainich* forest area (Central Germany, 51°38’N, 10°78’E), in the frame of the so-called *Biodiversity Exploratories*, a priority program of the Deutsche Forschungsgemeinschaft (DFG) (Fischer et al. 2010). A set of 13 logs (1 log per species) was exposed each in 3 spatially separated beech (*Fagus sylvatica* L.) forest sites of a “selection forest” management type with wide age distribution of beech trees. In total, we sampled runoff from 39 logs. The experimental plots are located between 420 and 520 m a.s.l. and the average annual temperature is 6.5-8.0 °C.

The soil at the sites developed from loess deposits over calcareous bedrock and is classified as Luvisol (WRB 2006). The forest floor is mull type with an Oi layer and a shallow (<1 cm) Oe layer. The averaged cumulative throughfall during the 17 months observation period was 536 mm.

Runoff solution from each log was collected using small gutters (0.1 × 0.3 m) installed beneath the logs. Solutions were sampled in 2.0 L bottles which were located in buckets in the mineral soil next to the logs, avoiding exposition to high temperatures and light. All runoff and throughfall samples were stored in the laboratory at 2 °C and filtered using Millipore water prewashed cellulose acetate filters (0.45 µm, Whatman OE 67, GE Health Care Europe, Freiburg, D). The filtrates were kept frozen until analysis of total nitrogen (N/C 2100 Analyzer, Analytik Jena, D), NH_4 and NO_3 (Flow injection analysis FIA-LAB, MLE Dresden, D). Dissolved organic nitrogen was calculated as difference: Total N – (NH_4-N + NO_3-N.).

Runoff and throughfall were collected during 13 sampling dates from July 2011 until November 2012 in the third to fourth year of log decomposition. Fluxes of N with runoff from each log were calculated by multiplying the N concentration in runoff at a single sampling date with the respective throughfall amount at each of the three plots. Fluxes were referred to m^{-2} projected log area yr^{-1}. Projected log area was calculated from stem diameter and length. Evaporation from logs under the forest canopy is considered negligible at the annual scale. The net release of N from each log results from the difference of the N fluxes in runoff and in throughfall.

Initial chemical properties of sapwood and bark (C/N ratio, water soluble carbohydrates, and water soluble phenols) were determined for each log (for methods and data see Bantle et al. 2014).

Statistics

All statistical analysis was conducted using the open source software R 3.0.1 (R Core Team 2013). All nitrogen flux data were log-transformed, and normal distribution was tested using the Shapiro-Wilkinson test. Subsequent to an ANOVA, differences in N release from CWD between tree species were determined using the Tukey’s post-hoc test.

For analysis of differences, data were grouped to deciduous and coniferous when no significant species effects were determined. To identify the seasonal dependency of the N budget, the net release of the different N forms was first normalized per mm precipitation. Seasonality of N release was then tested using a paired t-test, comparing data from July 2011-Oktober 2011 and March 2012-October 2012 for the growing season and from November 2011-February 2012 and November 2012 for the dormant season.

3.4 Results

Average initial C/N ratios ranged from 242 to 1569 in sapwood and from 38 to 169 in bark (Fig. 3.1). The C/N ratios were significantly larger in coniferous than in deciduous tree species both for bark and sapwood ($p < 0.05$).

The concentrations of total N in runoff from the logs were about 2 times larger than in throughfall for all tree species, with the exception of *Pseudotsuga* where concentrations were similar (Fig. 3.2). The variation of total N concentration in runoff among the tree species was rather small and differences were not significant. The major proportion of the dissolved N in runoff was provided by DON.

The cumulative N fluxes with runoff reflected the concentration patterns with much larger fluxes in runoff than in throughfall for all tree species except *Pseudotsuga* (Fig. 3.3). Runoff fluxes of total N were in the range of 2-3 g yr^{-1} m^{-2} projected log area, while about 1.2 g N m^{-2} yr^{-1} was measured with throughfall. Hence, we observed a net release of N from all logs except from *Pseudotsuga*. The largest proportion of the net release was due to DON for all tree species. The net DON release ranged from 0.4 to 1.5 g m^{-2} yr^{-1}, the largest net release was observed for *Prunus, Carpinus* and *Quercus,* whereas *Pseudotsuga* yielded the minimum release (Fig. 3.3). However, due to large intraspecific variations, the differences between tree species were not significant at the $p < 0.05$ level. The budget for mineral N (NH_4-N + NO_3-N) also revealed a net release from all logs except for *Pseudotsuga* and *Fagus*. Net release of mineral N ranged from 0.2 to 0.8 g yr^{-1} m^{-2} projected log area. Differences were not significant, neither between tree species nor between deciduous and coniferous species.

After normalization of the N net release by precipitation amount, a seasonality of the NH_4 budget became obvious. The net release of NH_4 was generally larger in the dormant period than in the growing season (Fig. 3.4). In addition, the net release of NH_4 was often negative for deciduous trees during the growing season. The differences between coniferous and deciduous CWD in seasonality of NH_4 net release were significant ($p < 0.05$). The seasonality of NO_3 release was opposite to NH_4: For most tree species, the net release was larger in the growing season than in the dormant season, differences being most pronounced for deciduous species. No such seasonality was found for the net release of DON.

Throughfall amounts for the single sampling intervals during the growing season ranged from 10 to 170 mm. The correlation of net DON release to throughfall amount was low (Table 3.1) (except of *Fagus*: $r^2 = 0.54$), but significant for *Acer*, *Betula*, *Fagus*, *Picea* and *Pinus* ($p < 0.05$).

The average ratio of DOC/DON in runoff from the different logs ranged from 55 to 75 for coniferous tree species, being consistently higher ($p < 0.05$) than for deciduous species (range from 35 to 50) (Fig. 3.5a). The correlation between DOC and DON concentrations at single sampling dates was significant for all tree species but the r^2 ranged from 0.27 (*Larix*) to 0.91 (*Quercus*) (Table 3.2). The r^2 was generally higher for broadleaved species than for the coniferous species, but the slope of the regression was lower ($p < 0.05$) for coniferous species than for deciduous species. The ratio of DOC/DON did not vary with throughfall amount.

While the correlation was significant, the range of DOC/DON ratios at single sampling dates was substantial (Table 3.2). DOC/DON ratios for runoff from single logs were <5 in some cases and maxima of >100 were also observed. The variation of DOC/DON ratios was generally larger for coniferous species, but was almost one order of magnitude for all tree species. The low DOC/DON ratios were observed at relatively low DOC concentrations, but were mostly caused by relatively high DON concentrations.

The average ratios of NH_4-N/NO_3-N in runoff ranged between 0.5 and 1.5 for the different tree species (Fig. 3.5b). No significant differences were found between coniferous and deciduous species. Significant differences of NH_4-N/NO_3-N ratios were found for the couples *Prunus*-*Acer* and *Prunus*-*Tilia*. There was a tendency for larger NH_4-N/NO_3-N ratios during the dormant season than during the growing season ($p = 0.07$).

When comparing the 13 tree species, the net release of DON, NH_4 and NO_3 from the logs was not related to the measured initial sapwood and bark parameters (phenols, carbohydrates, C/N ratio). Only the DOC/DON ratio in runoff clearly reflected the C/N ratio of bark ($r^2 = 0.42$) and sapwood ($r^2 = 0.32$; $p < 0.05$, $n = 13$). While the DOC/DON ratios in runoff correlated to those in bark and sapwood, the ratios were only about 50% of those in bark and 10% of those in sapwood.

3.5 Discussion

Our findings did not support the hypothesis that CWD acts as a sink for mineral N from throughfall in the early phase of decomposition due to the immobilization of N by microorganisms. In fact, we observed the opposite: CWD was a net source of N with DON as the dominating form. Even for mineral N, CWD was a net source. DON as the dominating form of N in runoff from CWD was also reported in previous studies (Yavitt and Fahey 1982; Hafner et al. 2005). If the DON leached from CWD is a product of microbial activity or results from the leaching of the initial soluble DON pool in the CWD remains open as we have no information on the DOC/DON ratio of the initial water soluble wood and bark compounds. The DOC in runoff was partly microbially modified and oxidized in relation to the DOC in undecomposed CWD (Bantle et al. 2014). The DOC/DON ratios in runoff were much smaller than in the solid phase C/N of the bark and sapwood, confirming findings of Yavitt and Fahey (1985). This can be seen as an effect of preferential net mineralization of C in relation to N, leading to the decrease of C/N ratios of the remains. The DOC/DON ratios in runoff seem to reflect the leaching from already decomposed parts of bark and sapwood.

The solute budget of mineral N suggested ongoing net N mineralization in the initial phase of decomposition for most tree species. Given the huge DON release from CWD, the question arises, if the net release of mineral N can be caused by mineralization of DON in the samplers during storage of the solutions in the field for several days. This would also influence the DOC/DON ratios and cannot be ruled out, since we have no information on the stability of DON from CWD against microbial use. In case of DON extracted from forest floors of different tree species and different O-horizons, the proportion of mineralized DON ranged from 0 to 50% of the initial pool in 20 days at 20 ^{o}C (Schmidt et al. 2011), but was similar to the decomposition of DOC. Qualls and Haines (1992) also found DON to be as refractory as DOC.

The absolute rates of mineral N net release (0.2 to 0.8 g m^{-2} yr^{-1} projected log area) can be explained by release from the N stock in bark and sapwood. Stocks of N in bark were calculated from measured bark thickness, initial N content and bark density (density data from Dietz 1975). The annual net release of total N amounted to 2-10% of the initial N stock in bark for all species except *Pinus* (here 45% due to shallow bark with low N content). Similar relations can be found for the N stock in the outer sapwood. However, the source of mineral N and DON in runoff remains unclear and needs to be resolved in future studies: Besides decomposition of bark and sapwood, N in runoff might originate from N_2 fixation or from fungal translocation of N from the surrounding soil (Schimel and Hättenschwiler 2007; Chigineva et al. 2011).

Despite substantial variations in the initial bark and wood C/N ratios and contents of soluble phenols and carbohydrates, the net release of DON, NH_4 and NO_3 was not related to any of these parameters when the 13 tree species are compared. Only the positive relation of the average DOC/DON ratios in runoff to the C/N ratios of bark and sapwood, with larger ratios under coniferous than under deciduous species, support the influence of initial wood and bark parameters.

The net release of N of the different tree species were not statistically different due to large intraspecific variation among the 3 replicates of each tree species. This intraspecific variation might be due to several reasons. First the sampling area of the runoff gutters was very small and we had only installed one throughfall sampler at each site. A more detailed analysis of the exact amount and composition of throughfall close to each runoff sampler might reduce the variability. Moreover variations of chemical composition of bark and wood between single logs of one species might account for the spatial variability. But also other factors are likely involved in the individual N budget, like the morphology of bark, contact time of the throughfall water and CWD, hydrophobicity of surfaces, pathways of water on the logs, spatial variability of throughfall, and invasion of decomposers. Also the huge temporal variation of the DOC/DON ratios in runoff remains to be explained by these factors, as no relation to throughfall amount and temperature was observed.

The net release of DON was similar in the growing and dormant season when normalized to the amount of precipitation. DON behaves different to DOC in runoff from CWD as the DOC net release form theses logs was found larger in the growing season than in the dormant season (Bantle et al. 2014). The lack of correlation to temperature indicates that the release of DON is not directly controlled by the activity of decomposers and seems to be driven mainly by other factors. There are no data on net release of DON from CWD in dependence of temperature, but DON concentrations in CWD leachate were also not related to temperature (Hafner et al. 2005).

Opposite to DON, the net release of mineral N was larger in the growing season than in the dormant season which points to the temperature dependency activity of decomposer activity and the resulting net mineralization. On top, for the deciduous tree species, the seasonality of NH_4 release was often characterized by negative net release during the growing in relation to the dormant season while the NO_3 release was increased in the growing season. This points to ongoing net nitrification in the growing season in the bark and wood, but again, nitrification in the samplers cannot be ruled out. The average pH of the runoff solutions was generally larger in runoff from deciduous CWD than from coniferous CWD (data not shown), indicating more favorable conditions for nitrifiers in deciduous CWD.

Only weak relations were found between DON net release and throughfall amount. Our findings confirm Hafner et al. (2005) who also reported a lack of correlation between DON concentrations under CWD and precipitation amount. The conditions preceding the precipitation events (previous leaching rates, water content of the bark/sapwood, temperature, wettability of surfaces) seem to be more important for the DON net release than the actual precipitation. Moreover, the net N release might be kinetically restricted by the short contact time of throughfall water with CWD and by slow diffusion of N in the bark and sapwood tissue into the runoff solution.

The high N solute fluxes with runoff from CWD in relation to throughfall add to the spatial heterogeneity of soil conditions in forest soils and may influence the N cycling, N availability and sequestration in the soil underneath CWD. The high inputs of DON, but also of NH_4 and NO_3 should increase the overall turnover and availability of N in the soil. However, the opposite was observed: Busse (1994) found less inorganic N beneath logs, and Spears et al. (2003) reported less gross N mineralization beneath logs. Hafner and Groffman (2005) found that microbial biomass N was lower, microbial biomass C/N was higher and rates of N_2O production were reduced in soil beneath CWD. Despite high N concentrations, the quality of runoff from CWD (rich in DOC and phenols, low pH) seems to inhibit the N turnover in the soil beneath CWD rather than having triggering effects.

3.6 Conclusions

During the early phase of decomposition CWD is a source for N with DON as the dominating form, but also mineral N is net released. This causes larger inputs of solute N to the soil underneath CWD than with throughfall. No significant differences in total N release were found between single tree species due to high intra-specific variation. Net N release was not influenced by C/N ratio of bark and sapwood. Only the DOC/DON ratios in runoff being larger under coniferous than under deciduous CWD were positively related to the initial C/N ratio of bark and sapwood. No seasonality was found for DON release, whereas net release of NH_4 was larger in the dormant than in the growing season, opposite to the release of NO_3. As the relations to temperature and precipitation were weak, the drivers being responsible for intra- and interspecific variation and temporal patterns of N release and DOC/DON ratios need further research.

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Tables chapter 3

Table 3.1: Relation of DON net release at single sampling dates to throughfall amount in the snow free period.
Coefficients of determination (r^2) and p-values.

wood type	tree species	r^2	p
coniferous	*Larix decidua*	-0.02	0.44
	Picea abies	0.14	0.03
	Pinus sylvestris	0.12	0.04
	Pseudotsuga menziesii	0.09	0.08
deciduous	*Acer sp.*	0.09	0.04
diffuse porous	*Betula sp.*	0.16	0.02
	Carpinus betulus	-0.03	0.62
	Fagus sylvatica	0.54	< 0.001
	Populus sp.	-0.03	0.57
	Prunus avium	-0.03	0.71
	Tilia sp.	0.01	0.26
deciduous	*Fraxinus excelsior*	-0.04	0.87
ring porous	*Quercus sp.*	-0.04	0.85

Table 3.2: Correlation of DOC and DON concentrations in runoff from CWD and in throughfall at single sampling dates. Coefficients of determination (r^2), slope of linear regression and p-values. Samples with DON <0.4 mg L^{-1} were not considered because of uncertainties in determining DON.

wood type	tree species	r^2	p	slope	range DOC/DON
coniferous	*Larix decidua*	0.27	< 0.001	0.007	9-82
	Picea abies	0.76	< 0.001	0.009	7-97
	Pinus sylvestris	0.54	< 0.001	0.016	9-87
	Pseudotsuga menziesii	0.44	< 0.001	0.005	6-170
deciduous	*Acer sp.*	0.72	< 0.001	0.018	11-140
diffuse porous	*Betula sp.*	0.69	< 0.001	0.014	4-58
	Carpinus betulus	0.51	< 0.001	0.016	9-51
	Fagus sylvatica	0.91	< 0.001	0.018	12-55
	Populus sp.	0.63	< 0.001	0.021	8-52
	Prunus avium	0.78	< 0.001	0.017	26-180
	Tilia sp.	0.74	< 0.001	0.014	9-64
deciduous	*Fraxinus excelsior*	0.56	< 0.001	0.022	6-79
ring porous	*Quercus sp.*	0.91	< 0.001	0.015	10-72
--	throughfall	0.66	< 0.001	0.029	5-26

Figures chapter 3

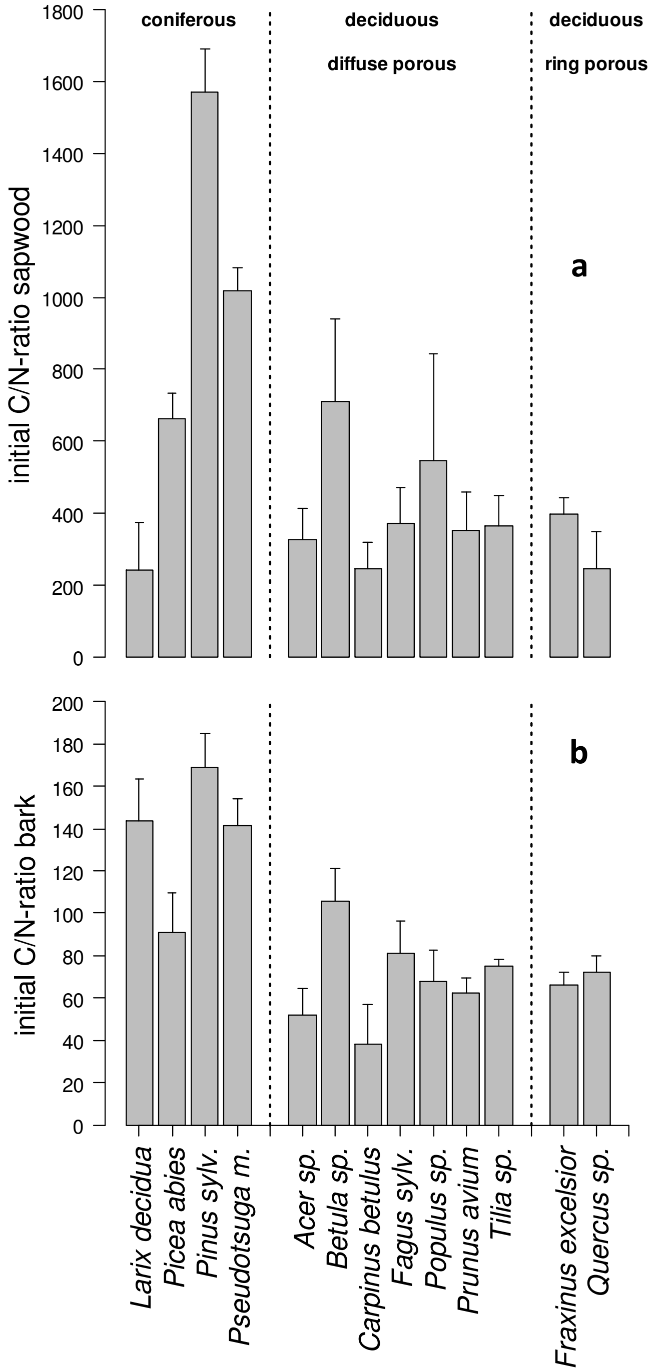

Figure 3.1: Initial C/N-ratios of sapwood (a) and bark (b) of 13 tree species.

With n = 3 per species, ±SD.

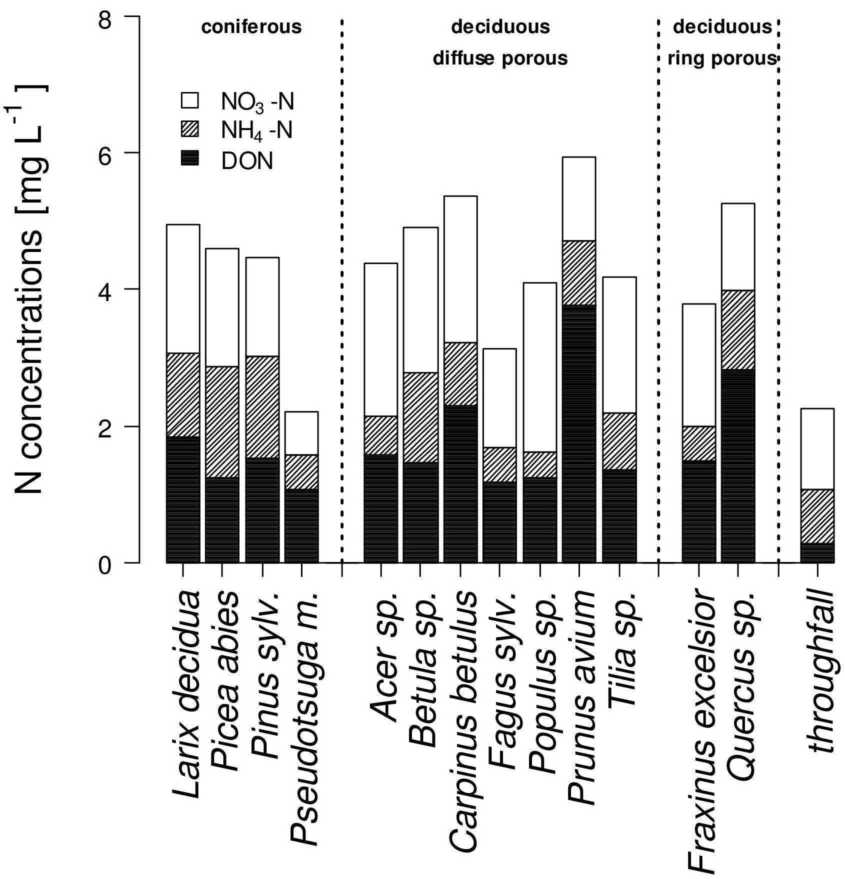

Figure 3.2: Flux-weighted average concentrations of nitrogen in runoff from CWD of 13 tree species.
With n = 3 per species.

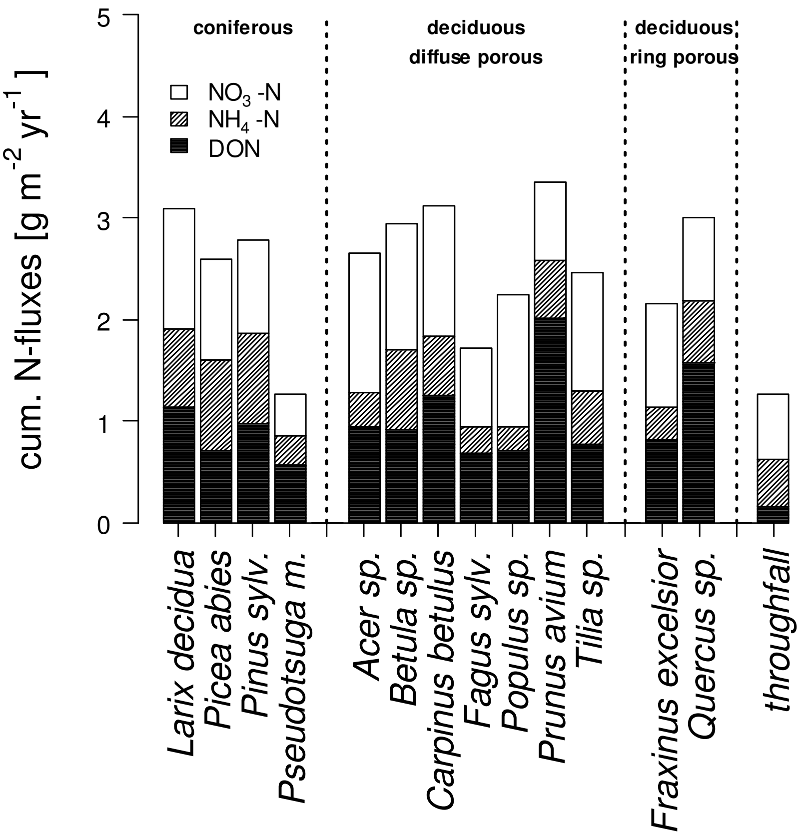

Figure 3.3: Cumulated average N fluxes with runoff from CWD of 13 tree species.

With n = 3 per species.

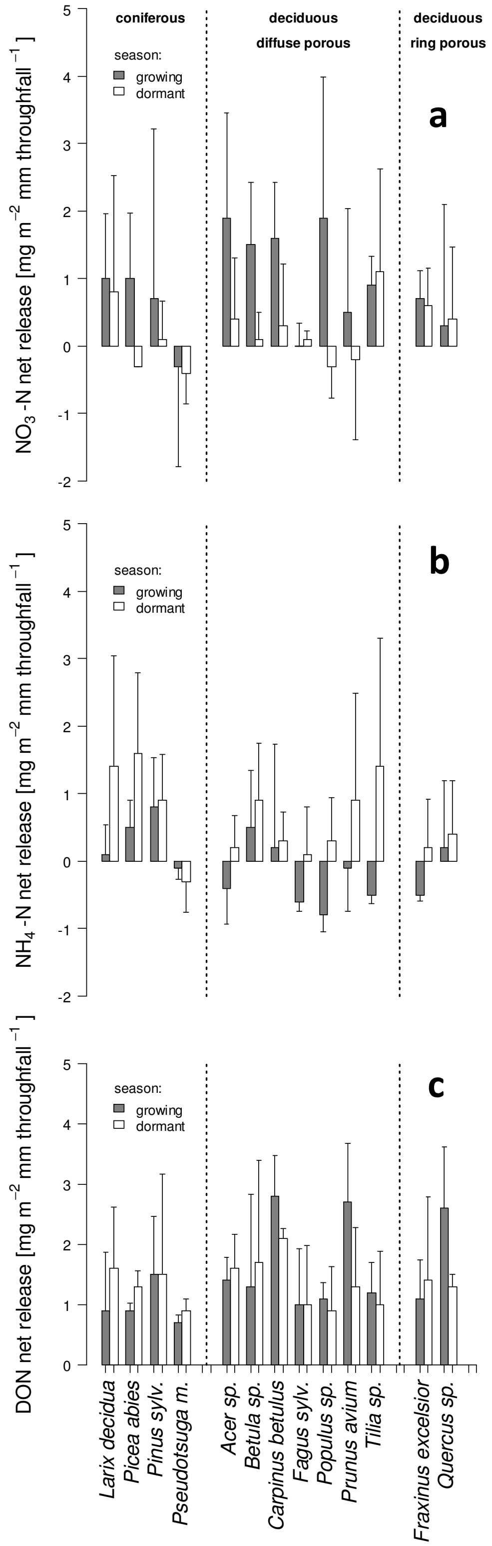

Figure 3.4: Flux weighted net release of NH_4, NO_3 and DON from CWD of 13 tree species in the growing and dormant season.

With n = 3 per species, ±SD.

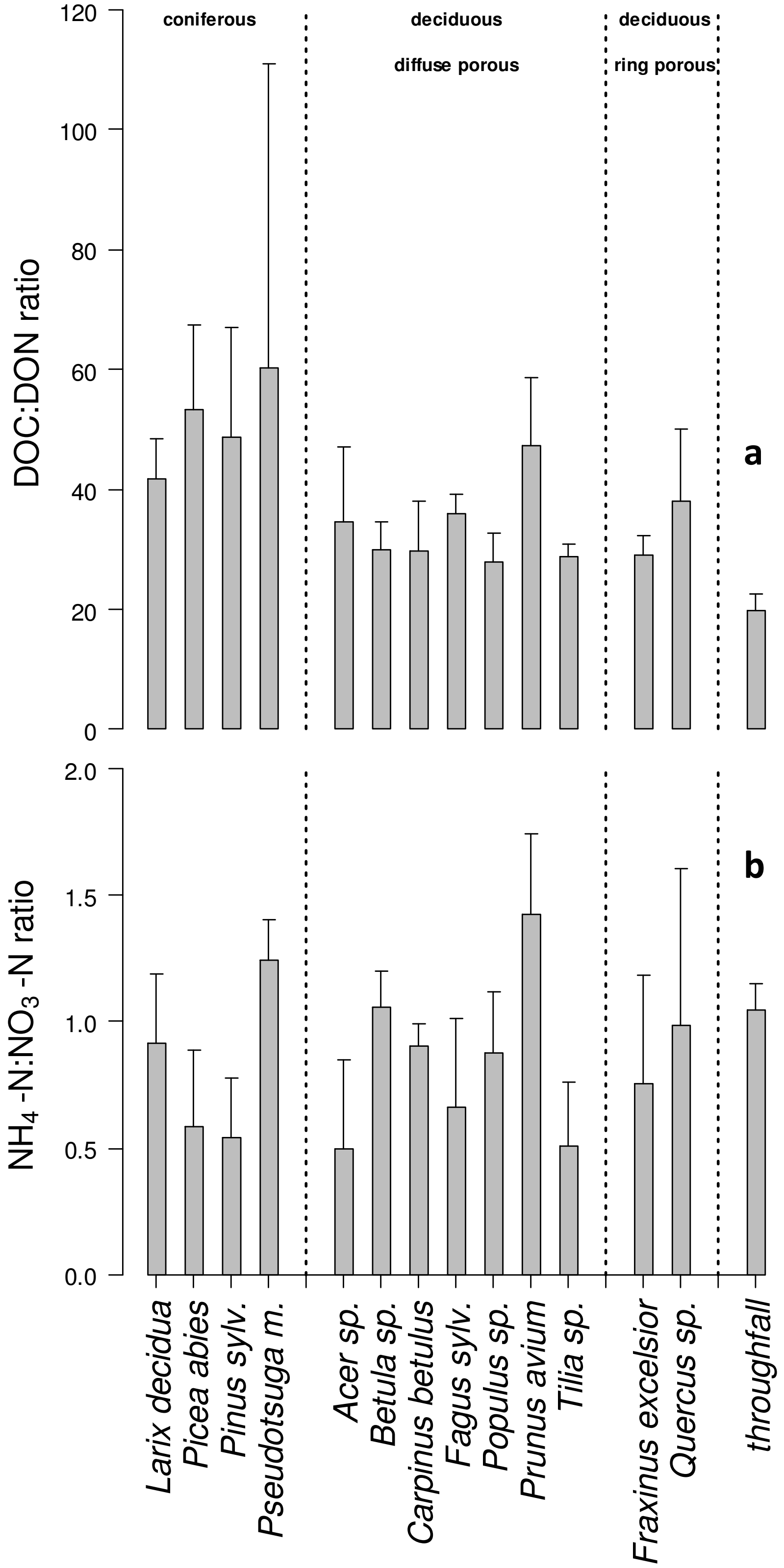

Figure 3.5: Average flux weighted ratios of DOC/DON (a) and NH_4-N/NO_3-N (b) in runoff from CWD of 13 tree species.
With n = 3 per species, ±SD.

4. Degradability of dissolved organic carbon derived from coarse woody debris of different tree species

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Keywords: coarse woody debris, biodegradability, decomposition, dissolved organic carbon, tree species.

4.1 Abstract

The leaching of dissolved organic carbon (DOC) from coarse woody debris (CWD) contributes to the decomposition of CWD and results in substantial inputs of DOC to the soil underneath CWD. The effect of the DOC input on soil processes and soil organic matter pools largely depend on the microbial decomposition kinetics of the DOC.

Here we investigated the biodegradability of dissolved organic carbon (DOC) in leachates from logs of 13 coniferous and deciduous European tree species.

Logs had been exposed to the soil for 3 to 4 years. DOC was collected as runoff solutions from CWD in the field and incubated in the laboratory for 64 days at 20 °C with a soil microbial inoculum. As proxy for biodegradability, the CO2 production was measured. The kinetics of CO_2 production was adapted to a 2-phase first order kinetic decay model. The quality of the DOC was characterized by spectroscopic properties and its hydrolysable carbohydrate content.

The amount of non-biodegradable DOC during the incubation ranged from 71 to 86% of total DOC and was not significantly different between coniferous and deciduous CWD. Labile DOC contributed 13.7 to 28.9% of the biodegradable DOC. The fraction of labile DOC and the mean residence times of the labile and stable fractions of biodegradable DOC did not differ between coniferous and deciduous species.

The DOC derived from CWD is largely recalcitrant and will likely add to the soil organic matter pools underneath CWD.

4.2 Introduction

During the decomposition of coarse woody debris (CWD) a major product besides CO_2 is dissolved organic carbon (DOC) leached from CWD. Concentrations of DOC underneath CWD were reported to be up to tenfold larger than in throughfall (*Bantle* et al, 2014, *Spears* and *Lajtha*, 2004). With increasing decomposition stage the release of DOC from CWD seems to increase (*Hafner* et al., 2005; *Kuehne* et al., 2008). Under logs of European beech, *Kahl* et al. (2012) found peak concentrations of >500 mg L^{-1}. The amount of DOC released is also tree species specific: The average DOC concentrations in runoff from logs of 13 different tree species in Germany ranged from 30 to 120 mg L^{-1} (*Bantle* et al., 2014).

The DOC input from CWD may influence the soil microbial community (*Brant* et al., 2006; *Crow* et al., 2009) and soil organic matter pools (*Kalbitz* and *Kaiser*, 2008) as well as the rates of soil respiration. The potential effect of DOC from CWD on soil processes largely depend on its biodegradability. DOC of low biodegradability may result in a larger sequestration of soil organic matter, but less contribution to soil respiration and vice versa for DOC of high biodegradability. Biodegradability of DOC varies widely with DOC properties (*Boyer* and *Groffman*, 1996; *Marschner* and *Kalbitz*, 2003; *Fellman* et al., 2008, *Qualls* and *Haines*, 1992; *Kalbitz* et al., 2003a) and microbial community composition (*Young* et al., 2005). DOC biodegradation has been studied in incubation experiments in the laboratory with varying incubation time from several days to one year. The biodegradable portions of total DOC in such incubations varied from 60-90% for DOC in extracts of fresh litter, to only 7% of the total DOC from Oa leachates (*Kalbitz* et al., 2003b; *Don* and *Kalbitz*, 2005, *Kiikkilä* et al. 2005).

Studies on leachate from litter of different ages (*Don* and *Kalbitz*, 2005) and on forest floor percolates (*Strobel* et al., 2001; *Kaiser* et al., 2001; *Kalbitz* et al., 2007; *Kiikkilä* et al., 2014) revealed the influence of tree species on the quality and biodegradability of DOC. DOC derived from birch leaves and birch forest floor degraded faster than DOC derived from spruce needles and forest floor (*Kiikkilä* et al., 2011). Coniferous forest floors comprised more water soluble ferulic and *p*-coumaric acid and phenolic acids in comparison to deciduous (*Suominen* et al., 2003). In water extracts from coniferous forest floors, *Ohno* et al. (2014) found higher proportions of condensed aromatic compounds and tannins than in deciduous forest floors.

Differences in the quality of DOC from CWD of coniferous and deciduous species can be expected since coniferous CWD usually has a larger C/N ratio and smaller decomposition rates than deciduous CWD (*Weedon* et al., 2009). Moreover, lignin of coniferous CWD is built up mostly by guaiacyl-units, whereas lignin of deciduous CWD is formed by syringyl- and guaiacyl-units in the ratio of 1:1 (*Adler*, 1977, *Wong*, 2009).

Up to now, the biodegradability of DOC from CWD has not been investigated. Here we studied the biodegradability of DOC derived from CWD of 13 different tree species in the early state of decomposition (3-4 years after exposure in the field). The hypotheses driving our experiment were that mineralization rates of DOC differ between coniferous and deciduous tree species and are related to spectroscopic properties, carbohydrate and phenol content of DOC.

4.3 Material and Methods

We collected DOC from coarse woody debris of 13 different tree species (coniferous: *Picea abies, Pinus sylvestris Pseudotsuga menziesii, Larix decidua,* deciduous: *Acer sp., Betula sp., Carpinus betulus, Fagus sylvatica, Fraxinus excelsior, Populus nigra, Prunus avium, Quercus sp., Tilia sp.).* Logs (4 m of length, 30–40 cm in diameter) of these species were exposed to decomposition on the soil on 3 plots at the *Hainich Exploratory* beech forest in winter 2008/2009 (for more details on the experimental design and locations, see *Bantle* et al., 2014).

Sampling and incubation

Logs of 13 species (3 replicates per tree species, 39 logs in total) were irrigated in June 2013 with an artificial precipitation solution free of DOC. The irrigation was performed using glass burettes for the drop-wise application of the artificial precipitation for several hours. The burettes were installed directly above the runoff sampling gutters (10 x 30 cm PVC) underneath the logs. The irrigation amount was about 2.5 L per log simulating a precipitation event of about 10 mm.

Runoff from the logs was filtered using prewashed cellulose acetate membrane filters (0.45 µm, Whatman OE 67, GE Health Care Europe, Freiburg, D). Until analysis and further processing, the samples were stored in a climate chamber at 2 °C in the dark. The DOC concentrations were analyzed by combustion using a C-Analyzer (N/C 2100 Analyzer, Analytik Jena, D).

Before incubation, the 3 runoff samples of the same tree species were merged obtaining one pooled sample per species. This procedure was necessary given the small volume of some runoff samples due to the loss of solution by bark structure and slope at the field site. To ensure comparability, DOC concentrations were adjusted in all merged samples prior to 15 to 20 mg L^{-1} prior to incubation.

After merging, 3 replicates per tree species of 40 mL each were incubated in glass bottles (Müller-Krempel, 120 mL, Bülach, CH). A glass fibre filter (Ø 55 mm, 47.5 cm^2, Schleicher & Schuell, GF 55, München, D) was added to each incubation flask providing a surface for the establishment of microbial biofilms (*Qualls* and *Haines*, 1992). Ensuring the nitrogen supply of the mixed microbial inoculum (that was extracted with 0.01 molar $CaCl_2$ from Oi + Oe horizons mixed from spruce and beech sites) 50 µL of a 0.5 molar NH_4NO_3 solution was added to each sample. A pressure of 80 hPa was applied to the bottles. The incubation was conducted in the dark at 20 °C for 64 days. During incubation, headspace samples were taken periodically at 10 occasions and CO_2 was measured by gas capillary chromatography equipped with a flame ionization detector (SRI 8610C, SRI Instruments Europe GmbH, D).

The amount of CO_2 in the headspace of the incubation flasks was calculated using the general gas equation. Additionally, the physically dissolved CO_2 in the solution phase was calculated by

$$n_F = \alpha * p_{CO2} \qquad \text{(equation 1)}$$

with: n_F: amount of CO_2 physically dissolved in the solution phase
α: Bunsen'scher absorption coefficient of CO_2 in water
(0.88 [1 bar^{-1}], at 20 °C).
p_{CO2}: partial pressure of CO_2 in the gas phase

The amount of CO_2 in solution was added to the headspace CO_2. Physically dissolved CO_2 accounted for 15 to 26% of the total CO_2 evolution.

The chemically dissolved CO_2 (HCO_3^-) was calculated using equation 2:

$$n(CO_{2\ chem}). = n_F * 10 \exp(-pK_{a1} + pH) \qquad \text{(equation 2)}$$

with: n_F: amount of physically dissolved CO_2 in the solution phase
pK_{a1}: pK_a of CO_2 / HCO_3^- system at 20 °C
pH: measured at the beginning and at pH 6.4 at the end of incubation

During the incubation an increase of pH was observed especially for the coniferous samples. The final pH at atmospheric CO_2 was between 6.1 and 6.9. Due to the closed system it was impossible to measure the pH of the solution during incubation at the in situ CO_2 pressure. Solutions were not acidified at the end of the incubation in order not to manipulate spectroscopic properties of the DOC. Therefore the final pH was assumed to be 6.4 for all samples and the chemically dissolved CO_2 was computed accordingly. The difference between initial and the final HCO_3^- was added in equal amounts to the CO_2 evolution at each measuring date. Chemically dissolved CO_2 accounted for 5.4 to 29% of the total CO_2 evolution.

The kinetic of total CO_2 production (CO_2 in headspace + physically dissolved CO_2 + HCO_3^-) was adapted to a 2-phase exponential model using a least square optimization:

$$y = a * (1 - e^{-k_1 * x}) + ((100 - a) * (1 - e^{-k_2 * x})) \qquad \text{(equation 3)}$$

with: a: labile fraction of the biodegradable DOC [%]
100-a: stable fraction of the biodegradable DOC [%]
k_1: mineralization constant of the labile fraction [d^{-1}]
k_2: mineralization constant of the stable stable fraction [d^{-1}]
x: day of incubation [d].

Humification index, specific UV absorption, phenolic carbon and hydrolysable carbohydrate carbon

Before and after incubation, the following solution parameters were measured (Table 1): The pH of the solutions was measured by a glass electrode at atmospheric CO_2 pressure. The pH of the solutions during incubation was recalculated based on the CO_2 concentration in the headspace. Fluorescence emission spectra of the DOC were recorded (SFM 25, BIO-TEK Instruments, Bad Friedrichshall, D) and the humification index (HIX_{em}) was calculated according to the method of Zsolnay (1999). The HIX_{em} is a measure of the complexity and condensation of the molecules. Additionally, the specific UV absorbance (UVIKON 930, BIO-TEK Instruments, Bad Friedrichshall, D) at 280 nm was measured as an estimate of aromaticity of DOC. The total amount of phenolic carbon was detected following to the method of Box (1983). Furthermore, the content of hydrolysable carbohydrates was determined using the procedure of Johnson and Sieburth (1977) and Johnson et al. (1981).

Statistics

All calculations were performed using the R software version 3.01 for statistical computing (R Core Team 2013). Subsequent to an ANOVA, significances were tested using a Tukey's post-hoc test. Normality was proved by Shapiro-Wilk test and homogeneity of variances was tested by Levene's test. Data were grouped for coniferous vs. deciduous species.

4.4 Results

The initial amount of carbohydrates in the DOC was in the range of 61.8 (*Larix*) to 121 (*Prunus*) µg mg DOC^{-1} and tended to be higher for deciduous than for coniferous samples ($p = 0.06$) (Table 1). Following the incubation, the CH content of DOC decreased significantly ($p < 0.001$) (Table 1, Figure 1c).

The contribution of phenols to DOC initially ranged from 22.6 (*Quercus*) to 163 µg mg DOC^{-1} (*Larix*) (Table 1). No significant difference was found between deciduous and coniferous species, neither before nor after incubation. The content of phenol C also did not change significantly during the incubation when expressed in µg mg DOC^{-1} (Figure 1b). The DOC normalized humification index (HIX_{em}) of DOC was initially higher on average for the coniferous CWD (Table 1), but the differences to deciduous DOC were not statistically significant. The HIX increased significantly ($p < 0.001$) during the incubation in all cases (Figure 1e). The initial DOC normalized specific UV absorption ($SUVA_{280nm}$, Table 1) was larger for DOC from coniferous than from deciduous CWD ($p < 0.05$) and increased during incubation with the exception of *Acer*, *Betula* and *Prunus* (Figure 1d). Largest increase of SUVA was observed for DOC from *Larix* and *Picea*.

The initial pH value of the incubation solutions was higher (average pH = 6.27) in samples from deciduous than from coniferous CWD (average pH = 4.73).

The kinetic of CO_2 evolution was rather similar for coniferous and deciduous species (Figure 2). However, the DOC from *Fagus* CWD was more rapidly and to a larger degree mineralized. The DOC loss calculated from initial and final DOC concentrations was always larger than the observed CO_2 evolution (Table 1). Compared to the CO_2 evolution the absolute loss of carbohydrates contributed on average 44% while the absolute loss of phenols was on average 23% of the total CO_2 evolution. Overall, about 23% of the CO_2 evolution resulted from the mineralization of non-defined DOC compounds.

The proportion of the non-degraded (recalcitrant) DOC (y_{stable} in Table 2) varied between 68 (*Fagus*) and 92.7% (*Populus*) and was similar for coniferous and deciduous DOC. The labile fraction of biodegradable DOC ("a" in Table 2) ranged from 8.7 to 21% for coniferous and from 7.1 to 29% for deciduous tree species (Table 2), the differences between the groups being not significant. The largest proportion of the labile fraction was observed for *Fagus* while the lowest was found for *Populus*. Since there were only minor differences in the proportion of easily degradable DOC, the decomposition rates k_1 was also not statistically different between coniferous and deciduous DOC and resulted in mean residence times

($MRT_1 = 1/k_1$) of 11 to 48 days for the labile fraction. The calculated MRT_2 of the stable biodegradable DOC fraction was much longer, ranging from 25 (*Larix*) to 685 (*Populus*) years. The mineralization constant k_2 was significantly larger for the coniferous DOC ($p < 0.05$) and significantly related to the normalized initial carbohydrate and phenol content ($p < 0.05$). The mineralization constant k_1 (Figure 3a-d) and the labile proportion of the biodegradable DOC (Figure 3e-h) were not significantly related to the DOC quality parameters hydrolysable carbohydrate C, phenol C, HIX and $SUVA_{280nm}$ except of the relation of k_1 to the normalized initial carbohydrate content ($p < 0.05$). The quality parameters were also not related to the non-degradable DOC (y_{stable}, Table 2).

4.5 Discussion

Our results did not confirm the hypothesis that DOC from coniferous CWD is less biodegradable than DOC from deciduous CWD. The proportions of biodegradable DOC (7–29% of initial DOC) were quite similar for coniferous and deciduous DOC. No other study on the decomposition of DOC from CWD is available and we have to compare our results to findings on DOC from litter and soil extracts. Comparing results from studies on DOC biodegradation is complicated by different incubation times that ranged from a few days (e.g.: *Marschner* and *Bredow*, 2002) up to 90 (*Kalbitz* et al., 2003a) or 365 days (*Kalbitz* et al., 2005; *Qualls*, 2005; *Marschner* and *Kalbitz*, 2003). With respect to the proportion of biodegradable soil derived DOC, a wide range is reported depending on the substrate used as a DOC source (*Kiikkilä* et al. 2013). Differences between tree species were however rather low when DOC was extracted from decomposed litter. *Kiikkilä* et al. (2005) found 12-17% (birch<spruce<pine) of the total DOC from forest floor extracts being degradable. Likewise, the biodegradable fraction of DOC in forest floor percolates was 20% (pine) and 17% for hardwood (*Yano* et al., 2000) which corresponds to our data on DOC from CWD. Hence, literature findings on DOC biodegradation using extracts from decomposed litter correspond to our findings of similar degradability of DOC from coniferous and deciduous CWD. The similar DOC decomposition rates contradict the general decomposition kinetics for CWD, since decomposition of coniferous is slower than of deciduous CWD (Russell et al., 2014; Adler, 1977; Harmon et al., 1986; Currie et al., 2002; Angers et al., 2012; Herrmann and Bauhus, 2013). The major proportion of DOC leached from CWD is likely a recalcitrant residue of microbial activity, since the easily decomposable fractions of the CWD have been already utilized by microorganisms.

The labile proportion "a" (Table 2) of biodegradable DOC from CWD were lower than those reported for DOC from Oi layer leachates (57-59%, *Kalbitz* et al., 2003b) and correspond to DOC from more decomposed litter, like from Oe and Oa layers (*Kiikkilä* et al. 2006, *Bowen* et al., 2009). However, the mineralization rates k_1 for the labile DOC from CWD (range from 0.051 to 0.088 d^{-1}) correspond to those of DOC in Oi and Oe percolates (*Kalbitz* et al., 2005; *Qualls* and *Haines*, 1992). In contrast, for Oa layer leachates of spruce and beech, *Kalbitz* et al., (2003b) found k_1 values one order of magnitude lower than for CWD.

For the stable proportion of biodegradable DOC, we calculated k_2 rates from 0.000021 to 0.000064 d^{-1}. These rates are one order of magnitude lower than those given by *Kalbitz* et al. (2003b) for DOC derived from Oa layers. The incubation time in our experiment was rather short in relation to the calculated mean residence times which should be considered with caution. In addition, the observed losses of DOC from the incubation solution were always larger than the CO_2 evolution. Beside the formation of precipitates, this discrepancy might be attributed to microbial DOC assimilation (*Bowen* et al., 2009) and growing microbial biomass. The proportion of DOC that is assimilated into the microbial biomass would cause an overestimation of the recalcitrant DOC as the turnover time of microbial biomass is much shorter than the proposed k_2 values. If the loss of DOC is fully attributed to microbial growth, the y_{stable} fraction would be in the range of 45-81%, instead of 68-93%. However, while the absolute rates can be questioned, the findings suggest that leachates from CWD have a substantial proportion of DOC with a long mean residence time.

Effects of DOC quality on biodegradability

The initial $SUVA_{280nm}$ of the coniferous DOC was significantly higher than of deciduous DOC ($p<0.01$) indicating a larger aromaticity of DOC from coniferous CWD. However, this had no effect on the biodegradable proportions of DOC. Furthermore, ratios of C=O:COC functional groups in DOC from coniferous CWD were higher than for deciduous CWD (*Bantle* et al., 2014), indicating a stronger modification and decomposition degree of DOC from coniferous CWD. This coincided with lower ratios of CH/C=O for coniferous samples (*Bantle* et al., 2014). These differences in chemical structure of DOC also did not influence the biodegradability of coniferous DOC compared to deciduous DOC.

The DOC normalized initial HIX_{em} was significantly lower ($p < 0.05$) for deciduous DOC, but no significant relation to biodegradability resulted. In other studies, HIX_{em} was found to be a good predictor for the degradability of DOC from soils (*Kalbitz* et al., 2003b). Furthermore, CO_2 evolution was not related to the initial $SUVA_{280nm}$ of DOC which is likely due to the low variation of DOC normalized initial $SUVA_{280nm}$ values. However, the increase of $SUVA_{280nm}$ during the incubation points to the relative accumulation of aromatic compounds.

While the degradation of carbohydrates provided a major proportion of total CO_2 evolution, our second hypothesis was not supported, as the CO_2 evolution did not correlate significantly with the loss of carbohydrates if all tree species are considered. The largest proportion of CO_2 resulted from the mineralization on non-defined DOC compounds. The proportion of carbohydrate C in the initial DOC was rather low is likely due to the mineralization of soluble carbohydrates during the exposition of the logs in the field. Additionally, inhibitory effects of non-specified DOC compounds (e.g. tannins) may modify the decomposition kinetics and cause the lack of correlation to measured DOC quality parameters.

The pH of the coniferous incubation solution increased substantially during the incubation indicating microbial mineralization of organic acids. The final pH measured after opening the incubation flasks was higher than the pH in the surface soil. The biodegradation of DOC is pH dependent (*Chang* and *Alexander*, 1984; *Marschner* and *Kalbitz*, 2003; *Curtin* et al., 1998; *Hansson* et al., 2013) and the mineralization rates in the incubation might be higher than under field conditions. Furthermore the final pH of the incubation solution was set to 6.4 which is a rough estimate in the absence of direct pH measurements in the closed incubation system. Small changes of the pH around the value of 6.4 strongly affect the HCO_3^- concentration and hence create uncertainty in the total mineralization rates. This shortcoming needs to be considered in future studies.

While the biodegradation of DOC from CWD in the soil differs from the kinetics observed in our laboratory incubation, the DOC from CWD was found to be largely recalcitrant. Recalcitrant DOC from CWD might thus contribute to the buildup of soil organic matter underneath CWD (Kalbitz and Kaiser 2008), while the labile parts of DOC might modify microbial growth and the soil microbial community (*Brant* et al., 2006; *Crow* et al., 2009). The labile compounds of DOC might – however –also cause priming effects on recalcitrant proportions of soil organic matter (Kuzyakov 2010) and the net effect of DOC from CWD on soil organic matter remains to be determined in future studies. Investigations on changes in the soil organic matter pool underneath CWD are scarce and can hardly be generalized: *Kahl* et al. (2012) did not find an increase of soil organic matter content in the upper mineral soil underneath *Fagus* logs that were exposed for 8-16 years. In contrast, larger stocks of soil C and N were found underneath *Eucalyptus* CWD (*Goldin* and *Hutchinson*, 2013).

4.6 Conclusions

The decomposition of CWD results in large DOC inputs to the soil underneath CWD. No significant differences in DOC biodegradation between coniferous and deciduous species were observed, and the overall variation between species was low. The majority of DOC from CWD seems rather recalcitrant and the input of DOC to the soil likely influences soil organic matter pools underneath CWD. The pH-effect on DOC mineralization rates and HCO_3^- solubility needs to be considered in future experiments that compare different DOC sources.

4.7 Acknowledgements

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Tables chapter 4

Table 4.1: Solution parameters before (initial) and after (final) incubation.

Hydrolysable carbohydrates (CH), phenolic carbon (PHE), specific UV absorption at 280 nm (SUVA) and humification index (HIX) were normalized to the initial or final DOC concentrations. DOC loss is the difference between initial and final DOC amount in the solution, CO_2 evolution represents CO_2 in headspace + physically dissolved CO_2 + HCO_3^-.

tree species		$DOC_{initial}$ [µg]	DOC_{final} [µg]	DOC loss [µg]	CO_2 evolution [µg]	$CH_{initial}$ [µg mg DOC^{-1}]	CH_{final} [µg mg DOC^{-1}]	$PHE_{initial}$ [µg mg DOC^{-1}]	PHE_{final} [µg mg DOC^{-1}]	$SUVA_{initial}$ [L mg DOC^{-1} cm^{-1}]	$SUVA_{final}$ [L mg DOC^{-1} cm^{-1}]	$HIX_{initial}$	HIX_{final}	$pH_{initial}$
Larix decidua	coniferous	925	668	257	123	61.8	34.3	162.6	72.5	0.0445	0.2738	5.02	14.54	4.97
Picea abies		952	616	337	186	75.5	34.0	77.8	79.1	0.0532	0.1397	5.63	9.68	5.17
Pinus sylvatica		1020	559	461	290	75.8	56.0	63.9	80.1	0.0466	0.0537	4.70	5.75	4.61
Pseudotsuga m.		1033	551	482	229	98.1	52.3	60.9	69.8	0.0436	n.d.	3.20	4.76	4.49
Acer sp.	deciduous	960	437	522	226	108.4	66.5	43.9	60.7	0.0287	0.0274	3.04	7.85	6.08
Betula sp.		944	506	438	179	91.6	43.4	64.6	53.5	0.0360	0.0316	4.01	8.26	6.39
Carpinus betulus		983	575	408	157	110.9	55.4	62.8	75.0	0.0379	0.0782	4.76	8.28	6.2
Fagus sylvatica		880	535	345	283	110.7	39.6	68.8	96.6	0.0469	0.0542	4.12	8.20	6.39
Fraxinus excelsior		967	527	441	74	75.6	51.5	88.0	67.9	0.0415	0.0646	4.67	7.52	6.31
Populus sp.		913	599	313	63	93.5	61.7	73.2	65.8	0.0413	0.1101	2.77	7.71	6.37
Prunus avium		857	531	326	177	121.0	48.1	84.7	122.3	0.0421	0.0377	3.40	7.28	6.07
Quercus sp.		1031	583	448	63	97.1	22.6	65.3	88.5	0.0396	0.1029	5.16	9.34	6.59
Tilia sp.		931	547	385	131	97.2	55.7	82.3	53.2	0.0350	0.0476	3.87	9.31	6.27

Table 4.2: Parameters given by the 2-phase exponential model of DOC mineralization.

Mineralization rates k_1 of the labile fraction, k_2 of the stable fraction of biodegradable DOC, mean residence times (MRT_1, MRT_2), proportions of labile biodegradable DOC (“a”), stabile biodegradable DOC (“b”), and non-degradable DOC (“y_{stable}”).

tree species		k_1 [d^{-1}]	k_2 [d^{-1}]	MRT_1 [d]	MRT_2 [yr]	a [%] of initial DOC	b [%] of initial DOC	y_{stable} [%] of initial DOC
Larix decidua	coniferous	0.041	0.000110	24.4	25	8.69	4.58	86.7
Picea abies	coniferous	0.060	0.000063	16.7	43	13.7	5.75	80.6
Pinus sylvatica	coniferous	0.062	0.000059	16.1	46	21.1	7.33	71.6
Pseudotsuga m.	coniferous	0.063	0.000062	15.9	44	15.8	6.38	77.8
Acer sp.	deciduous	0.067	0.000033	14.9	83	20.0	3.50	76.5
Betula sp.	deciduous	0.087	0.000007	11.5	391	18.9	0.47	80.6
Carpinus betulus	deciduous	0.073	0.000019	13.7	144	15.0	1.03	84.0
Fagus sylvatica	deciduous	0.089	0.000021	11.2	130	29.1	3.07	67.8
Fraxinus excelsior	deciduous	0.021	0.000016	47.6	171	10.2	1.79	88.1
Populus sp.	deciduous	0.095	0.000004	10.5	685	7.10	0.20	92.7
Prunus avium	deciduous	0.067	0.000030	14.9	91	17.4	3.25	79.4
Quercus sp.	deciduous	0.089	0.000013	11.2	211	7.19	0.97	91.8
Tilia sp.	deciduous	0.076	0.000012	13.2	228	13.1	0.62	86.3

Figures chapter 4

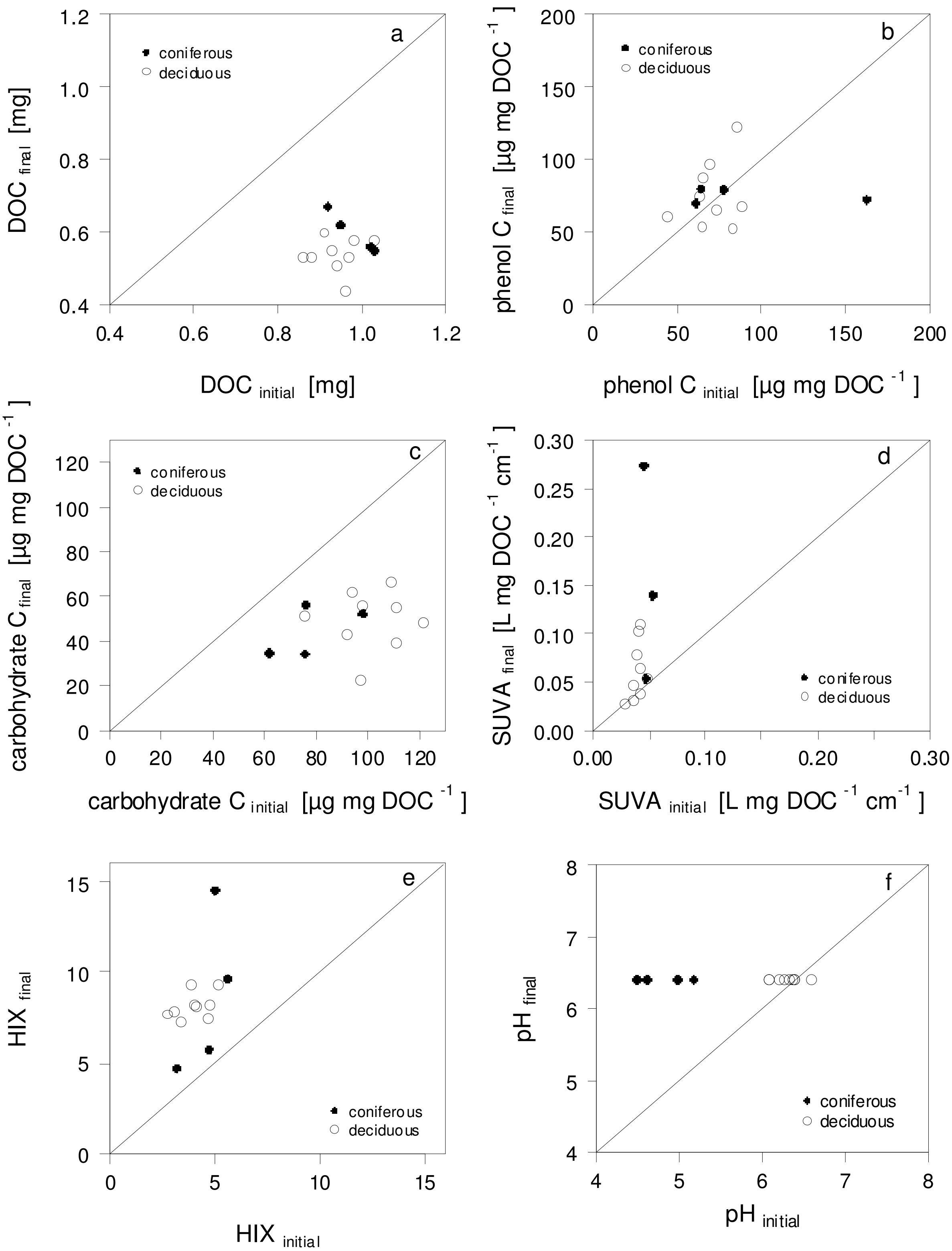

Figure 4.1: Correlation of final versus initial content and properties of DOC. With n = 4 for coniferous, n = 9 for deciduous species.

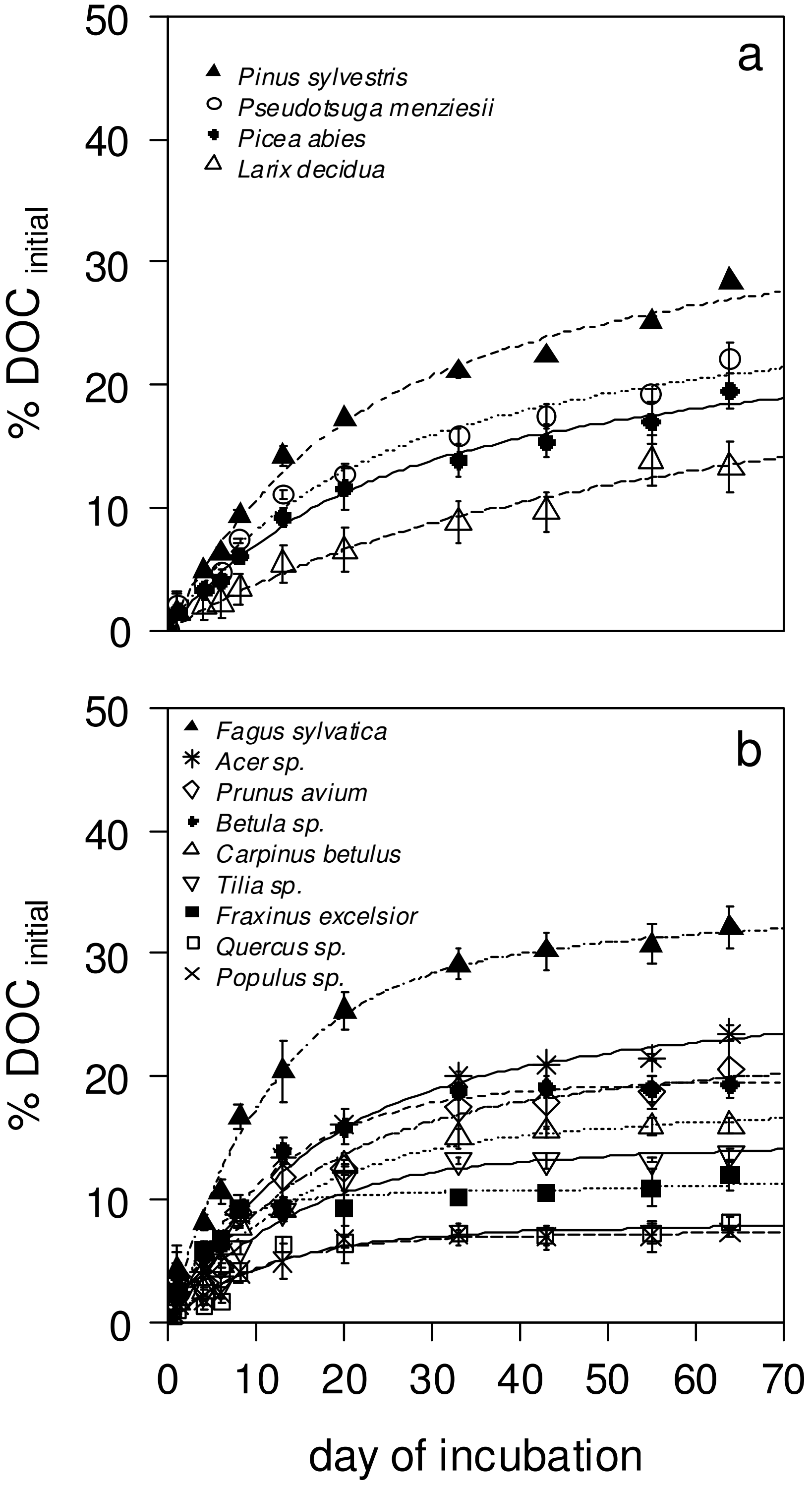

Figure 4.2: Kinetics of CO_2-evolution during the incubation of log runoff samples from coniferous (a) and deciduous (b) tree species. With n = 3 per species, ±SD, adjusted to final pH 6.4.

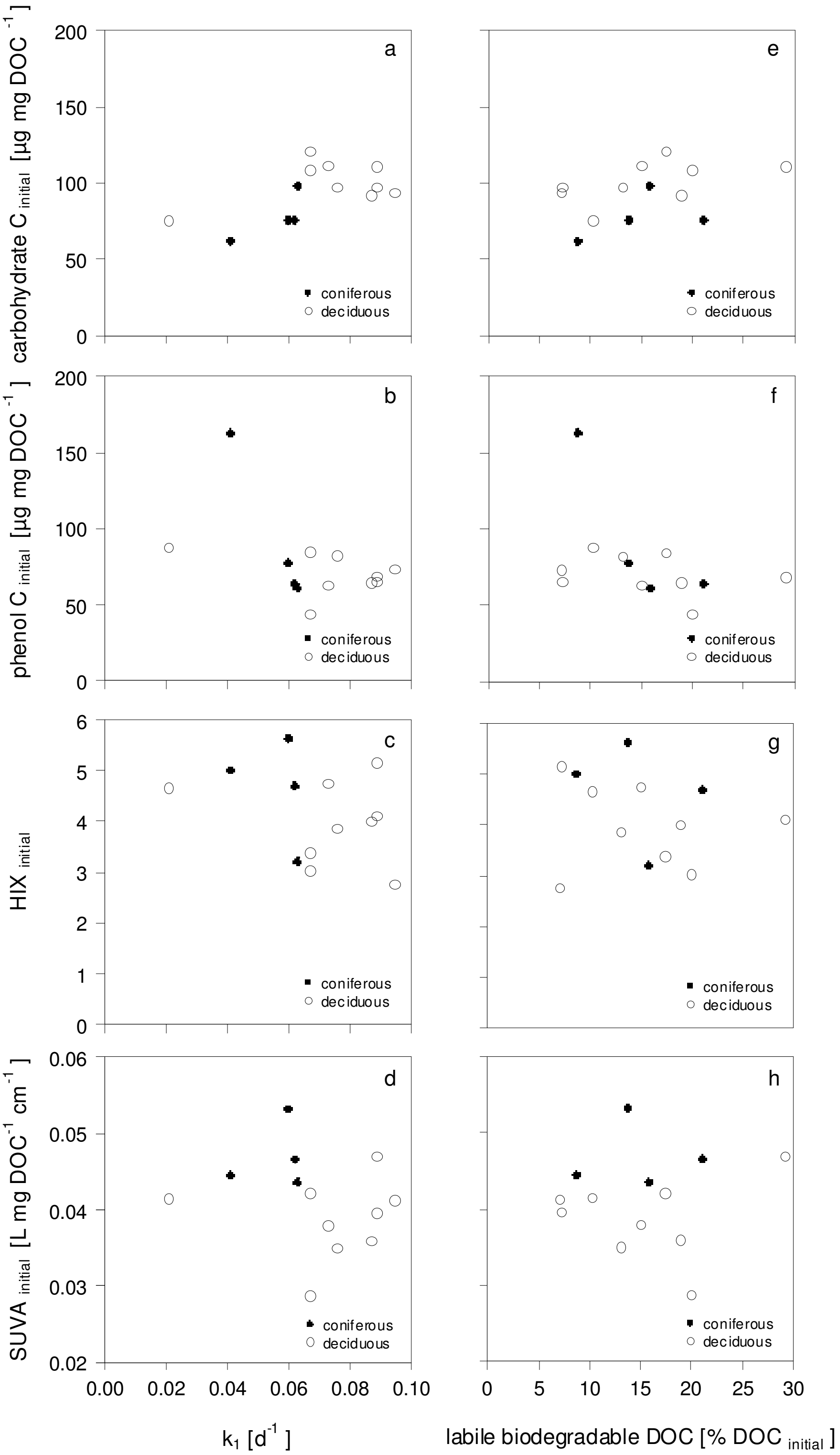

Figure 4.3: Mineralization rate constant k_1 and proportion of labile biodegradable DOC versus initial DOC quality parameters.

Quality parameters: hydrolysable carbohydrate C, phenol C, HIX_{em} and $SUVA_{280nm}$.

5. Appendix

Contributions to the included manuscripts

Table 5.1: Record of contributions [%] of each author to the included manuscripts.

With respect to different aspects:

a: concept and experimental design
b: field and laboratory work
c: data evolution and statistical analysis
d: discussion and interpretation of results
e: manuscript preparation.

manuscript	author	a	b	c	d	e
"Quantity and quality of dissolved organic carbon released	Bantle	40	90	70	60	40
from coarse woody debris of different tree species in the early	Borken	10	0	10	10	10
phase of decomposition"	Ellerbrock	0	10	0	10	10
	Schulze	5	0	0	0	0
(FOREST ECOLOGY AND MANAGEMENT, 329 (2014) 287-294)	Weisser	5	0	0	0	0
	Matzner	30	0	20	20	40
"Dissolved nitrogen release from coarse woody debris of	Bantle	50	100	65	60	50
different tree species in the early phase of decomposition"	Borken	20	0	5	10	10
(FOREST ECOLOGY AND MANAGEMENT, 334 (2014) 277-283)	Matzner	30	0	30	30	40
"Degradability of dissolved organic carbon derived from	Bantle	90	50	80	90	90
coarse woody debris of different tree species"	Schmid	10	50	20	10	10

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Declaration

§ 5, 4 PromO:

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

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Datum, Unterschrift

Publications

Bantle A, Borken W, Ellerbrock R-H, Schulze E-D, Weisser WW, Matzner E (2014): Quantity and quality of dissolved organic carbon released from coarse woody debris of different tree species in the early phase of decomposition. Forest ecology and management 329:287-294.
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Bantle A, Borken W, Matzner E (2014): Dissolved nitrogen release from coarse woody debris of different tree species in the early phase of decomposition. Forest Ecology and Management 334:277-283.
DOI: 10.1016/j.foreco.2014.09.015.

Bantle A, Schmid B (2015): Degradability of dissolved organic carbon derived from coarse woody debris of different tree species. *In preparation*.