Potential of above- and below-ground coarse woody debris as a carbon sink in managed and unmanaged forests

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All that is gold does not glitter,
Not all those who wander are lost;
The old that is strong does not wither,
Deep roots are not reached by the frost.

JRR Tolkien

Contents

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Glossary

a.s.l.	Above sea level, corresponds to German NN (über Normalnull)
AMS	Accelerator mass spectrometry
C	Carbon
C density	Carbon content of coarse woody debris per volume unit
CWD	Coarse woody debris, defined as all lying and standing woody debris with a diameter > 7 cm at their widest point
DC	Decay class
Disappearance time	Time period between death and decay of tree or branch to fractions < 7 cm in diameter
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
EPS	Expressed population signal
Fm	Fraction modern
FWD	Fine woody debris, defined as all woody debris with a diameter 0.2 <x< 7 cm
fPOM	Free particulate organic matter (ρ < 1.6 g cm^{-3})
GC	Gas-chromatography
Glk	Gleichläufigkeit
HIX	Humification index
IAEA	International Atomic Energy Agency
MaOM	Mineral associated organic matter (ρ > 2.0 g cm^{-3})
N	Nitrogen
NPOC	Non-purgable organic carbon
NSC	Non-structural carbohydrates
oPOM	Occluded particulate organic matter (1.6 < ρ < 2.0 g cm^{-3})
Rbar	Mean inter series correlation
SOC	Soil organic carbon
SOM	Soil organic matter
SPT	Sodium polytungstate
$SUVA_{254}$	Specific UV-absorption at a wavelength of 254 nm
TT	Turnover time

Summary

With respect to climate warming, carbon (C) sequestration is of important public and political interest. Forests represent important terrestrial C sinks. Their management can have direct and indirect influence on forest characteristics, including to some extent C sequestration. One direct effect of forest management is an increase in the stock of coarse woody debris (CWD). CWD represents a short- to middle term C sink that is of particular importance in natural and old-growth forests. Its impact on the soil organic carbon (SOC) stock is largely unknown.

To investigate the impact of management, a case study was conducted in three adjacent managed and unmanaged forests with similar geological and micrometeorological conditions as well as similar tree species composition. In each forest, the C pools of the forest floor, the mineral soil and the CWD as well as their turnover times (TTs) or disappearance times (in case of CWD) were investigated. The unmanaged forests were withdrawn from management 40-100 years ago. The dominant tree species of temperate forests, European beech, Sessile oak and Norway spruce were considered. The experimental set-up permits to estimate how the C pools of a forest evolve within decades following its withdrawal from forest management.

In each forest, the above-ground CWD stocks were inventoried. The volume and the decay class of each CWD piece was determined on an area of 1 ha. For each decay class, a representative number of samples of logs was sampled to measure wood density and C concentration. In addition, radiocarbon analysis and dendrochronological cross-dating were used to determine the time of tree death for CWD logs. From these data, disappearance times were calculated for the three tree species.

In the unmanaged forests, the C stocks in the CWD accumulated to 10 Mg ha^{-1} in the spruce forest and to 24 – 30 Mg C ha^{-1} in the beech-oak forests. As such, the C stock in the CWD was 2 to 6 times greater in the unmanaged forests than in the managed forests where the C stocks in the CWD were around 5 Mg C ha^{-1} at all study sites. Average disappearance times of 30 and 70 years were calculated for beech and spruce CWD respectively. Oak CWD yielded a great variability of time since tree death at similar C densities of individual CWD pieces. The calculation of a decay function was thus not possible. However, the time since tree death of the dated oak CWD pieces indicated that oak CWD has the potential to remain in forests for more than 70 years.

In addition to the field study, CWD samples of the three tree species and of three decay classes were incubated in a laboratory experiment under controlled conditions for a period of 380 days. In regular intervals, the CO_2 production was measured and a leachate was produced to estimate the C fluxes

from CWD in the gaseous and in the liquid phase.

The yearly C loss was specific to the tree species and decay class. Beech CWD had the greatest C loss followed by oak and by spruce CWD. C loss generally increased with decay class for all tree species. The CO_2 release represented the most important pathway of C loss, however, dissolved organic C (DOC) contributed between 1 and 25% of the total C loss. The DOC production was most important for oak CWD and for heavily decayed wood of all tree species.

The C stock of below-ground CWD was estimated by uncovering stumps of known age. For each tree species, five stumps were sampled in their entity for two or three different times of tree death. Total mass and volume as well as C concentration of a representative number of sub-samples were measured.

The great differences in volume, wood density and C concentration expressed the variability in the properties of below-ground CWD. For this reason, a calculation of the below-ground CWD mass in relation to the stump diameter was not possible. The number of stumps and snags was multiplied by an average C mass per stump to calculate below-ground CWD stocks. As a result of regular thinning and felling of trees and the resulting higher number of stumps, the below-ground CWD stocks in the managed forests were greater than in the unmanaged forests. The C stocks in the below-ground CWD ranged from 0.3 to 1.4 Mg C ha^{-1} in the managed and from 0.1 to 0.4 Mg C ha^{-1} in the unmanaged forest in one of the beech-oak forest. This corresponded to 16 % of the total CWD C stock in the managed forest and to 1 % of the total CWD C stock in the unmanaged forest.

Soil samples were taken at 30 points on a regular raster plot on an area of 2 ha. The forest floor samples were separated by horizon in the field. The mineral soil was sampled up to a soil depth of 100 cm and separated by depth into 4 sub-samples. Of each sample, the organic C concentration was measured. Density fractionation in three fractions (<1.6 g cm^{-3}, 1.6-2.0 g cm^{-3}, >2 g cm^{-3}) was carried out for one mixed sample of each soil depth. Radiocarbon signatures were measured of the mixed samples as well as of each fraction.

The SOC stocks showed greater differences among the study sites than between the management forms. The SOC stocks ranged between 4.3 and 15.9 Mg C ha^{-1} in the forest floor and between 50 – 260 Mg C ha^{-1} in the mineral soil down to a depth of 1 m. At all study sites, the radiocarbon signatures of the O_e horizon indicated a shorter TT of SOC in the unmanaged than in the managed forests. The difference is attributed to a change in the decomposing community induced by the enhanced CWD stocks. Differences between managed and unmanaged forests in TT of SOC in the O_a horizon and the bulk mineral soil were not consistent across all study sites. Either potential management influences are overshadowed by other effects or the time since withdrawal from management is not sufficient to result in significant changes. Of the density fractions, only the light fraction <1.6 g cm^{-3} exhibited consistent differences across soil depths between management forms. No consistent patterns were found for the denser fractions.

In dependence of tree species, CWD has the potential to substantially contribute to the C stocks of forest ecosystems. A withdrawal from management results in a significant increase in the CWD stocks within decades. However, SOC stocks did not increase as a result of enhanced CWD C stocks. A potentially greater input of C from CWD to the forest floor was compensated by a shorter TT of SOC in the O_e horizon. CWD and forest management had no effect on the SOC stocks or TT of the mineral soil. Most C from CWD is probably lost to the atmosphere as CO_2 before it reaches the soil.

Zusammenfassung

In Hinblick auf die Klimaerwärmung ist das Verständnis des globalen Kohlenstoffkreislaufes und Kenntnis über die Möglichkeiten anthropogener Einflussnahmen unverzichtbar. Ein Bereich, in dem der Mensch durch sein Handeln den Kohlenstoffkreislauf beeinflussen kann, ist die Waldwirtschaft. Wälder stellen in terrestrischen Ökosystemen wichtige Kohlenstoffspeicher dar. Die Bewirtschaftungsform hat direkten und indirekten Einfluss auf die Kohlenstoffvorräte. Eine direkte Einflussgröße ist der Vorrat an Totholz, das im Wald verbleibt. Totholz stellt, vor allem in Naturwäldern, einen wichtigen kurz- bis mittelfristigen Kohlenstoffspeicher dar. Des Weiteren besitzt Totholz das Potential auch andere Kohlenstoffpools, vor allem den Boden, zu beeinflussen.

Zur Untersuchung des Einflusses der Bewirtschaftung wurde eine Fallstudie mit drei unbewirtschafteten und benachbarten bewirtschafteten Wäldern mit jeweils ähnlichen Standorteigenschaften wie Ausgangsgestein, mikrometeorologischen Eigenschaften, Neigung und Baumartenzusammensetzung durchgeführt. In jedem Wald wurden Kohlenstoffvorräte und --umsatzzeiten erfasst. Besonderer Fokus wurde dabei auf die Kohlenstoffvorräte im Totholz gelegt. Die unbewirtschafteten Wälder werden seit 40-100 Jahren nicht mehr bewirtschaftet. Mit Buche, Eiche und Fichte sind die dominierenden Baumarten der feucht-gemäßigten Zone berücksichtigt. Das Versuchskonzept ermöglicht eine Abschätzung, wie sich die Kohlenstoffvorräte innerhalb von einigen Jahrzehnten in einem nicht mehr bewirtschafteten Wald entwickeln im Vergleich zu bewirtschafteten Wäldern.

In jedem der Wälder wurden auf Flächen von rund 1 ha die oberirdischen Totholzvorräte in einer Gesamtinventur erhoben. Volumen und Zersetzungsgrad jedes Totholzstückes wurden erfasst. Für Totholzstämme von fünf definierten Zersetzungsgraden wurde aus einer repräsentativen Stichprobenmenge Holzdichte und Kohlenstoffgehalt bestimmt. Außerdem wurden Radiokarbonanalysen und dendrochronologische Kreuzdatierungen durchgeführt um das Absterbejahr von Totholzstämmen zu bestimmen. Aus diesen Daten wurden artspezifische Abbaukurven für Totholz berechnet.

In den unbewirtschafteten Wäldern waren mit 10 Mg C ha^{-1} im Fichtenwald und 24 bzw. 30 Mg C ha^{-1} im Buchen-Eichenwald die Kohlenstoffvorräte im oberirdischen Totholz zwei- bis sechsmal größer als in den bewirtschafteten Wäldern, in denen die Kohlenstoffvorräte im oberirdischen Totholz rund 5 Mg C ha^{-1} betrugen. Die Verbleibzeiten von oberirdischem Totholz waren artabhängig. Buchentotholz hatte mit rund 30 Jahren eine kürzere Verbleibzeit als Fichtentotholz mit rund 70 Jahren. Für Eichentotholz unterschieden sich die erwarteten Verbleibzeiten einzelner

Totholzstücke so stark, dass die Berechnung einer allgemeinen Abbaufunktion nicht möglich war. Jedoch deuteten die datierten Eichentotholzstämme daraufhin, dass Eichentotholz das Potential aufweist, genauso lange oder länger in Wäldern zu verbleiben wie Fichtentotholz.
Zusätzlich zu den Feldaufnahmen wurde im Labor der Abbau von oberirdischen Totholz unter kontrollierten Bedingungen untersucht. Totholzstücke der drei Baumarten in drei verschiedenen Zersetzungsgraden wurden über eine Zeitspanne von 380 Tagen bei 15°C inkubiert. In regelmäßigen Abständen wurde die CO_2 Produktion gemessen und ein Holzextrakt gewonnen, um die Flüsse aus Totholz in der Gas- und Flüssigphase zu ermitteln.
Der jährliche Kohlenstoffverlust aus Totholz war art- und zersetzungsgradabhängig. Der größte Kohlenstoffverlust wurde für Buchentotholz gefolgt von Eichen- und Fichtentotholz festgestellt. Der jährliche Kohlenstoffverlust aus Totholz nahm mit dem Zersetzungsgrad zu. Die Mineralisierung zu CO_2 stellte den Hauptanteil des Kohlenstoffverlusts dar, jedoch machte Auswaschung als gelöster Kohlenstoff bis zu 25% des Kohlenstoffverlusts aus. Die höchste Produktion an gelöstem Kohlenstoff hatte Eichentotholz sowie stark zersetztes Totholz aller Baumarten.
Der Kohlenstoffvorrat im unterirdische Totholz wurde durch Ausgraben von Wurzelstöcken bekanntem Todesjahres ermittelt. Pro Baumart und Todesjahr wurden im bewirtschafteten Wald fünf Wurzelstöcke beprobt. Die Wurzelstöcke wurden vollständig entnommen und das Totholzvolumen im Labor durch Wasserverdrängung ermittelt. Eine repräsentative Probenanzahl wurde auf ihren Kohlenstoffgehalt untersucht.
Unterirdisches Totholz zeigt eine große Variabilität im Abbau, die durch Unterschiede in Totholzvolumen, -dichten und Kohlenstoffgehalten der Wurzelstöcke von Bäumen des selben Todesjahres gekennzeichnet war. Aus diesem Grund war eine sichere Berechnung der unterirdischen Totholzmasse aus dem Stumpfdurchmesser von Totholz des selben Todesjahres nicht möglich. Vielmehr erwies es sich als sinnvoll, die unterirdischen Totholzvorräte durch Multiplikation der Anzahl an Totholzstücken, die dem stehendem Totholz und den Stümpfen zugeordnet wurden, mit der durchschnittlichen Kohlenstoffmasse pro Stumpf zu berechnen. Aufgrund der regelmäßigen Durchforstung und der daraus resultierenden größeren Anzahl an Stümpfen, war der Vorrat an unterirdischem Totholz in den bewirtschafteten Waldern höher als in den unbewirtschafteten. Der Kohlenstoffvorrat betrug im unterirdischen Totholz 0.3 – 1.4 Mg C ha^{-1} im bewirtschafteten Wald und 0.1 – 0.4 Mg C ha^{-1} im unbewirtschafteten Wald. Dies entsprach im bewirtschafteten Wald rund 16% und im unbewirtschafteten Wald 1% des Gesamttotholzkohlenstoffvorrats.
Bodenproben wurden auf jeder Fläche an 30 Punkten auf einem regelmäßigen Raster mit einer

Fläche von 2 ha genommen. Die Humusauflage wurde nach Horizonten getrennt beprobt. Der Mineralboden wurde bis in eine Tiefe von 100 cm beprobt und in 4 Tiefenstufen getrennt. Von jeder der Proben wurde der Kohlenstoffgehalt bestimmt. Des Weiteren wurde für jeden Wald und jede Tiefenstufe eine Mischprobe zur Dichtefraktionierung in drei Fraktionen (<1.6 g cm^{-3}, 1.6-2.0 g cm^{-3}, >2 g cm^{-3}) angefertigt. Radiokarbonsignaturen der Mischprobe sowie jeder Fraktion wurden gemessen.

Im Boden wiesen die Kohlenstoffvorräte größere Unterschiede zwischen den Versuchsflächen auf als zwischen den Bewirtschaftungsformen. Die Kohlenstoffvorräte betrugen zwischen 4.3 – 15.9 Mg C ha^{-1} in der Humusauflage und zwischen 48.1 – 261.4 Mg C ha^{-1} im Mineralboden bis in 1 m Tiefe. Radiokarbonanalysen der Humusauflage zeigten für den Of Horizont an allen Versuchsstandorten eine kürzere Umsatzzeit in den unbewirtschafteten als in den bewirtschafteten Wäldern. Dies wird durch eine Stimulation des Streuabbaus durch die erhöhten oberirdischen Totholzvorräte erklärt. Im Oh-Horizont und im Mineralboden sind die Unterschiede zwischen den Wäldern jedoch nicht konsistent. Es wurde angenommen, dass andere Faktoren einen Totholzeffekt überschatten bzw. die Umsatzzeiten im Vergleich zur Zeitspanne seit Änderung der Bewirtschaftungsform zu lang sind, um sich nach Jahrzehnten signifikant auf die Umsatzzeit im Oh Horizont und Mineralboden auszuwirken. Von den Dichtefraktionen waren nur die Unterschiede zwischen Bewirtschaftungsformen in der leichten Fraktion <1.6 g cm^3 für jeden Versuchsstandort über alle Tiefenstufen konsistent.

Totholz hat das Potential substantiell zur Kohlenstoffspeicherung im Wald beizutragen, wobei die Eignung Baumarten abhängig ist. Durch eine Beendigung der Bewirtschaftung können die Totholzvorräte innerhalb von Jahrzehnten signifikant gesteigert werden. Jedoch hat Totholz keinen Einfluss auf die Kohlenstoffvorräte im Boden. Ein eventuell bestehender größerer Input von Kohlenstoff in die Humusauflage wird durch eine kürzere Umsatzzeit im Of-Horizont ausgeglichen. Im Mineralboden sind keine konsistenten Unterschiede zwischen den Bewirtschaftungsformen in Kohlenstoffvorräten und Umsatzzeiten feststellbar.

Chapter 1

On this thesis

Introduction

Motivation

With regard to climate warming, carbon (C) sequestration is of particular political and public interest. Forests store 50 % of the terrestrial C stocks (Jandl et al. 2007) and are thought to have the potential to increase their C stock through anthropogenic impact. Management can influence different site characteristics, including soil properties. One substantial result of management represents the accumulation of coarse woody debris (CWD) (Christensen et al. 2009). While CWD constitutes an important short to middle term C sink in forest ecosystems (Laiho & Precott 2004), its influence on other C pools in forest ecosystems including the forest floor and the mineral soil are subject of speculations (Harden et al. 2000, Manies et al. 2005). Likewise, management impact on the soil organic carbon (SOC) stocks isn't clear (Nave et al. 2010). The aim of this study was to investigate the impact of a withdrawal from management on the SOC stocks of forests within decades. Special focus was given to CWD.

Forests as carbon stocks

Forests represent an important C sink and contribute approximately 90% of the terrestrial above-ground and 40% of the terrestrial below-ground C storage (Waring & Schlesinger 1985). Globally, two thirds of the C in forest ecosystems is stored in soils (Dixon et al. 1994) as soils contain more than twice the amount of C in vegetation or in the atmosphere (Batjes 1996, Schlesinger & Andrews 2000). More than 50% of the SOC stocks in mineral soils is stored within deep mineral horizons below 10 cm depth (Jobbágy & Jackson 2000). Changes in the SOC content of deep soil horizons thus greatly influence the global C budget.

C gradually accumulates in soil, forest floor, as well as biomass and by consequence C stocks reach their maximum values in old-growth stands (Böttcher & Springob 2001, Cerli et al. 2006). Strategies to enhance C sequestration in forest ecosystems, most importantly in the soil, might be important to counteract changes in the atmospheric CO_2 concentration (Lal, 2005). Land use, land use change and forestry can sequester C from the atmosphere. (Vankooten et al. 2004). Forestry is estimated to have the potential to enhance the C sequestration capacity of forest ecosystems to correspond to 11-15% of the actual fossil fuel emission at the global level and to 5-11% in Europe (Brown & Sathaye 1996, Cannell 2003).

Land use change and forest management

Land use and land use change, including conversion from forest to crop- or grassland or vice-versa

(Poeplau et al. 2011), have major impacts on the C budget of an ecosystem (Guo & Gifford 2002, Houghton 2003). Protection of formerly managed forests represents a smaller change than afforestation or deforestation. A meta-analysis indicates that few management practices are clearly positive or negative in regards to C sequestration (Jandl et al. 2007). Management effects are divers and include tree species selection as well as different chemical and physical treatments of the forest sites. Chemical treatments comprise nitrogen (N) fertilization and liming. Physical treatments of the forest soil include clearing operations like prescribed burning, soil tillage or ploughing (Raulund-Rasmussen et al. 2006). Management practices vary in their rotation length, the handling of logging residues and the amount of timber removed. The removal of timber represents a substantial loss of nutrient and C from the forest ecosystem (Ballard 2000). Post-harvest, depletion of C from the ecosystem is assumed to occur as respired CO_2. In addition a smaller flux exists as dissolved organic carbon (DOC) (Kalbitz & Kaiser 2008).

Forest management has greater effects on the forest floor than on the mineral soil (DeGryze et al. 2004). A depletion of forest floor C following management procedures is noticeable (Aussenac 1987) unless thinning residues are left on the site (Hendrickson et al. 1989, Mattson & Swank 1989). Chronosequence studies conducted in New England showed that the forest floor lost over 50% of its mass in the 15 years following clear cutting with a gradual recovery over the next 50 years (Covington et al. 1981). More recent cut stands had lower forest floor mass than older stands (Federer et al. 1984).

Relatively little data is available on the effects of management on mineral soil (Jandl et al. 2007, Luyssaert et al. 2010). It results in a mixing of forest floor C with stable mineral soil C and leads to an increase in SOC in the mineral soil. On the other hand, mechanical site preparation can cause problems as the soil structure is degraded (Ballard 2000).

A meta analysis yielded that the forest floor was significantly smaller in harvested sites, but that harvesting had no effects on shallow or deep soil (Nave et al. 2010). Thinning influences the C stock of the forest floor and the mineral soil oppositely and results in no effect on total SOC (Skovsgaard et al. 2006). Overall, the effects on the SOC stocks are small and mostly depend on the residue management (Johnson & Curtis 2001). There is no evidence that thinning and harvest operations have a long term effect on SOC (Johnson & Curtis 2001, Misson & Tang 2005, Vesala 2005, Jandl et al. 2007), as most effects on the soil seem short-lived.

Coarse woody debris as a carbon stock

CWD is defined as dead woody material with a minimal diameter between 2 and 20 cm (Topp et al.

2006, Ellis et al. 2008). CWD can occur as above-ground and below-ground CWD. Above-ground CWD is further differentiated into lying CWD (logs and branches), standing CWD (snags) and stumps. In some cases, only lying logs in contact with the soil are considered as CWD (Ligot et al. 2012). In this study, CWD is defined as lying and standing woody debris with a diameter of at least 7 cm at the widest point. In Germany, wood with a diameter above 7 cm is commonly defined as merchantable (Kramer 1988).

CWD can result from natural mortality and disturbances like fire or storms. In managed forests large amounts of CWD are created during thinning procedures. With stocks of up to 550 m^3, unmanaged forests generally have higher CWD stocks than managed forest where stocks of 10 m^3 are common (Christensen et al. 2005). CWD stocks start to accumulate at yearly rates of 0.1 – 19 m^3 ha^{-1} a^{-1} when a forest is taken out of management (Vandekerkhove et al. 2009).

Forest management greatly affects the amount, size and quality of CWD that remain in forest ecosystems. Historically few woody debris were left in managed forests and CWD was considered a trait unique to old-growth forests (Harmon 2009). CWD management has gained importance since the 1990s (Harmon 2001) as the ecological functions of CWD were recognized and its economic value was identified (Heilmann-Clausen & Christensen 2004). Today, CWD is considered a key indicator of the sustainability of forest management (Ligot et al. 2012). The ecological functions include its role as a habitat for insects and fungi and its part in the nutrient cycle of forest ecosystems (Harmon et al. 1986). Furthermore CWD can enhance soil stability, increase natural regeneration and improve the quality of aquatic ecosystems (Ligot et al. 2012). Last but not least, it represent a short to middle term C sink (Laiho & Prescott 2004).

During its decay CWD undergoes a transformation that results in highly divers physical, chemical and biological characteristics. Theses changes are mostly caused by biological decomposition. While many insects take part in the decomposition of CWD, the decomposition of CWD is mostly attributed to basidomycetes (Käärik 1974, Swift 1977, Harmon 2001). Basidiomycetes are commonly separated into white rot and brown rot fungi (Schmidt 2006). Abiotic decay processes like photo-degradation play minor roles in decomposition of CWD.

CWD decay is a relatively slow process, that takes decades to several centuries (Rock et al. 2008). Mean decomposition rates decrease with altitude (Kueppers et al. 2004) and increase from boreal to temperate to tropical forest ecosystems (Harmon et al. 2001). Decomposition rates are controlled by site conditions most importantly temperature and moisture (Herrmann & Bauhus 2012) as well as wood characteristics including wood lignin, dry matter content or wood pH (Fréschet et al. 2012). Further effects of CWD size and exposition to the soil on decomposition rates have been described though published results are contradictory (Harmon 2009).

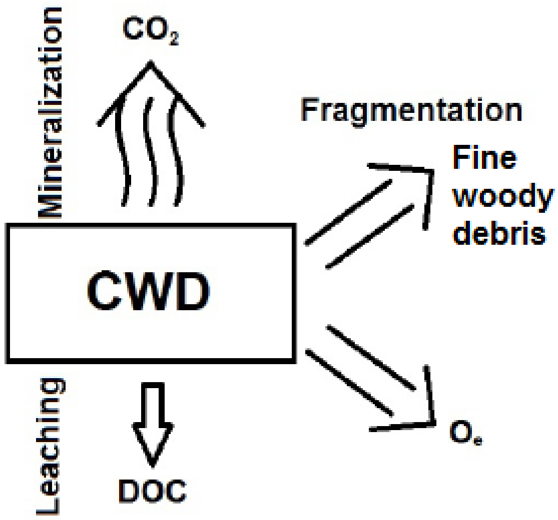

Fig. 1.1: Pathways of C loss from CWD

CWD decay can be separated in three main factors: mineralization, leaching, as well as biological and chemical fragmentation (Fig. 1.1). Mineralization is the main pathway of CWD decay and is assumed to account for 76% of the total C loss from CWD in the tropics over the whole decomposition period (Chambers et al. 2001). With CO_2:DOC ratio of 12:1, leaching of C as DOC is the second important pathway of C loss (Mattson et al. 1987). Fragmentation has hardly ever been quantified, but Lambert et al. (1980) calculated that 63% of the biomass loss from boles is due to fragmentation. While mineralized C is lost to the atmosphere, leaching and fragmentation represent potential C inputs to the forest floor and the mineral soil (Spears & Lajtha 2005, Crow et al. 2007).
Further C pathways include C loss to the atmosphere as methane (Mukhin & Voronin, 2008) or as a variety of carbohydrates during forest fires (Hyde et al. 2011). Fungi can transfer C to the soil through mycellium (Boddy & Watkinson 2005) and animals contribute to nutrient loss in heavily decayed wood (Swift 1977). These pathways have not been quantified and are of minor importance for the C budget of CWD.
CWD has the capacity to modify a range of soil characteristics including the heterogeneity of organic compounds (Strukelj et al. 2012), the pH value (Klinka et al. 1995) and the microbial community of the soil (Rajala et al. 2012). An elevated CWD stock can increase the size of the fungal community in the soil and result in a shift in the fungal:bacterial ratio, which may result in a better utilization of organic compounds that a bacterially dominated microbial community is less

able to degrade (Brant et al. 2006). Effects of CWD have been measured after only two years in degraded eucalpyt woodlands indicating that they originate from indirect structural effects rather than direct inputs through leachates (Goldin & Hutchinson, 2013). An increase of SOC stocks underneath CWD has never been reported, nonetheless CWD is incorporated in many soil and forest models as a C input pool (Parton et al. 1988, Cramer et al. 2001, Tuomi et al. 2011).

Forests as nitrogen stocks

N is a mineral nutrient required for tree growth. In soils, 90 % of N occurs in solid, organic forms (Stevenson 1982). Global amounts of soil N in the upper 100 cm are estimated at 133-140 Pg (Batjes 2005). N stocks are between 6 and 10 Mg ha^{-1} in temperate forests (Gerstberger et al. 2004). Most terrestrial ecosystems used to be N limited (Date 1973). The increased N deposition in the past decades due to human activities like industrial combustion processes and fertilizer application (Vitousek et al. 1997, Gruber and Galloway 2008) resulted in a N saturation in temperate forest ecosystems (Aber 1992). On the other hand, anthropogenic influence through forest management has little or no effect on N stocks of the soil (Johnson and Curtis 2001).

Studies on the N cycle of forest ecosystems give contradictory on the importance of CWD. While CWD has been reported as an important regulator of N availability in forest ecosystems (Hafner & Groffmann 2005), other studies suggest that CWD does not make a significant contribution to the N cycle (Laiho & Precott 1999). N concentration of above-ground CWD is low (<0.2 %) in its initial state (Holub et al. 2001), but increases during its decay through microbial fixation of atmospheric N_2 (Larsen & Neal 1978, Jurgensen et al. 1990, Jurgensen et al. 1992, Brunner & Kimmens 2003). Heavily decayed CWD might serve as a N source, with N release from stumps occurring at slower rates than N release from logs or branches (Palvianien et al. 2010).

Objectives

The study was conducted with the aim of investigating the role of CWD as a C sink and its influence on the SOC stock. To this end, managed forests were compared with unmanaged forests with an elevated CWD stock. Site characteristics between managed and unmanaged forests are assumed to be similar. All differences were attributed to management in general and especially CWD. The specific objectives of this thesis were:

1) To test the suitability of two different methods for determination of time of tree death. Time of tree death is an essential parameter to calculate disappearance times of CWD and to evaluate the potential of tree species as middle-term C stocks.

Chapter 2

2) to quantify the C loss from CWD as CO_2 and as DOC under laboratory conditions for samples of different tree species and decay classes.

Chapter 3

3) to quantify the C stocks in above-ground CWD, forest floor and mineral soil in managed and unmanaged forests and to calculate the influence of enhanced CWD stocks on the SOC turnover in the forest floor and the mineral soil.

Chapter 4

Material and Methods

Study sites

The thesis compromises field studies and one laboratory study. Samples used in the laboratory study originate from the study sites the field work was conducted on and thus relate to the same forest systems. At each study site, an unmanaged and an adjacent managed forest were investigated.

The unmanaged forests are protected by law from management procedures with the goal of economical gain. No regular management procedures were conducted for several decades. However, exceptional procedures were carried out in order to influence the natural succession towards a favoured direction. Motivations include the prevention of large scale bark beetle infestation or the removal of beech trees to reduce their dominance in comparison to oak. The unmanaged forests are shaped by previous human cultivation and management, which are visible in current species distribution and age structure of the unmanaged forests. For this reason, the unmanaged forests are not considered old growth or natural forest ecosystems.

The managed forests are high forests. They undergo procedures such as thinning and selective felling that are commonly applied in Bavarian state forests at regular intervals.

In contrast to a comparison of managed forests with natural or old growth forest systems, this set-up gives insights on how forests that were previously managed can evolve within time periods of decades, if a management change occurs.

Grübel

Grübel (49°07' N 013°07' E) is a Norway spruce (*Picea abies* (L.) H. Karst.) forest situated at 1250 m a.s.l. in the Bavarian forest. The unmanaged forest has an area of 56.3 ha and was declared at natural reserve in 1978. The soil type is Podzol. Soil moisture greatly varies across the study area: parts of the study area are considered poorly drained. The forest floor is highly variable and can reach a depth of over 1 m in the poorly drained parts of the study area. Mean annual temperatures are 3-4°C and mean precipitations are 1500 mm a^{-1}. The forest reserve is situated on the south slope of the Kleiner Arber massif. Due to the microclimatically advantaged morphology, the spruce-dominated highland forest starts at 1150 m a.s.l., which is about 100 m higher than in less favourable parts of the Bavarian forests. While the samples were taken in an area with sheer spruce forests, single trees of mountain ash, sycamore maple, fir and beech are scattered over the reserve. The forest is even aged with a mean tree age estimated at 260 years. Due to the infestation with bark beetles, single trees were removed in the past years. Generally the bark was removed and the wood left as logs in the forests. However, in 2010, a dozen dominant trees were felled and the timber extracted from the forest. The investigated managed forest is situated in close proximity to the forest reserve in northern direction. Species distribution and stand age are similar to the unmanaged forest. Information of stand history is scarce, but it is assumed that no thinning procedures were conducted in the past 20 years.

Ludwigshain

Ludwigshain (49°55' N 011°48' E) is a beech-oak forest situated at an altitude of 460 m a.s.l. in the Hienheimer Forst near Kelheim. Mean annual temperature is 7-8°C and mean precipitations are 950-1100 mm a^{-1}. Geologically it is situated on the Swabian Jura. The soil is calcareous Luvisol. Ludwigshain is a nature reserve with an area of 2.4 ha. It is most famous for its ancient oaks, that were used in the construction of several famous German buildings, including the Cologne Cathedral and the fortress of Ingolstadt. It was first declared a nature park by kKing Ludwig III of Bavaria in 1913 after a hunting-visit in 1906. Ever since, no thinning procedures were conducted, though the removal of oak timber of trees that had succumbed to natural mortality has been allowed until the mid-1960s. The area was proclaimed a natural reserve in 1939. While the forest was first protected for its imposable oak trees, their number is slowly declining as old trees die and few oak seedlings germinate. As part of natural succession, beeches rejuvenate successfully and gradually transform the forest in a beech forest. Currently the tree species distribution is 30% Sessile oak (*Quercus petraea* (Mattuschka) Liebl.) and 70% European beech (*Fagus sylvatica* L.). The mean tree age is 370 years. The oldest oak trees are up to 470 years old.
The managed forest has a higher amount of Sessile oak (70%) than European beech (30%). The mean tree age is 125 years. As far as historical records reach back, the area has been used for timber production. The last thinning procedure was conducted in the year 2002, when about 340 m^3 wood ha^{-1} were removed.

Rohrberg

Rohrberg (49°54' N 009°26' E) is an oak-beech forest situated 540 m a.s.l. in the Hochspessart. The soil is Cambisol on Sandstone. Mean annual temperature is 7-8°C and precipitations are 650-750 mm a^{-1}. Rohrberg is a nature reserve with an area of 9.9 ha. It is Bavaria's oldest nature reserve and has been protected since 1928. With a mean stand age of 550 years and single oak trees that are up to 840 years old, it is the oldest forest stand of Bavaria. It used to be a typical sparse oak forest, that evolved until 1803 due to management aiming to create favourable conditions for hunting. Glands were used as browsing for game animals. However, due to the natural dominance of beech under the site conditions, the abundance of beech is gradually increasing at the cost of oak trees. For this reason, a number of dominant beech trees were removed in accordance with the natural conservation authority in 2002. Currently, European beech makes up 30% and Sessile oak 70% of the biomass in the unmanaged forest. The managed forest is separated in two parts, one with a 100 years old beech forest and the other an 65 years old oak forest. The last thinning procedure took place in the year 2007 when 106 m^3 wood ha^{-1} were cut.

Waldstein

Waldstein (50°08' N 011°52' E) is a Norway spruce forest situated at 770 m a.s.l. in the Lehstenbach catchment in the Fichtelgebirge. Mean annual temperature is 5.3°C and the mean precipitations are around 1160 mm a^{-1} (Gerstberger et al. 2004). The Lehstenbach catchment is dominated by Norway spruce. The soil is classified as a Haplic Podzol with a sandy to loamy texture.

No complete C inventory was conducted at Waldstein. Solely below-ground spruce CWD was investigated. This decision was taken as an investigation of the below-ground CWD stocks at Grübel was restricted by morphological constraints of the study site and fragmentary forest records.

General concept and field sampling

The inventory of the C stocks in managed and unmanaged forests include a complete inventory of the C stocks in the forest floor, the mineral soil and the above-ground CWD stocks. Below-ground CWD was sampled in the Ludwigshain (beech and oak) and Waldstein (spruce) only. Sampling of below-ground CWD represents a huge invasion and was thus only possible in managed forests. The suitability of the study sites is further restricted by incomplete knowledge on time since thinning procedures.

Living timber biomass was not inventoried in detail. Forest records and measurements of diameter at breast height were used to estimate above-ground timber biomass in trees. Below-ground biomass was estimated through root:shoot ratios given in Offenthaler & Hochbichler (2006).

Above-ground coarse woody debris inventory

The assessment of above-ground CWD included the quantification of the above-ground CWD stocks, the identification of CWD quality (e.g. C density) and the determination of time of tree death. These parameters were used to calculate the CWD C stocks, the disappearance time of CWD, the C loss from CWD, the CWD production and the CWD accumulation (Fig. 1.2).

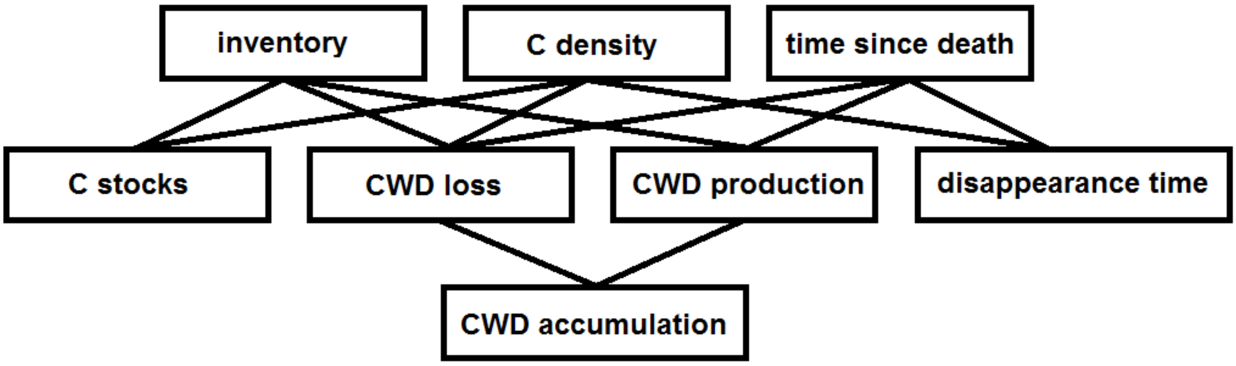

Fig. 1.2: Measured and calculated CWD parameters.

The inventory of above-ground CWD was conducted in each forest within an area of 0.5 – 1.2 ha. Lying logs and branches, standing snags as well as stumps with a diameter >7 cm were inventoried as CWD. Lying CWD was defined as all CWD with no fix connection to the soil, that was situated at an angle of less than 45° relative to the soil. Standing CWD was defined as CWD fixed to the soil and/or situated at an angle of more than 45° relative to the soil. Standing CWD had a height of more than 1 m. All CWD that was connected to the soil with roots and had a height of less than 1 m was defined as stumps. Usually stumps resulted from tree cutting.

Each piece of CWD was measured, characteristics like wood colour, penetrability with a knife, shape and insect infestation diagnosed and a decay class from 1 to 5 (Table 1.1) attributed in their accordance with a method adapted from Goodburn & Lorimer (1998).

Table 1.1: Decay class (DC) characteristics of coarse woody debris (CWD).

Decay class	Characteristics
1	Recently dead, bark intact, small twigs and leaves, no visible signs of decomposition
2	Bark mostly remaining, no leafs, wood not penetrable by a knife
3	Bark mostly missing, wood partly penetrable with knife, visible discolouration
4	No bark, wood completely penetrable with knife, deformation and discolouration
5	Wood soft, breakable with fingers, advanced humification

CWD volumes were calculated from multiple measurements of length and diameter using volume formulas under the assumption that CWD pieces were regular cones or cylinders (Bebber & Thomas 2003). It was assumed that over- and underestimations of individual pieces levelled errors out over the total stock.

To investigate CWD quality (wood density, water content as well as C and N concentrations), 722 CWD samples were taken by drilling holes of known volume and collecting all shavings. Sub-samples of 200 samples were ground with a ball mill for further analysis. For conversion of CWD volumes to C stocks, C densities were calculated from wood density and C concentration for each tree species and decay class. This was a necessary step as usage of values for fresh wood for conversion of CWD volumes to C stock leads to an overestimation of the C stocks (Weggler et al. 2012).

To determine the time of tree death of CWD that decayed under field conditions, the two methods radiocarbon analysis (see below) and dendrochronological cross-dating were compared. Both methods rely on the presence of the uttermost tree ring and thus restricted the method to CWD with an utter tissue layers that had not yet degraded.

Decay of CWD can be expressed in different sizes including decomposition rate constants (Rock et al. 2008), half-times (Olajuyigbe et al. 2011) and residence times (Holeksa et al. 2007). In this study, disappearance times were calculated. It considered the C density at different times since tree death. The disappearance time is reached when volume loss and fragmentation reduced the former CWD to pieces with diameters of less than 7 cm.

CWD C loss was calculated from CWD C stocks and the disappearance times with tree species specific linear function. Decadal CWD production was derived from time of tree death of current CWD stocks. Volume loss is assumed to play an inferior role in early stages of decay (Harmon et al. 1986). The combination of CWD production and CWD loss gave the CWD accumulation.

Below-ground coarse woody debris inventory

Five stumps, from two (oak and spruce) or three (beech) thinning procedures of known time of tree death, were completely excavated by hand. All roots with a diameter > 7 cm were recovered. The total volume of the samples was determined by water dispersion.

Soil sampling

30 regularly distributed plots on a representative area of 2 ha were measured for the soil sampling. The number was judged sufficient to represent the inhomogeneity of forest soils. The forest floor was separated in the O_i, O_e and, if existent, O_a horizon in the field. Fine woody debris (FWD), defined as woody pieces with a diameter between 0.2 - 7.0 cm and roots were separated in the laboratory and their mass and C concentration were determined separately.

The upper 10 cm of the mineral soil were sampled with a core cutter. Further soil samples up to 100 cm depth were taken with a percussion drill and separated by the depth intervals 10-20 cm, 20-50 cm and 50-100 cm under consideration of compression. The soil was separated by depth rather than horizons to facilitate statistical comparison of the study sites. Sampling by percussion drill can result to an uncertainty in the density determination of the bulk soil as well as an underestimation of the rock content. SOC stock estimates in this study should thus be considered upper limits of the potential SOC stock in the forests.

Twelve additional soil samples of the upper 10 cm of the mineral soil per tree species and study site were taken directly underneath heavily decayed CWD of beech and oak at Rohrberg and Ludwigshain. The CWD piece and, if present, organic material, were removed from the plot before sampling.

Sample preparation and analysis

Decay of woody debris under laboratory conditions

Twelve woody debris samples of decay class 1, decay class 3 and decay class 5 of the tree species beech, oak and spruce (108 samples total) were incubated on filtration units in glass jars at 15°C in a dark climate chamber for 380 days. In weekly intervals, the increase in CO_2 in the glass jars within a time period of 24 hours was measured by gas-chromatography to calculate respiration rates. Further leached C was measured in a constant quantity of artificial rain. This set-up enabled us to quantify the C loss as CO_2 and DOC in dependence of tree species and decay class.

Density fractionation

Changes in SOC are often hard to detect in bulk soil due to its high spatial variability (Schöning et al. 2006, Homann et al. 2008, Schrumpf et al. 2008). For this reason, a division in less heterogeneous chemical and physical fractions with different stability and turnover times (TTs) is useful to detect changes (Trumbore 2000, Kögel-Knabner et al. 2008). Commonly applied procedures include the separation of soil in dependence of its density in three fractions that are named free particulate organic matter (fPOM, $\delta<1.6$ g cm^{-3}), occluded particulate organic matter (oPOM, $1.6<\delta<2.0$ g cm^{-3}) and mineral associated organic matter (MaOM, $\delta>2.0$ g cm^{-3}). In this study, sodium-polytungstate (SPT) solution was used to separate the soil in its fractions.

The meaning of the fractions and the implications for processes occurring under natural conditions is controversially discussed. Generally, it is agreed upon that SOC in the lighter fractions originates from litter input and constitutes fragmented plant debris whereas the heavier fractions are higher in compounds derived from microorganisms (Wagai et al. 2008). The fractions respond to changes at varying rates with a faster reaction in the light fractions than in the heavy fractions (Hedde et al.

2008, Don et al. 2009). As density fractionation is a time intensive costly procedure, it was only done for one mixed sample per study site and soil depth.

Radiocarbon analysis

The application of radiocarbon analysis in environmental studies is often based on the so-called „bomb“ ^{14}C or modern ^{14}C. Due to above-ground thermonuclear weapon testing, the amount of ^{14}C in the atmosphere significantly increased during the 1950s. By 1963, the amount of ^{14}C in the atmosphere had almost doubled (Lassey et al. 1987). Since the limited Test Ban Treaty went into effect in October 1963, the ^{14}C in the atmosphere is continually diluted due to the burning of ^{14}C free fossil fuels and the mixing of atmospheric ^{14}C with terrestrial and marine C pools (Levin & Kromer 2004). This results in yearly differences of atmospheric ^{14}C that are above the sensitivity of radiocarbon measurements. Plants take up atmospheric C and bind it. The atmospheric ^{14}C signal is thus propagated first to the living biomass and than to litter pools and to the soil. This enables the study of the flow of C through the different pools on a decadal time-scale (Goh 1991).

In this study, radiocarbon analysis were incorporated in different ways. The time of tree death of CWD logs were studied by radiocarbon analysis of the uttermost tree ring. Further, the different radiocarbon signatures of CWD in comparison to leaf litter was used to model the influence of CWD on the forest floor. Finally, TTs of the SOC were calculated.

Modelling of soil organic carbon turnover in the forest floor and the mineral soil

TT of SOC pools can be calculated from radiocarbon signatures using different modelling approaches in dependence of the input pools, and whether a system is at steady state. All modelling approaches used in this study are based on Gaudinski et al. (2000). For the forest floor, non-steady state models are assumed. In addition to the radiocarbon signatures, the SOC stocks and their build up are considered for calculation of TTs. It is assumed that all input to the O_i horizon originates from fresh leaf litter. For the O_e horizon different scenarios were calculated with and without consideration of input from the O_i horizon, the FWD and the CWD. For the O_a horizon, input from the O_e horizon as well as from roots are considered. TTs of SOC in the bulk mineral soil and the density fractions were calculated with a steady state model.

Synthesis and discussion of results

Properties of above-ground coarse woody debris

The investigation of differences in C stocks in the managed and unmanaged forests gave special focus to CWD. CWD properties changed during its decay. Wood density decreased and C and N concentration as well as in *in situ* water content increasedin above-ground CWD of the three species European beech, Sessile oak and Norway spruce (Fig. 1.3). All characteristics were marked with high variations between samples of the same decay class as well as between samples from the same log highlighting the natural variance in decay of CWD.

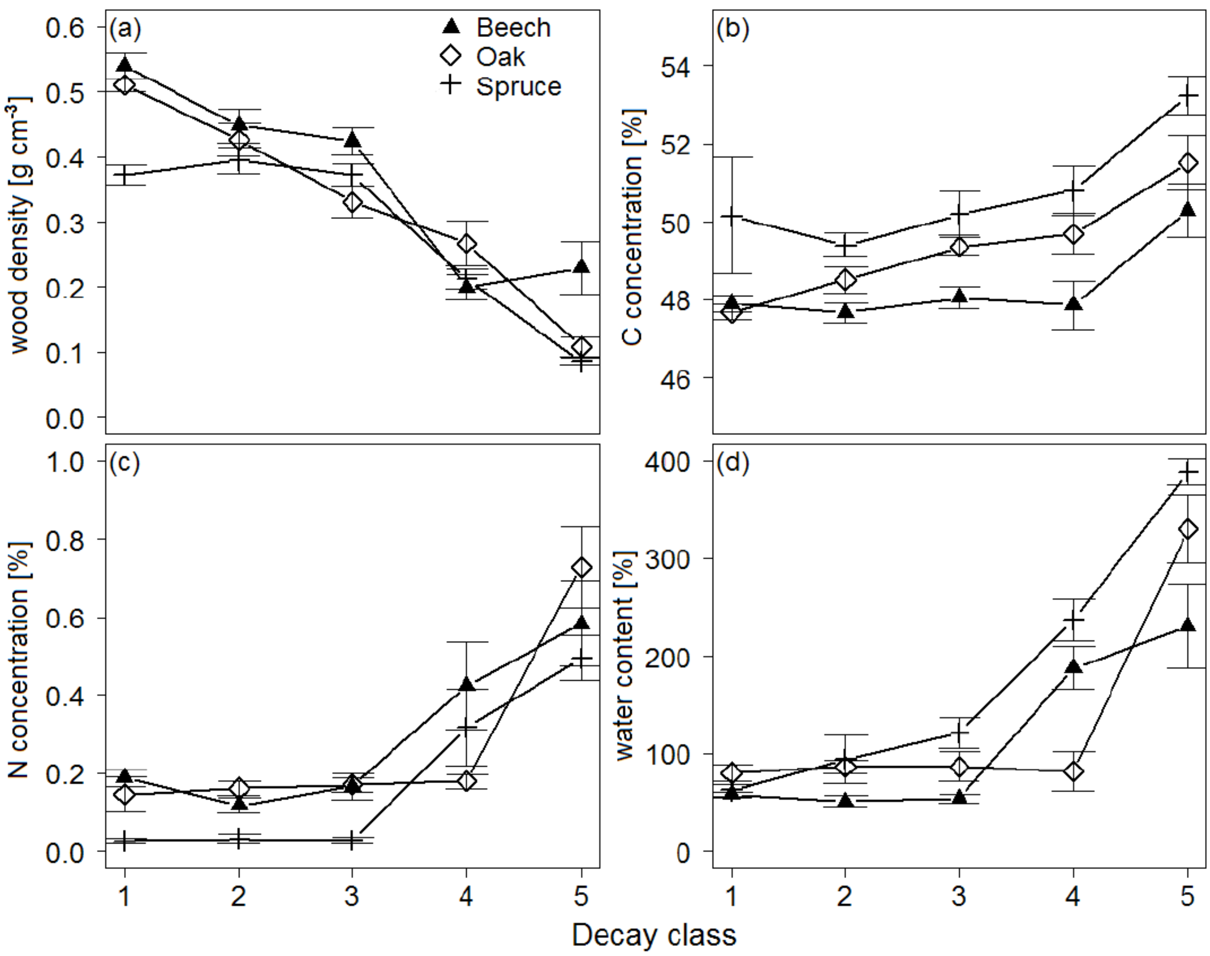

Fig. 1.3: Wood density (a), C concentration (b), N concentration (c) and gravimetric water content (d) at decay classes 1-5 for the tree species European beech, Sessile oak and Norway spruce. Error bars give standard errors.

Wood density of CWD of decay class 1 significantly differs between spruce (0.38 g cm^{-3}) and beech as well as oak (0.51 g cm^{-3}). It is lower than wood density of undecomposed wood (spruce: 0.43 g cm^{-3}, beech: 0.72 g cm^{-3}, oak: 0.65 g cm^{-3}) (Trepkau 2003). Wood density exhibits a great variation depending on environmental and climatic variables, the cambial age and radial position of the wood and the tree height and location relative to the crown (Lei et al. 1996, Gartner et al. 2001, Swenson & Enquist 2007). The high variation in wood density of decayed wood could thus partially stem from initial differences in wood density. As a result of fragmentation by wood-dwelling insects and of consumption by wood decomposers (Harmon et al. 1986), wood density of heavily decayed wood decreased to values of 0.1 g cm^{-3} (Fig. 1.3a). Decrease in wood density is the most important property for estimation of C stocks in CWD (Weggeler et al. 2012).

The increase in C concentration from 48.6 to 51.7 from decay class 1 to 5 (Fig. 1.3b) corresponds to published results (Holub et al. 2001) and can be attributed to a change in the chemical composition of wood following microbial decay. Some wood decomposing organisms, including brown rot fungi, transform the constituents of wood lignin, cellulose and hemicellulose at different paces (Song et al. 2012). White rot fungi simultaneously decompose lignin and cellulose (Leonowicz et al. 1999). Beech CWD is mostly decomposed by white rot fungi (Schmidt 2006), resulting in only slight alteration of the cellulose:lignin ratio in CWD and consequently no significant change in C concentration at decay class 1 to 4. Oak and spruce CWD on the other hand is mainly decomposed by brown rot fungi (Schmidt 2006). Brown rot fungi do not have the capacity to decompose lignin, but metabolize cellulose (Schmidt 2006). By consequence the amount of lignin in comparison to cellulose increases in CWD. Pure lignin has a C concentration between 63 and 72 %, while cellulose and hemicellulose have C concentrations around 42 % (Crawford 1981).

N concentration of CWD remained at a low and constant level for decay class 1 to 3 (or 4 in case of spruce) (Fig. 1.3c). The relative increase in N concentration at decay class 4 and 5 was more distinctive for spruce CWD than it was for beech and oak CWD. This pattern corresponds to published results on CWD of other tree species (Krankina et al. 1999, Fukasawa et al. 2009). An increase in N concentration can result from a relative accumulation of N in consequence of density loss or by an uptake of N by wood decaying organisms from the soil (Hafner & Groffman 2005) or N_2 fixation from the atmosphere (Cowling & Merill 1966). In case of spruce CWD, the increase in N concentration cannot be explained by a relative accumulation of N in CWD due to density loss alone and must thus result from an N uptake or fixation by wood decaying fungi. Depending on its stage of decay, CWD can serve as both a sink and a source of N in aquatic systems (Creed et al. 2004). A similar behaviour is assumed in terrestrial ecosystems (Palviainen et al. 2010).

CWD possesses a great water holding capacity that resulted in *in situ* water contents of up to 15 times its dry mass (Fig. 1.3d). The *in situ* water content increased with decay class showing that especially heavily decayed served as a water stock. Moisture content affects the decay of CWD (Herrmann & Bauhus 2012) and might explain potential differences in C loss from CWD between early and advanced decay classes. The water holding capacity of CWD can also be of importance to SOC turnover in the top soil especially during drought periods, when CWD can slow evaporation of soil moisture (Stevens 1997).

Properties of below-ground coarse woody debris

Significant ($p < 0.001$) differences in mean below-ground CWD density were found between beech (0.26 g cm^{-3}), spruce (0.41 g cm^{-3}) and oak (0.64 g cm^{-3}). Below-ground CWD had a lower wood density for beech, a higher wood density for spruce and a similar wood density for oak than above-ground CWD.

With average C concentrations of 42.9 (spruce) to 46.3 (beech) and 46.9 % (oak), average C concentrations of below-ground CWD were lower than of above-ground CWD of the same tree species. N concentration of below-ground CWD was lower than N concentration of above-ground CWD for oak (0.23 %), but higher for beech (0.48 %) and for spruce (0.87 %). No agreement of N concentration with time since tree death was found. These findings do not correspond to results from Olajuyigbe et al. (2001) who described an increase in N concentration with increasing density loss and time since tree death.

Above-ground coarse woody debris decay

Knowledge on decay is essential to estimate the potential of CWD as a middle-term C stock in forest ecosystems and to assess the potential contribution of C originating from CWD to the soil. To study CWD decay two different approaches were used in this study: a field study and a laboratory incubation experiment.

Due to the short duration of this study in comparison to the decay of CWD, a chronosequence approach was implemented to study CWD decay in the field. Chronosequence approaches require knowledge of the time since tree death of CWD (Harmon et al. 1986). As forestry record did not provide sufficient information on the time of tree death of individual trees, other methods for age determination were used: dendrochronological cross-dating and radiocarbon analysis of the outermost tree ring. Both methods require the presence and the ability to identify the outermost tree ring and thus restricted decay studies to CWD with an at least partially intact outermost tree ring.

The laboratory experiment enabled the observation of decay under controlled conditions and the measurement of C loss through different pathways namely as leached DOC and as mineralized CO_2. However, the sample had no soil contact in the implemented design and by consequence any interaction with the soil including mycellium growth or N transfer was prevented. Microbial decay is considered the main driver of C loss from CWD (Swift 1973), but other factors also contribute including insect infestation (Swift 1977) and photo-degradation (Pandey 2005). In the experiment, wood disks were cut to create samples of equal size in order to get several replications of similar quality. New surfaces were created and samples significantly reduced in size in comparison to the original CWD logs. Further samples were dried, re-wet and inoculated prior to the experiment. Temperature and moisture regimes in the experiment did not represent field conditions and effects resulting from the sample treatment could not be distinguished from natural decomposition processes.

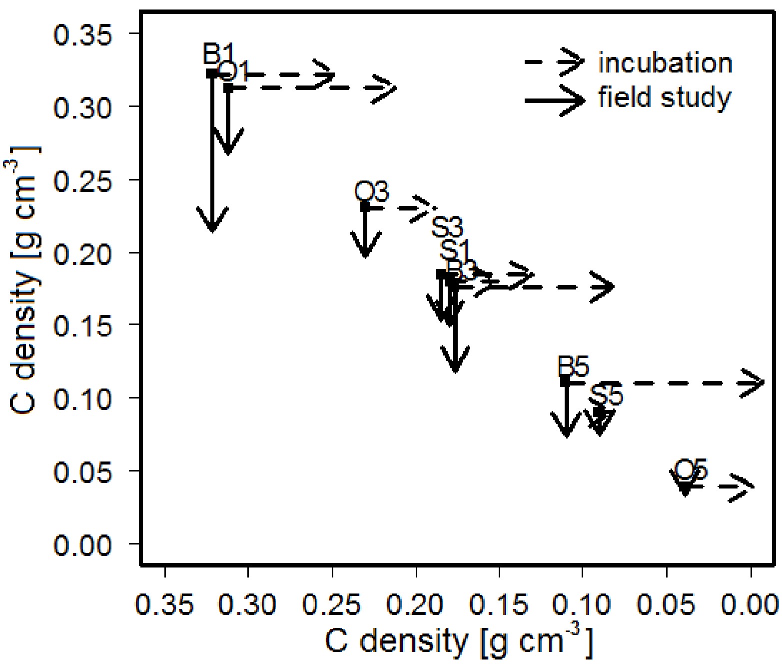

Fig. 1.4: Extrapolation of C loss over a ten years period in the incubation experiment and under field conditions for samples of beech (B), oak (O) and spruce (S) of decay class 1, 3 and 5.

Results of the field and the laboratory study differed in total annual C loss as well as effects of tree species and decay class. Calculated annual C loss (1.5 – 11 % of initial C) was in average two times higher under laboratory conditions than under field conditions (Fig. 1.4). This was partially attributed to a temperature effect as the samples were incubated at 15°C while yearly averages in the field range between 3 and 8°C. Q_{10} values for CWD of 2.7 - 3.4 (Yatskov et al. 2003) would explain the difference. Under laboratory conditions, C loss through leaching contributed between 1 and 25% of the total C loss. Contributions were highest for oak CWD and for decay class 5 of all tree species.

The experimental set-up might have enhanced C loss through leaching due to the increased surface:volume ratio resulting from the smaller sample size in comparison to logs. Nonetheless, mineralization to CO_2 was the main pathway of C loss.

CWD decay was tree species dependant. The order of tree species differed in the field and in the laboratory. Under field conditions the order beech > spruce > oak corresponded to other observations in temperate forests (Rock et al. 2009). Beech CWD samples remained in the forest for no longer than 30 years. Samples of spruce and oak CWD had disappearance times of over 70 years. The high C density of oak CWD indicated the potential of oak CWD to remain in forests longer than spruce CWD. The mean annual temperature of the studied spruce forest is 4 K colder than mean annual temperatures of the beech-oak forests. The long disappearance time is thus partially due to climate effects rather than intrinsic CWD characteristics.

In the laboratory, C loss decreased in the order beech > oak > spruce. Sample preparation might have favoured the decomposition of oak CWD more than of spruce CWD, as the distinct chemical composition of oak with a high content of extractable substances (Bianco & Savolainen 1994) results in a higher potential C loss through leaching from CWD.

Exponential functions are common to describe the decay of CWD (Harmon et al. 1986), indicating a decrease in C loss relative to the initial amount of C. However, depending on the tree species, sigmoid or linear functions are more suitable to describe CWD decay (Fréschet et al. 2011). Under field conditions, there was a statistically significant linear correlation between time since tree death and C density for beech and spruce CWD, but not for oak CWD. A linear decay function indicates that absolute C loss remains constant at all decay classes. Under laboratory conditions, C loss increased with decay classes with significant differences in annual C loss between heavily decayed CWD and less decayed wood. As heavily decayed wood was not considered under field conditions, neither was the potential increase in C loss.

Under laboratory conditions, all samples for each decay class originated from the same wood disk of the same tree. Despite the relatively uniform material, standard deviation of samples of the same kind were around 30% of the measured average C loss. Under field conditions, standard deviations of several orders of magnitude are common (Kuehne et al. 2008), rending the finding of statistically significant differences between decay classes more unlikely. The lack of correlation between time since tree death and C density for oak CWD was caused by the natural variability of oak CWD. Oak has a stong differentiation in heart- and sapwood that results in CWD size effects on decay (Harmon 2009). Heartwood of oak contains high concentrations of fungi-toxic extractables (Hillis 1987, Puech et al. 1999), that inhibit colonization by wood decaying fungi. Further, natural variability is increased by differences in decay between snags and logs (Harmon 2009) and by old oak trees that partially die and decay while new tissue is still being formed (Ranius et al. 2009).

Below-ground coarse woody debris decay

Below-ground CWD exhibited a great variability in C mass per stump (beech: 1 – 8 kg C, oak: 1 – 20 kg C, spruce: 2 – 36 kg C). There was no agreement between above-ground stump diameter and below-ground C mass. No correlation between time since tree death and below-ground C mass was found (data not shown).

Variations in below-ground C mass was highest for below-ground oak CWD. Below-ground CWD of about 80 % of oak trees cut 14 years prior to sampling, was considerably reduced in mass and volume, while below-ground CWD of the remaining stumps were in a state similar to fresh CWD notable by a high wood density and presence of fine roots. The resistance to decay in the years following tree cutting was attributed to the high content of tanning agents in the CWD that became visible during sampling through discolouration of metal objects. This points to a long lag-period of several years followed by a rapid decay of below-ground oak CWD. Lag-periods result from the time needed for wood-decaying fungi to colonize the CWD (Harmon et al. 2000) and have been described for above-ground CWD decay of various tree species (Grier 1978, Yatskov et al. 2003, Olajuyigbe et al. 2012). Decay of below-ground CWD of coniferous tree species and birch on the other hand occurs without a lag-period (Melin et al. 2009, Fréschet et al. 2011). The data were not sufficient to calculate statistically significant decay functions for any tree species.

Coarse woody debris carbon stocks

Differences in above-ground CWD stocks between management types as well as tree species were relevant. In the unmanaged forests, C stocks of CWD were between 11 and 30 Mg C ha^{-1}. In the managed forests, there were around 5 Mg C ha^{-1} of CWD. The CWD C stocks have accumulated in the unmanaged forests since they were withdrawn from management between 40 and 100 years ago. CWD production is still anthropologically influenced as exceptional management practices were conducted in the past years with preservation motives. In all forests, removal of wood resulting from natural mortality was allowed until the mid-1960s. CWD stocks in all unmanaged forests have the potential to further increase and are not yet at steady state.

CWD accumulation is known to be a highly variable process that is tree species specific (Vandekerkhove et al. 2009). The reconstruction of past CWD accumulation was restricted by the number of CWD samples whose time of tree death was determined. A reconstruction by decades was considered a good compromise between the needs of the study and the vulnerability to errors.

Over the last decades, CWD accumulated at yearly rates of 0.2 to 1.2 Mg C ha^{-1} a^{-1} (Fig. 1.5). In the unmanaged forests, accumulation rates were greater than in the managed forests. The increase in CWD stocks in the managed forests was attributed to management practices that leave crowns in the forests for ecological reasons.

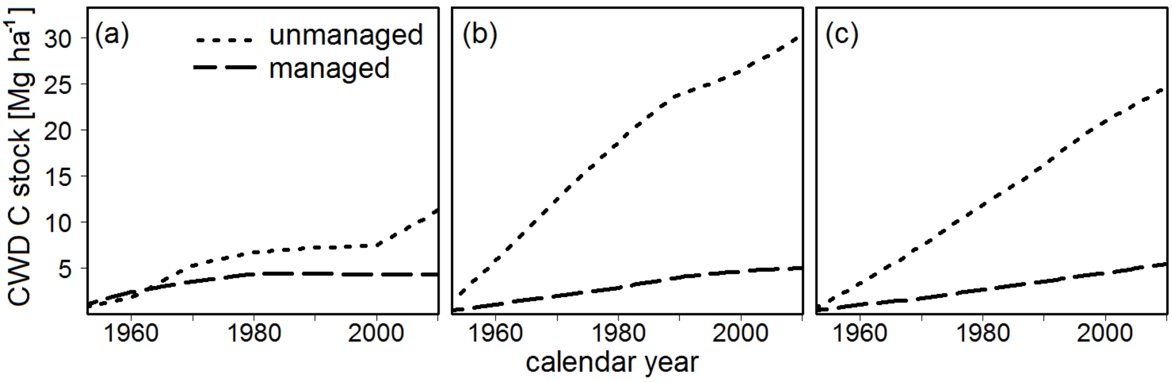

Fig. 1.5: Estimated build up of the CWD stocks and cumulative C loss from CWD since 1950 at Grübel (a), Ludwigshain (b) and Rohrberg (c).

At Ludwigshain, C stocks in the below-ground CWD ranged between 0.3 and 1.4 Mg C ha^{-1}. This corresponded to about 16 % in the managed and to less than 1 % in the unmanaged forest of the total C stock of CWD. In accordance with the amount of standing CWD and stumps, the C stocks in the managed forest were estimated 2.3 times higher at Rohrberg and 1.8 times higher at Grübel than in the unmanaged forests. With a contribution of at least 10 % to the total CWD stocks in the unmanaged and over 50 % in the managed forest, below-ground CWD was of more importance in the spruce forest at Grübel than in the beech-oak forests. This corresponds to literature values that estimate that up to 85 % of the total CWD stocks in managed Sitka spruce forests are below-ground (Olajuyigbe et al. 2011).

Influence of coarse woody debris on soil organic carbon stocks

Influence of elevated CWD stocks on the SOC stocks was tested by comparing the SOC stocks and TTs in the managed and unmanaged forests and by measuring the SOC stocks directly underneath heavily decomposed CWD. CWD can contribute to the SOC stock of the soil through fragmentation (Crow et al. 2007) and through leaching of C as DOC (Spears et al. 2003). Fragmentation of above-ground CWD contributes to the SOC stock of the O_e horizon first. Fragmentation of below-ground CWD has the potential to increase the SOC stock, especially in the fPOM fraction, at all soil depths. Leaching of C as DOC is likely to contribute to the SOC stock in the whole mineral soil including the MaOM fraction.

The SOC stocks in the forest floor and the mineral soil did not differ between managed and unmanaged forests. SOC stocks of the forest floor ranged between 4 and 15 Mg C ha^{-1}. FWD represents an additional C stock of 0.3 – 1.1 Mg C ha^{-1}. The C stocks of the CWD were about six times higher than the SOC stocks in the forest floor in the unmanaged beech-oak forests and about half of the SOC stock in the forest floor in the unmanaged spruce forest.

With a sample size of 30 replicates, SOC stocks of the O_e horizon have to differ by 30 % between managed and unmanaged forests to be statistically significant. A model calculation yielded, that an input of 5 % of the total C loss from CWD would be sufficient to cause such an increase at equal TT of the SOC in the O_e horizon. As no significant differences in SOC stocks of the O_e horizon were measured, the contribution to the O_e horizon from CWD is either smaller than 5 % or other factors level out the additional input (see below).

The SOC stocks in the mineral soil up to 1 m soil depth (50 and 260 Mg C ha^{-1}) corresponded to the range found in the Bavarian soil inventory for similar site conditions (Wiesmeier et al. 2012). C concentrations and bulk density of soil samples taken directly underneath heavily decayed CWD of beech and oak at Ludwigshain and Rohrberg did not differ from soil samples taken as part of the SOC stocks inventory. This indicated that CWD does not influence the SOC stocks in the mineral soil, even on a punctual level. This result corresponds to findings by Kahl et al. (2013) who measured no increase in the SOC stock beneath beech logs despite an increased DOC flux.

Total carbon stocks

Total C stocks of the above- and below-ground timber biomass, CWD, forest floor including FWD and mineral soil up to 1 m soil depth amounted to 240 to 410 Mg C ha^{-1} (Fig. 1.6). C stocks in the unmanaged forests were higher in Grübel and Rohrberg, but lower in Ludwigshain. The differences between management types are not substantial. C stocks of CWD contributed 3, 12 and 8 % in the unmanaged forests Grübel, Ludwigshain and Rohrberg respectively. In the unmanaged forests, the contribution of CWD to the total C stocks was between 2 and 3 %. The values in the managed forests were lower than the average contribution of CWD to the C stocks of European forests of about 5 % (Goodale et al. 2002). The total C pool of European forests including living timber biomass, CWD, forest floor and SOC, is reported at 22.4 Pg C with 1.0 Pg stored in CWD (Goodale et al. 2002).

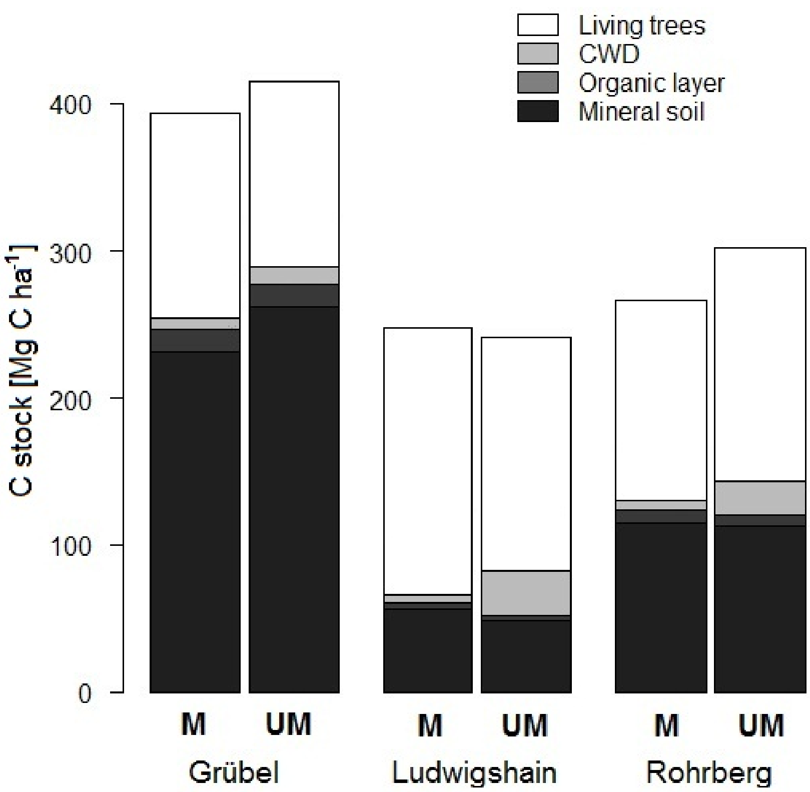

Fig. 1.6: C stocks in living timber biomass, CWD, forest floor including FWD and the mineral soil up to 1 m soil depth in the managed (M) and unmanaged (UM) forests Grübel, Ludwigshain and Rohrberg.

Coarse woody debris nitrogen stocks

N stocks of above-ground CWD were substantially smaller in the spruce forests than in the beech-oak forests. At Grübel, N stocks of above-ground CWD are around 10 kg N ha^{-1} in both the managed and unmanaged forests. In the managed forest at Grübel, the CWD is more heavily decayed With around 90 and 115 kg N ha^{-1} in the unmanaged Rohrberg and Ludwigshain respectively, N stocks in above-ground CWD were about five times higher in the unmanaged beech-oak forests than in the managed beech-oak forests (20 kg N ha^{-1}). In the unmanaged beech-oak forest, N stocks were in the same order of magnitude than described for temperate beech forests (Müller-Using & Bartsch 2007).

N stocks of below-ground CWD were below 10 kg in the managed and unmanaged forests in Rohrberg and Ludwigshain. At Grübel, N stocks of below-ground CWD were estimated around 35 kg N ha^{-1} in the unmanaged forest and around 65 kg N ha^{-1} in the managed forest. At Grübel, N stocks in below-ground CWD were thus greater than in above-ground CWD. So far, no studies on N stocks of below-ground CWD have been published.

Average C:N ratios of above-ground CWD were between 250 and 300 in the beech-oak forests and between 500 and 1000 in the spruce forests. Below-ground CWD has substantially lower C:N ratios of 100 (European beech), 200 (Sessile oak) and 60 (Norway spruce). The observation that C:N ratios of below-ground CWD are lower than of above-ground CWD corresponds to published studies (Olajuyigbe et al. 2011). A possible explanation for the lower C:N ratio of below-ground in comparison to above-ground CWD is the higher soil contact that might result in a greater fungal translocation of N (Palviainen et al. 2011). C:N ratio is one of the variables that controls N release during litter decomposition (Parton et al. 2007). Below-ground CWD thus has a greater potential as a N source than above-ground CWD.

Influence of coarse woody debris on soil nitrogen stocks

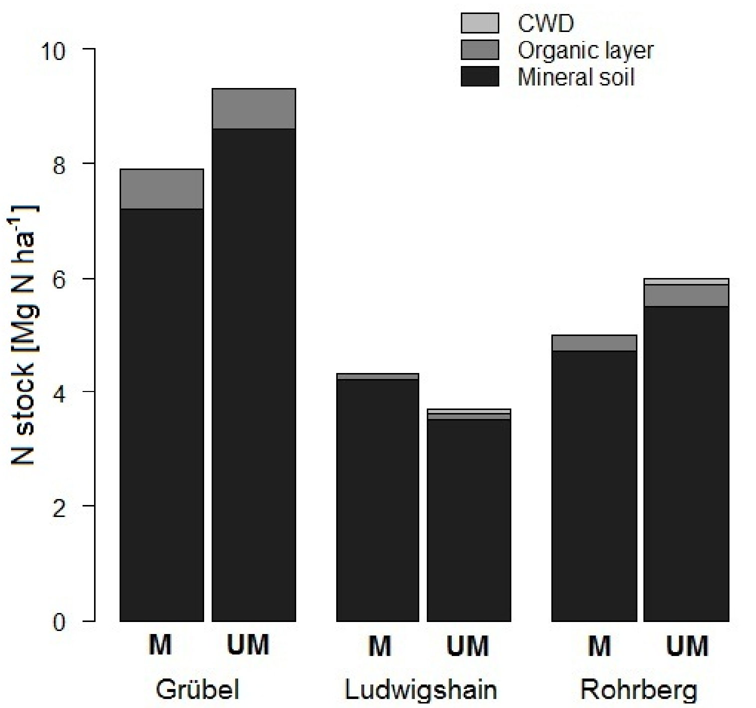

Fig. 1.7: N stocks in CWD, forest floor including FWD and the mineral soil up to 1 m soil depth in the managed (M) and unmanaged (UM) forests Grübel, Ludwigshain and Rohrberg.

N stocks in the forest floor were between 0.1 and 0.7 Mg N ha^{-1} (Fig. 1.7). Values were lower than described for the forest floor of Bavarian forests between 0.8 and 2.9 Mg N ha^{-1} (Gerstenberger et al. 2004). Differences between study sites were more important than between management types. In the

O_i and O_e horizon at Rohrberg and Ludwigshain, N concentration significantly differed between managed and unmanaged forests in 2009. However, the trend could not be confirmed in samples taken in 2011. Differences in N concentration were greater between sampling years than between management types.

N stocks of the forest floor were of similar range than the N stocks of the above-ground CWD in the unmanaged forest at Ludwigshain, four times greater in the unmanaged forest at Rohrberg and seventy times greater in the unmanaged forest at Grübel. The wide range demonstrates the differing role of above-ground CWD in the N cycle of forest ecosystems. The low N stocks in Grübel corresponded to results published on North American coniferous forests, where a contribution of 3 % or less of the N pool of the soil has been attributed to above-ground woody debris (Fahey et al. 1983, Busse 1994, Laiho & Prescott 1999).

N stock in the mineral soil ranged from 3.5 and 8.6 Mg N ha^{-1}. Differences in N stocks in managed and unmanaged forests showed no distinct patterns, nor did N concentrations or N stocks in soil samples directly underneath CWD differ from soil sampled as part of the inventory. An influence of CWD on the N stocks of forest systems had been suggested (Hafner & Groffman 2005), but this result could not be confirmed in this study.

Soil organic carbon turnover in the forest floor

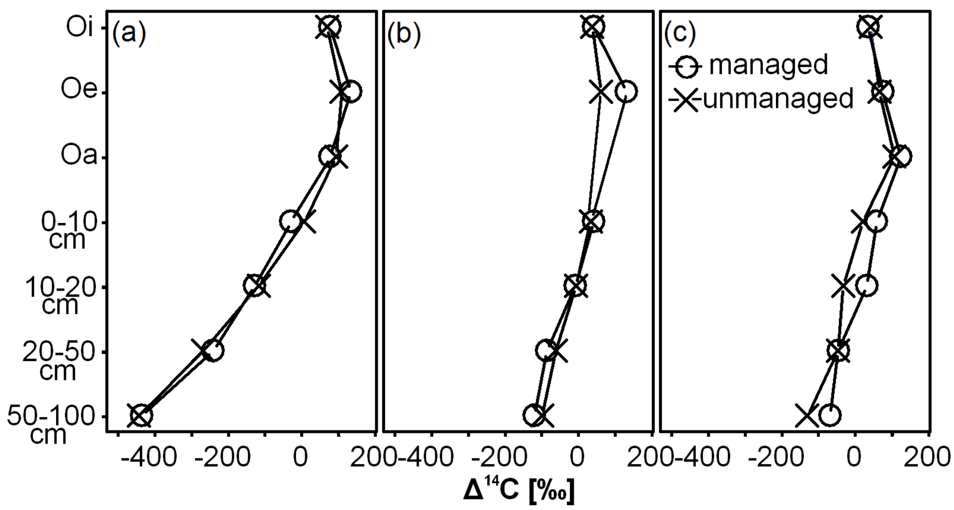

Fig. 1.8: Radiocarbon signatures of the forest floor and the bulk soil organic matter in the managed and unmanaged forests at Grübel (a), Ludwigshain (b) and Rohrberg (c).

Radiocarbon signatures of SOC in the forest floor and bulk soil samples showed no consistent differences across all study sites between managed and unmanaged forests except in the O_e horizon (Fig. 1.8). The differences might be explained by differences in the radiocarbon signatures of the input pools or differences in TTs of SOC in the O_e horizon. To test the likeliness of the possibilities, a non-steady state model with three input pools (leaf litter, FWD and CWD) was implemented for the O_e horizon. CWD contains a relatively high amount of pre-bomb C and thus possesses a lower radiocarbon signature than leaf litter and FWD. By consequence, an elevated input of C from CWD would result in a lower radiocarbon signature in the O_e horizon at the same TT of SOC.

Most model calculations of the O_e do not consider input from FWD and CWD (e.g. Gaudinski et al. 2000, Schulze et al. 2009), though variability in radiocarbon signatures of the forest floor have been attributed to the presence of CWD (Trumbore & Harden 1997). In this study, the applied model was restricted by a lack of information on the proportion of total C loss that enter the O_e horizon from each input pools. The classic modelling approach without consideration of C input from FWD and CWD to the O_e horizon gave TTs of SOC in the O_e horizon between 5 and 19 years. At all study sites, TTs of the SOC in the O_e horizon were shorter in the unmanaged forests than in the managed forests. Scenarios with different proportions of total C loss from CWD and FWD that enter the O_e horizon resulted in TTs of SOC in the O_e horizon differing by up to 5 years. Model runs with more than one data point would enable to help clarify which model scenario is most accurate. No scenario gave equal or longer TTs of SOC in the O_e horizon in unmanaged and/than in managed forests.

While the calculation could not quantify the amount of C originating from CWD in the O_e horizon, they permitted to show that the CWD stocks and their C loss are not sufficient to cause the difference in radiocarbon signatures through C input alone. It is speculated that a change in the decomposing community could stimulate decomposition of leaf litter and result in shorter TT of SOC in the O_e horizon. CWD has the capacity to influence the microbial community of the soil (Rajala et al. 2012), to affect soil yeast abundance and community composition (Yurkov et al. 2012) and to increase the size of the fungal community in the soil and cause a shift in the fungal:bacterial ratio (Brant et al. 2006).

The increase in TT of SOC in the unmanaged forests was only visible in the O_e horizon. There was no significant management effect on the TT of SOC in the O_a horizon. As the build up of CWD is a gradual process and the release of C from CWD equally slow, it is possible that the time since management change has not been sufficient to affect the O_a horizon.

Soil organic carbon turnover in the mineral soil

The TT of SOC in the mineral bulk soil increased with soil depth. The upper 10 cm have TT of SOC of 130-470 years. This time period is longer than the time since management change and the period since an elevated CWD stock has accumulated in the unmanaged forests. The differences in the TT of SOC in the bulk soil cannot be attributed to a management effects. Differences in radiocarbon signatures between the forests were probably existent before the management change. The same was true for the fPOM fraction at Grübel as well as the oPOM and MaOM fractions at all study sites.

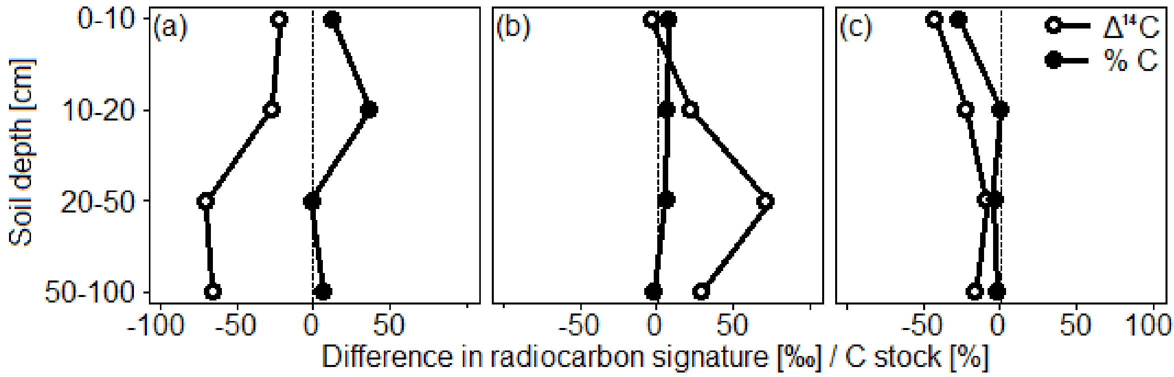

Fig. 1.9: Differences between managed and unmanaged forests in radiocarbon signatures and SOC stocks of the fPOM fraction in Grübel (a), Ludwigshain (b) and Rohrberg (c).

At Rohrberg and Ludwigshain, the TTs of SOC of the fPOM horizon were generally less than 250 years. Management could thus affect this soil fraction. There were consistent patterns in differences between managed and unmanaged forests across all soil depths at each forest. At Rohrberg, the radiocarbon signatures of the fPOM fraction were higher in the unmanaged than in the managed forest. At Ludwigshain however, the radiocarbon signatures of the fPOM fraction were lower in the unmanaged than in the managed forest (Fig. 1.9). The differences in SOC stocks between managed and unmanaged forests in the fPOM fraction also showed consistent patterns across all soil depths. However, their direction differed between the two study sites. An explanation might be less input of litter in the unmanaged than in the managed forest at Rohrberg and a shorter TT of SOC in the fPOM fraction in the unmanaged than in the managed forest at Ludwigshain. Which factors cause the specific changes could not be evaluated with this study. As the soil type differs between the two study sites, an opposing effects of enhanced above-ground and reduced below-ground CWD stocks cannot be excluded. A potential explanation for the lower SOC input to the fPOM fraction in the unmanaged forest at Rohrberg is a lower SOC stock of below-ground CWD than in the managed forest. At Ludwigshain, the shorter TT of SOC might be explained by differences in the decomposing community (see above).

Conclusions

This thesis aimed at comparing the C sequestration potential of managed and unmanaged forests as influenced by CWD stocks. The study specifically considered Bavarian site conditions. CWD decay is greatly influenced by biotic and biotic factors that differ between geographical regions of the world. So far, relatively few studies on CWD have been conducted in temperate forests.

Differences in above-ground CWD properties and disappearance times indicate the differing potential of European beech, Sessile oak and Norway spruce as lasting CWD pools. Linear models were used to describe C loss from CWD, despite differences in C loss between decay classes. Natural variation in CWD properties is important and an easy model sufficient to model C loss from CWD on a stand level. Beech CWD has a shorter disappearance time than oak and spruce CWD and by consequence is not as suitable as a lasting CWD stock as the other tree species. CO_2 mineralization is the main pathway of C loss, showing that the most C is lost to the atmosphere before it can contribute to other C pools of the forest ecosystem. However, leaching as DOC can make up to one forth of the C loss from CWD. A significant C input to the soil is thus possible. As the amount of C lost from oak CWD through leaching is highest of the investigated tree species, oak CWD could potentially contribute most to the SOC stocks of the soil.

Below-ground CWD exhibits a greater variability in properties than above-ground CWD. Calculation of functions to describe decay was not possible. Properties and potential as lasting C stocks differ between tree species with spruce offering the greatest potential C masses per stump.

Above-ground CWD accumulates, when a forest is withdrawn from management and represents an important C stock in unmanaged forest ecosystems. Above-ground CWD stocks of 10 to 30 t C ha^{-1} have accumulated within decades. The CWD stocks continue to increase, showing the potential for an even higher C sequestration potential. In the managed forests, above-ground CWD stocks increased in the past decades, however the accumulation occurred at a slower rate than in the unmanaged forest.

Below-ground CWD represents an additional C stock that is greater in the managed than in the unmanaged forests. Spruce forests have the potential to store more C in below-ground CWD than beech or oak forests. Despite the higher below-ground CWD stocks in the managed forests, the total CWD stocks are more important in the unmanaged forests.

Contributions of above-ground CWD to the N stocks of the forests are substantial in the beech-oak forests, but not in the spruce forest. Below-ground CWD stocks are greater than above-ground CWD stocks in the spruce forest, but slight in comparison to the N stock of the forest floor and the mineral soil.

It was assumed, that an elevated CWD stock in the unmanaged forests would increase the SOC stocks in the forest floor and the mineral soil. However, this was not confirmed in this study. Management has no influence on the SOC stocks in the forest floor and the mineral soil. Despite notable C loss as DOC, C from CWD is mostly lost to the atmosphere as CO_2, before it can contribute to other C pools. There were no differences in N stocks of the forest floor and the mineral soil between managed and unmanaged forests.

Consistent differences in TT of SOC exist between managed and unmanaged forests in the O_e horizon. The enhanced CWD stocks in the unmanaged forests result in shorter TTs of SOC in the O_e horizon possibly due to a change in the decomposing community that stimulates leaf litter decay. Differences in radiocarbon signatures in the mineral soil are not consistent between studied forests and cannot be attributed to management. This demonstrates that management impact on the SOC stocks and TT of the mineral soil is small or non-existent. Time periods of decades are not sufficient to result in relevant changes in SOC turnover in mineral soils. Whether longer time periods would result in significant changes remains open. However, results suggest that an increase in SOC stocks in unmanaged forests is not expected.

CWD is an important consistuent of forest biodiversity and seems to influence the decomposing community of the soil. In regards to conservation efforts, creation of unmanaged forest and efforts to augment CWD stocks in managed forests are thus of great importance. The potential of CWD to increase SOC stocks of the soil is slight. Managed forests are thus just as suitable as C sinks as unmanaged forests.

Record of contributions to this thesis

Chapter 1 and the summary of this thesis were written by me. This dissertation includes three publications that have been submitted to international peer-reviewed journals. The contributions of me and all co-authors are listed below.

Chapter 2 Age determination of coarse woody debris with radiocarbon analysis and dendrochronological cross-dating

Krüger I:	70 %	(concepts, field and laboratory work, interpretation, manuscript preparation)
Muhr J,	10 %	(discussions, contributions to manuscript preparation)
Hartl-Meier C:	5 %	(laboratory work and discussions)
Schulz C:	5 %	(contributions to manuscript preparation)
Borken W:	10 %	(concept, discussion, contribution to manuscript preparation)

Chapter 3 Effects of tree species and decay class on DOC and CO_2 production of woody debris

Krüger I:	70 %	(concepts, laboratory work, interpretation, discussion and presentation of results, manuscript preparation)
Borken W:	30 %	(concepts, discussion, contribution to manuscript preparation)

Chapter 4 Carbon stocks and turnover of coarse woody debris and soil in three managed and unmanaged forests

Krüger I:	65 %	(field and laboratory work, model calculation, interpretation, discussion and presentation of results, manuscript preparation)
Schulz C:	10 %	(concepts, discussion, contribution to manuscript preparation)
Borken W:	25 %	(concepts, discussion, contribution to manuscript preparation)

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Chapter 2

Age determination of coarse woody debris with radiocarbon analysis and dendrochronological cross-dating.

Age determination of coarse woody debris with radiocarbon analysis and dendrochronological cross-dating

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Abstract

To study the decay of coarse woody debris (CWD) in forest ecosystems, it is necessary to determine the time elapsed since tree death, which is difficult at advanced decay stages. Here, we compare two methods for age determination of CWD logs, dendrochronological cross-dating and radiocarbon analysis of the outermost tree ring. The methods were compared using samples from logs of European beech, Norway spruce and Sessile oak decomposing *in situ* at three different forest sites. For dendrochronological cross-dating, we prepared wood discs with diameters of 10-80 cm. For radiocarbon analysis, cellulose was isolated from shavings of the outermost tree rings. There was an overall good agreement between time of death determined by the two methods with median difference of one year. We found no increase in uncertainty with carbon density, despite an increased nitrogen concentration in the extracted cellulose resulting from incomplete separation of chitin and other organic nitrogen compounds. A correlation between time since tree death and carbon density of wood was found for beech and spruce, but, due to the high natural variability, not for oak. Disappearance times, defined as the period until a piece of woody debris has been reduced to a size when it is no longer considered as CWD, of 30 years (beech) and 90 years (spruce) were estimated. The uncertainty of disappearance times results mainly from huge natural variability in carbon density of CWD rather than uncertainty in the age determination. The results suggest that both methods are suitable for age determination of CWD.

Keywords: Radiocarbon, Coarse woody debris, CWD, dendrochronological cross-dating, cellulose

extraction, time of tree death

Introduction

Coarse woody debris (CWD) has several ecological functions (Harmon et al. 1986) as habitat for insects, fungi and mosses, and through its role in the nutrient and carbon (C) cycle of forest ecosystems. The decay rate of CWD is highly variable in dependence of exposure, tree species and environmental factors (Harmon et al. 1986). Residence times of few decades to centuries are common in temperate forests (Rock et al. 2008). As long-term experiments on CWD decay are rare (Stone et al. 1998), chronosequence approaches are often used to estimate residence times (Kueppers et al. 2004). One prerequisite for the estimation of decay is the age of CWD (i.e. the time elapsed since death of the tree or branch) (Harmon et al. 1986). In case the tree death is linked to distinct events like fire, storm or harvesting, historical records might be used to determine the time of tree death, but usually more sophisticated methods are needed. Dendrochronological cross-dating is commonly used for the determination of time of tree death of CWD (Daniels et al. 1997, Lombardi et al. 2008, Castagneri et al. 2010). We know of only one study by Kueppers et al. (2004) that used radiocarbon analysis.

The bomb-radiocarbon approach makes use of the annual change of the atmospheric radiocarbon signature triggered by nuclear weapon testing in the 1950s and 60s and subsequent dilution or uptake processes. Because of photosynthetic CO_2 fixation the radiocarbon signatures of tree rings correlate with the respective atmospheric radiocarbon signatures (Worbes & Junk 1989). As the annual rate of change of the atmospheric radiocarbon signature has been bigger than the current measurement precision for the last decades, we can clearly distinguish the radiocarbon signature of two subsequent years. Radiocarbon analysis requires only a small quantity of wood from the outermost tree ring.

Dendrochronological cross-dating exploits the similarity in weather-dependent patterns of tree ring width sequences or other growth ring characteristics in trees of the same species and from the same climatic region (Schweingruber 1988). It has proved to be a reliable age determination technique. This method can be difficult or even impossible at advanced decay stages, as decaying CWD loses its stability and density and the formation of holes is notable (Harmon et al. 1986), making the correct identification of the outermost tree ring difficult (Schweingruber 2007, Campbell & Laroque 2006). The combination of dendrochronology and radiocarbon analysis has been used to estimate annual changes in the radiocarbon signature of CO_2 in the atmosphere before the 1950s (Leavitt & Bannister 2009).

In this study we compared radiocarbon analysis with dendrochronological cross-dating of wood discs of European beech, Sessile oak and Norway spruce from three different study sites. We tested the suitability of both methods and investigated how tree ages relate to C density of CWD calculated from C concentration and wood density. Disappearance times of CWD, defined as the period until a piece of woody debris has been reduced by density loss and fractionation to a diameter of less than 7 cm when it is no longer considered as CWD, were calculated for each of the tree species.

Material and methods

Study sites

Samples were collected at three unmanaged forests in Bavaria, Germany: Grübel (49°07' N 013°07' E), Ludwigshain (49°55' 011°48' E) and Rohrberg (49°54' N 009°26' E). Grübel is a Norway spruce (*Picea abies* L.) forest reserve situated in the Bavarian Forest at an altitude of 1250 m a.s.l.. Mean annual air temperature is 3-4°C and mean annual precipitation is 1500 mm. The formerly managed forest has been protected since 1978 and the CWD stock amounted to 12 t C ha^{-1} in 2010 (Krüger et al. in prep). Ludwigshain is a beech-oak (*Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl.) forest that has been unmanaged since 1913 and is well known for ancient oaks of 450 years. Mean annual temperature is 7-8°C and precipitation accumulates to 650-750 mm a^{-1}. Total above-ground CWD stocks are 30 t C ha^{-1} in 2010 (Krüger et al. in prep). Rohrberg is a beech-oak forest that has been unmanaged since 1928. The oaks are up to 600 year old. Mean annual air temperature ranges from 7-8°C and precipitation from 950-1100 mm a^{-1}. The CWD stock was 24 t C ha^{-1} in 2010 (Krüger et al. in prep).

Sampling procedures

A total of 56 CWD logs of at least 20 cm in diameter were selected for analysis. For determining CWD characteristics (wood density, C concentration), up to 10 wood samples per log were taken with a power drill with a diameter of 2 cm. All wood shavings were collected and subsequently dried at 60°C until constant mass. Wood density was calculated from dry mass and the volume of the drill hole. Sub-samples were ground with a ball mill for C and N analysis (Elementar Vario EL, Hanau, Germany).

For radiocarbon analysis, we took samples of the outermost tree ring with a utility knife. The blade was exchanged between two samplings to avoid cross-contamination. The samples were ground before the cellulose extraction. One tree segment of each log was taken with a motor saw for dendrochronological cross-dating.

Radiocarbon dating

Cellulose is commonly isolated from wood for isotope analysis (Gaudinski et al. 2005). While non-structural wood compounds might cross tree ring boundaries, cellulose is synthesized with C fixed in the year of ring formation (Mazany et al. 1980). Lignification of wood tissue occurs after cellulose formation (Fritts 1976). We thus assume that contamination with lignin-containing compounds has no or little impact on radiocarbon signatures. For cellulose extraction, we used a method adapted from the Jayme-Wise protocol (Green 1963). Hereafter, 40-50 mg of wood was processed for extraction of α-cellulose. The milled samples were processed in cuvettes with glass fiber filters. Extractable wood substances were extracted with a 1:1 toluene-ethanol mixture in a soxhlet extractor. Subsequently, the remaining samples were treated with a CH_3COOH-$NaClO_2$ mixture and subsequently 5% NaOH solution at 80°C. Between extraction steps, the samples were rinsed with a 15% NaCl solution. These extraction steps were repeated at least three times and until the remaining sample had a white colour. The samples were then rinsed with 1% HCl and subsequently with distilled water for a period of at least 12h. The cellulose was freeze-dried until mass constancy. To assess the quality of cellulose, total C and N was measured with a with a CN analyser (Elementar Vario EL, Hanau, Germany) by the Central Analytics of the Bayreuth Center of Environmental and Ecological Research (BayCEER). Further, $\delta^{13}C$ of the cellulose was measured with a MAT 252 IRMS at the stable isotope lab of the Max Planck Institute for Biogeochemsitry in Jena. Industrial cellulose (Sigma chemicals, St Louis, USA), chitin and chitinose (Acros organics, New Jersey, USA) as well as Heidelberger Nullholz and the wood standards C-4 and C-5 from the International Atomic Energy Agency (IAEA) (Rozanski et al. 1992) were used as standards for radiocarbon analysis. The yield of cellulose is calculated from the difference of the original sample weight and the weight of the extracted cellulose.

Radiocarbon signatures of cellulose were measured by accelerator mass spectrometry (AMS). Subsamples of 0.7 - 1.1 mg C were combusted in sealed quartz tubes with CuO as oxidizer and silver wire for 2 hours at 900°C. The resulting CO_2 was cryogenically purified from water and non-condensable compounds and converted to graphite targets using the modified sealed tube zinc reduction method described by Xu et al. (2007). Radiocarbon data are expressed as $\Delta^{14}C$, which is the per mil deviation from the $^{14}C/^{12}C$ ratio of oxalic acid standard in 1950. The sample $^{14}C/^{12}C$ ratio has been corrected to a $\delta^{13}C$ value of -25‰ to account for any mass dependent fractionation effects (Stuiver & Polach 1977). $\Delta^{14}C$ signatures were dated to calendar years using the CALIBomb

Radiocarbon calibration online tool (Reimer et al. 2004). For post-bomb radiocarbon signatures, two calendar years are possible. The younger age was attributed to the time of tree death. The cellulose extraction and sample combustion were processed at the laboratory of ^{14}C analyses at the Max Planck Institute for Biogeochemistry in Jena. Graphite targets were prepared at the Department of Soil Ecology at the University of Bayreuth. The AMS measurements were performed by the Keck-CCAMS facility of the University of California, Irvine with a precision of 2-5‰.

Dendrochronological cross-dating

All wood segments were dried prior to further preparation. Heavily decomposed wood was immersed in paraffin at 60°C to prevent rupture and breaking (Hall 1939). Less decomposed wood was polished with sandpaper with granulation of 100 grit. Wet chalk was used to increase the visibility of tree ring boundaries (Schweingruber, 1983). Ring widths were measured to the nearest 0.01 mm using a measuring device (LINTAB 6; Rinntech, Heidelberg, Germany) with a stereo microscope (MZ 6; Leica, Wetzlar; Germany) and the TSAP-Win software package (Rinn 2003). Tree ring widths were measured along two radii following the longest and shortest radius.

Site chronologies were compiled from 6-12 wood disks of living trees for each tree species and study site, in order to build up reference chronologies for the CWD. The quality of the site chronologies were tested with the dplR package for R (Bunn 2008) using series inter-correlation (Rbar), Expressed Population Signal (EPS) and Gleichläufigkeit (Glk).

Tree ring sequences were measured along at least two radii at postions with a surely identified outermost tree ring and the smallest amount of major constraints including softness of wood or holes. All measurements were conducted at the Faculty of Forestry, University of Applied Science Weihenstephan-Triesdorf.

The dating of tree death was obtained through visual cross-dating of CWD samples with the corresponding site chronology with the software Corina 1.1 β (The Cornell Tree Ring Analysis System). Additionally, the software was used to calculate correlation analyses based on student’s t-test (t values), series inter-correlation (Rbar) as well as Gleichläufigkeit (Glk) to cross-date the tree ring sequence with the site chronologies. All results that gave an end of the sequence set after 2009 were excluded. Based on what is known about the decay rate of the observed tree species (Rock et al. 2008) as well as site history we also excluded all results that gave end dates before 1935. If uncertainties on the correct date remained, the tree ring sequences were visually compared with other sequences of CWD of the same tree species and the same study site. Precision of the method depends on the number of overlapping years and by consequence the length of the individual tree ring sequences.

Data analysis

The C density of CWD is calculated from the density and the C concentration of CWD. Decay of CWD is described through disappearance time defined as the time period from tree death to reduction in size to the point where the piece is no longer considered as CWD (less than 7 cm at the largest diameter). Differences between tree species were tested with a Student's t-test with a confidence interval of $p<0.05$. If not otherwise specified, calculations were performed with R 2.9.2 (R Development Core Team 2009).

Results

Properties of cellulose and radiocarbon dating

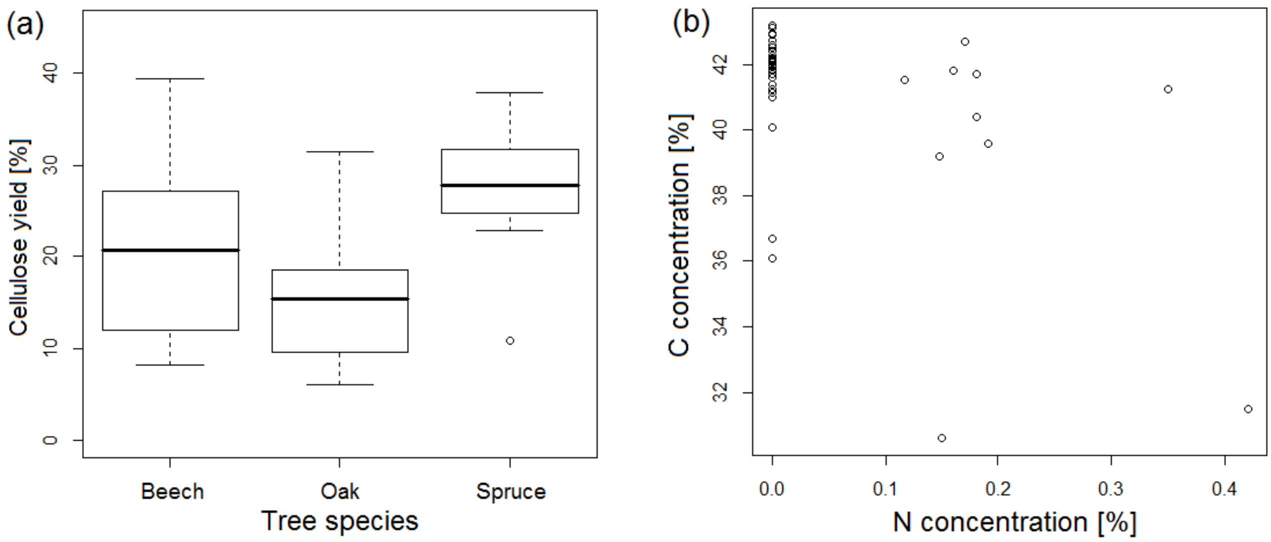

Fig. 2.1: Properties of extracted cellulose: Yields of cellulose extraction in % per tree species (a) and carbon and nitrogen concentration of extracted cellulose in % (b).

We found cellulose yields, defined as mass-% of the original sample after extraction, of 17 – 38 % for the different wood standards with a good reproducibility (data not shown). Pure industrial cellulose had a recovery rate of 81.2 ± 0.3 % (SD, n=4). For the CWD samples, cellulose yields ranged between 6 and 39 % (Fig 2.1a). We found significant differences between tree species ($p<0.001$), but no correlations with C density of CWD.
Mean C concentration (± SD) in the extracted cellulose was lower in oak (39.5 ± 3.9 %) than in beech (42.1 ± 0.7 %) and spruce (42.2 ± 0.6 %). In 6 out of 56 samples, the C concentration was

below 40 %. 13 samples contained measurable N concentrations (>0.05 %) whereas the N concentration of the remaining samples was below the detection limit (Fig 2.1b). Mean $\delta^{13}C$ of cellulose was -23.2 ‰ ± 1.3 ‰ without significant differences between the three tree species. $\Delta^{14}C$ signatures of the outermost tree rings ranged between -34 and 660 ‰. Five samples were dated to the time period before the bomb-peak. 51 samples could be attributed to calendar years between 1959 and 2006.

Dendrochronological cross-dating

The length of the site chronologies was between 94 and 244 years. The Rbar values range between 0.45 and 0.65 and EPS between 0.82 and 0.93, therefore the reference chronologies provide good data quality (Table 2.1). With respect to wood characteristics and tree age, between 43 and 286 rings were measured per CWD segment. Fig. 2.2 shows samples of the wood anatomy at different stages of decay and the tree species specific changes in CWD. Beech CWD becomes soft and tree rings gradually less visible. Oak CWD is marked by the formation of holes and spruce CWD by cracks along tree ring boundaries.

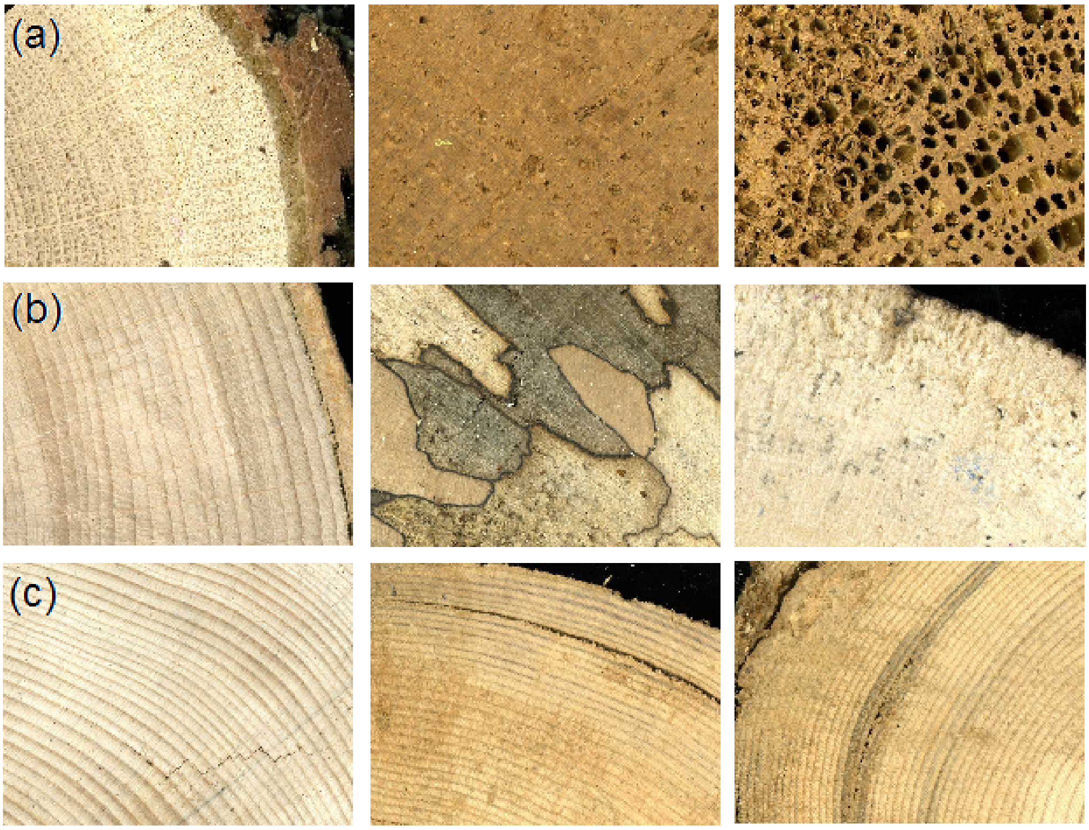

Fig. 2.2: Samples of coarse woody debris of Sessile oak (a), European beech (b) and Norway spruce (c) at different stages of decay.

Based on dendrochronological cross-dating, the investigated trees had died between 1942 and 2006.

The distribution differed between the tree species: for beech the oldest CWD originated from 1981, while four samples of oak and one sample of spruce were dated to the period prior to the bomb peak in the 1950s.

Comparison of radiocarbon and dendrochronological dating

We found a good correlation between year of death as determined by radiocarbon dating vs. dendrochronological cross-dating (R^2=0.96) (Fig. 2.3). The average difference between radiocarbon and dendrochronological dating were 2.05 years with a median value of one year. Radiocarbon dating revealed a younger time of death in 13 cases and an older death year in 17 cases. No differences between radiocarbon analysis and dendrochronological cross-dating were found for tree species, study sites or C density of CWD.

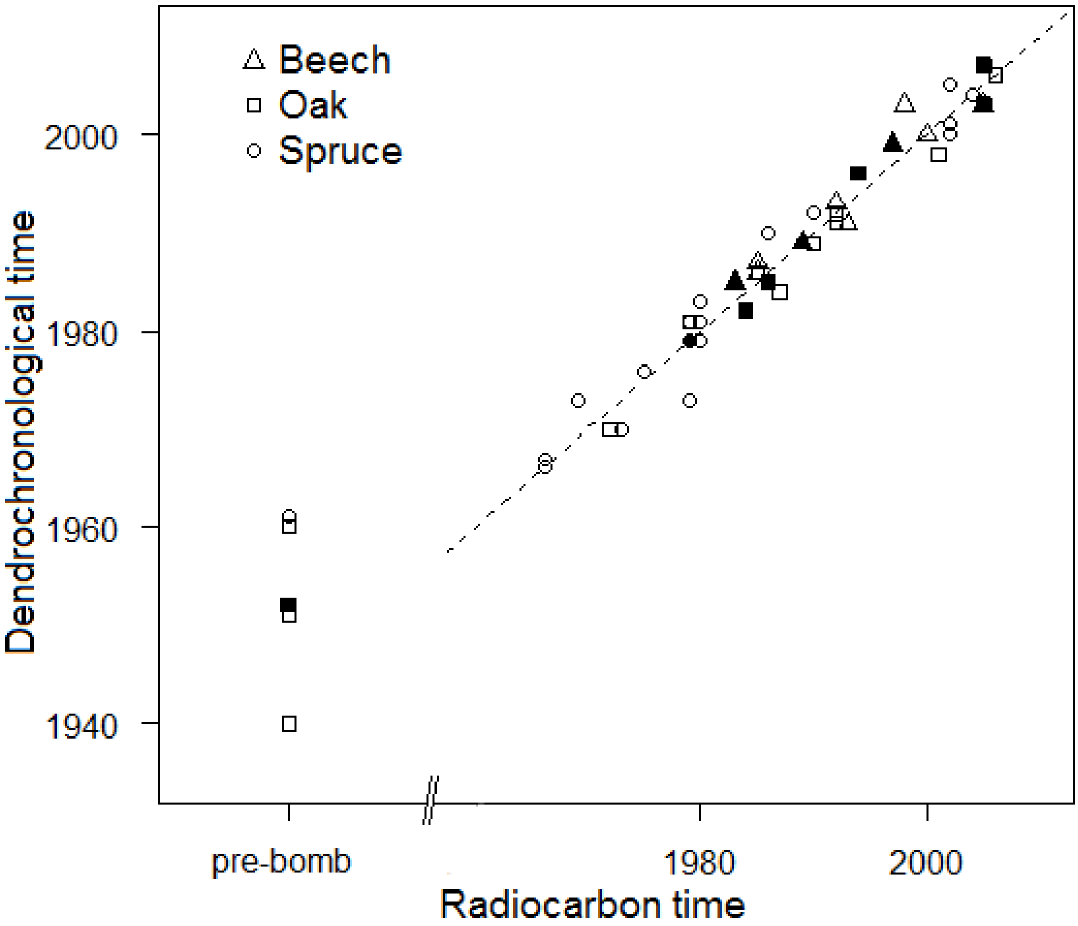

Fig. 2.3: Time of tree death as determined by dendrochronological cross-dating (dendrochronological time) and radiocarbon analysis of the uttermost year ring (radiocarbon time) for the tree species European beech, Sessile oak and Norway spruce. Full bullets designate enhanced nitrogen concentration in the cellulose.

Table 2.1: Characteristics of site chronologies.

Study site	Tree species	Period	Number of trees	rbar	EPS	Glk[%]
Grübel	Norway spruce	1759-2010	6	0.50	0.82	52
Ludwigshain	European beech	1916-2009	12	0.51	0.91	63
Ludwigshain	Sessile oak	1907-2009	8	0.65	0.93	64
Rohrberg	European beech	1938-2009	7	0.45	0.84	68
Rohrberg	Sessile oak	1848-2009	10	0.46	0.93	64

Table 2.2: Correlation between time of tree death and C density for the tree species European beech, Sessile oak and Norway spruce.

Tree species	Method		adjusted R^2	p	n	disappearance time [a]
European beech	average	y=-15916.0+8.0x	0.61	<0.001	22	33
	dendrochronoly	y=-15760.0+8.0x	0.62	<0.001	22	33
	radiocarbon	y=-15976.0+8.1x	0.60	<0.001	22	32
Sessile oak	average	y=-2294.4+1.2x	0.08	0.16	16	169
	dendrochronoly	y=-2279.5+1.2x	0.07	0.16	16	171
	radiocarbon	y=-2074.1+1.1x	0.05	0.19	16	182
Norway spruce	average	y=-5104.7+2.7x	0.57	<0.001	16	92
	dendrochronoly	y=-4853.6+2.5x	0.55	<0.001	16	95
	radiocarbon	y=-5194.5+2.7x	0.59	<0.001	16	90

CWD density varied between 80 and 630 kg m^{-3} for beech, 140 and 480 kg m^{-3} for oak and 60 and 510 kg m^{-3} for spruce. C concentration ranged between 46 and 56 % for all species, resulting in C densities of CWD of 29 to 307 kg C m^{-3}. Positive correlations between average time of tree death and C density were found for beech and spruce, but not for oak (Fig. 2.4). Differences in decay functions between dendrochronological data and radiocarbon data were slight (Table 2.2). Disappearance times are estimated at 30 years for beech and about 90 years for spruce.

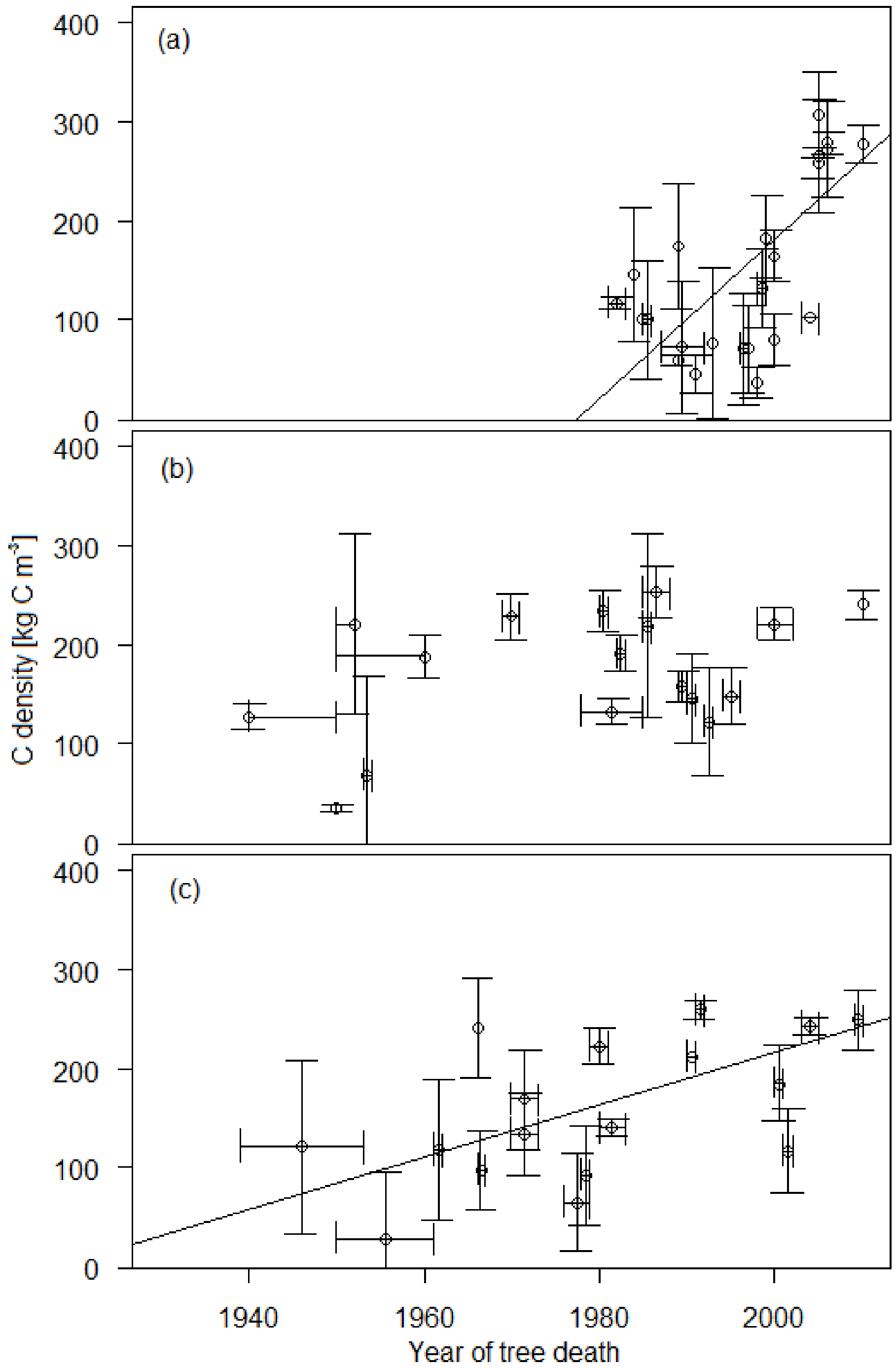

Fig. 2.4: Relation between time since tree death and C density of coarse woody debris for the tree species European beech (a), Sessile oak (b) and Norway spruce (c).

Discussion

Properties of cellulose and constraints of radiocarbon analysis

The observed cellulose yields for CWD samples between 6 and 39 % were considerably lower than the values reported for fresh wood samples of up to 68 % (Gaudinski et al. 2005). These differences can be explained only partly by incomplete extraction due to the method, as we measured a recovery rate of about 80% for the extraction of pure cellulose. Decay of wood usually results in the preferential loss of cellulose and thus a relative increase of lignin, resins and waxes (Preston et al. 2006), which could explain the low cellulose yields in the CWD samples. The lowest yield was found for oak CWD, likely for two reasons: (1) Live oak wood is known to have a smaller initial cellulose concentration (ca. 40%) than beech (43%) and spruce (49%) (Thygesen et al. 2005, Pettersen 1984, Kollmann & Fengel 1965, Fengel & Wegener 1984); (2) Decomposition of oak wood is dominated by brown-rot fungi, which preferentially decompose cellulose while leaving lignin mostly intact, whereas beech and spruce wood are known to be decomposed by white-rot fungi, which decompose cellulose and lignin at a nearly equal rate (Leonowicz et al. 1999).

With an average of 41 %, the C concentration of the extracted cellulose is lower than the 44 % C of pure cellulose polymer. Other methods of cellulose extraction do not have this problem, reporting C concentration in the extracted cellulose closer to the expected values (Brendel et al. 1999). The lower C concentrations in our measurements are most likely to be explained by a dilution effect: Weighing of the glass fibre filters that we used, before and after the extraction procedure, indicate a weight loss of the filters. As the filters are C-free, the addition of filter material to the samples would result in a decrease of the C concentration without affecting any of the isotopic measurements. The measured weight losses were big enough to explain the observed differences in C concentration. We found no correlation between ^{13}C signatures and C concentration , affirming that isotope measurements were not affected by a presumed contamination of the samples.

We speculate that chitin produced by fungi during the decay of CWD could explain the increased N concentrations found in some of the samples. The treatment of chitin revealed that chitin is not at all removed by the procedure we used (data not shown). The presence of chitin in wood samples is a problem for age determination by radiocarbon analysis of CWD samples as chitin has a different radiocarbon signature than cellulose of in the outermost tree ring. Undecayed wood contains only small amounts of chitin (Jones & Worrall 1995). Because of increasing colonization by fungi both the chitin and N concentration of CWD increases with decay (Holub et al. 2001). The increased amount of chitin or other organic N compounds might make the extraction of cellulose less effective in heavily decayed CWD samples. The C:N ratio of 210 to 80 found in the cellulose would be explained by a dilution of cellulose with about 3 to 8 % chitin. An increase in N concentration during cellulose extraction is commonly observed in most extraction methods (Gaudinski et al. 2005). As no N containing chemicals were utilized during sample preparation the N must originate from the CWD sample.

The within tree ring difference of $\delta^{13}C$ of cellulose is typically 1 – 2 ‰ (Leavitt & Long 1984). Measured differences between samples are thus within natural variations of tree rings. CWD is less depleted in $\delta^{13}C$ than cellulose extracted from undecayed wood (Leavitt & Danzer 1993). With increasing decomposition the $\delta^{13}C$ concentration of organic material increases due to microbial fractionation (Preston et al. 2009). Schleser et al. (1999) found a depletion of $\delta^{13}C$ of cellulose for thermally decayed wood corroborating the change of $\delta^{13}C$ signatures of CWD due to decay.

The five CWD samples with negative $\Delta^{14}C$ signatures, that correspond to calendar years before 1955, belong to the tree species spruce and oak. The CWD logs must have resided in the forests for at least 65 years, which is common for CWD of spruce and oak (Holeska et al. 2006, Harmon et al. 1986).

Constraints of dendrochronological cross-dating

Dendrochronological studies of CWD are more challenging than studies of living trees. The changes due to the decay of CWD affect the completeness of the outermost tree ring, the choice of radii position and the visibility of the tree rings. With advancing decay, density and stability of CWD decreases (Harmon et al. 1986). This affects the correct identification of tree ring boundaries resulting in missing tree rings or incorrect tree ring widths.

By extracting wood segments like disks instead of increment cores, the difficulties resulting from decay were remediated to some extent. As a disadvantage, segments are larger and more difficult to handle than core samples, but allow choosing the best suited radii after examination of the entire section. Nonetheless, the significance of the correlation analysis was affected by decay. Calculated algorithms are on the lower scale of what is commonly considered statistically significant for some of the CWD measurements.

We found the effects of decay on wood anatomy to be species-dependent. Samples of beech often showed symptoms of white-rot decay that disintegrates wood structure and reduces it to its components cellulose, hemicelluloses and lignin (Schweingruber 2008). Discoloration of wood, often the first visible effect of decay, does not affect the identification of tree rings. At later stages of decay, however, tree ring boundaries become difficult to see or even invisible. This process usually occurs from the outside to the inside, in consequence reducing the length of the usable sequence. In spruce CWD, the formation of cracks along tree ring boundaries was often noted and restricted the positioning of the recorded radii. Decay of oak CWD leads to the formation of holes, but it does not affect the visibility of tree ring boundaries until advanced stages of decay.

While sequences are statistically compared with standardized methods, dendrochronological cross-dating necessitates the restriction to a certain time interval. While such restrictions are based on scientific observations and reliable accounts, they remain to some extent subjective and might differ between users.

Comparison of analysis methods and coarse woody debris carbon density

We found a good correlation between radiocarbon analysis and dendrochronological cross-dating that was not affected by the state of decay, the tree species and the study sites. This indicates that despite constraints, both methods are equally reliable techniques to estimate the year of tree death. Radiocarbon analysis can be the favourable method for standing CWD that cannot be sampled by motor saw and for CWD were the outermost tree ring is only intact on a small area or decay occurs from the inner to the outer wood. Dendrochronological cross-dating is more suitable for CWD that is expected to have slow decay rates, as found in CWD of decay resistant tree species or at unfavourable study sites.

Besides practicability, the decision to apply a method is based on factors like time and cost. Both methods are time intensive and require special equipment. Their efficiency partially depends on the number of samples, age as well as their diversity regarding geographical origin and tree species. Each region and tree species requires an individual site or reference chronology that needs to be compiled from trees of known age. The compilation of a site chronology requires a need to record a certain number of tree ring width sequences in addition to the CWD samples. This is more worthwhile the more samples need to be dated. If a reference chronology is existent, dendrochronological cross-dating represents a cheaper way to date a large number of samples than radiocarbon analysis.

Age determination of tree rings by radiocarbon analysis is barely dependent on the geographical region and the tree species. In mixed forests with many tree species, classification of heavily decayed CWD logs to tree species is problematic if wood characteristics are similar. In such cases, radiocarbon analysis is an alternative method of age determination. Further radiocarbon analysis can be more time efficient if the number of CWD samples is small.

A correlation between time since tree death and C density of CWD was found for European beech and Norway spruce. For Sessile oak no correlation was found. Decay rates can greatly vary depending on the decomposition conditions and the contact of CWD to soil fungi (Holeska et al. 2008). Further, large branches or even parts of the stem of oak trees can die and decay while other parts of the trees are still alive for many decades, resulting in a non-uniform year of death for different parts of these trees (Ranius et al. 2009). In such a tree, some parts would already decay and loose C, while new tree rings could still be formed in others. For this reason, decay rate of CWD may vary within a tree. Despite differences of up to 5 years between radiocarbon analysis and dendrochronological cross-dating, both methods yield similar decay functions and disappearance times for beech and spruce. Overall, the variations in CWD characteristics cause a greater uncertainty for the calculation of decay rates than the both studied methods of age determination.

Conclusions

Our results show that radiocarbon analysis and dendrochronological cross-dating revealed similar year of tree death and are in most cases suitable for age determination of CWD. Both methods are constrained by CWD decay, though we found these not to affect the quality of the dating procedure. Radiocarbon analyses are less destructive and only require small samples. On the other hand, CWD can only be radiocarbon dated for the time period since the 1950s and the method is thus not suitable for old CWD of species with long turnover times. Calculation of disappearance times was possible for Norway spruce and European beech, but not for Sessile oak.

Acknowledgments

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Chapter 3

Effects of tree species and decay class on

DOC and CO2 production of woody debris.

Effects of tree species and decay class on DOC and CO_2 production of woody debris

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Abstract

Woody debris is an important component in the carbon (C) cycle of forest ecosystems, but the release of dissolved organic carbon (DOC) and CO_2 as influenced by tree species and decay class is widely unknown. A laboratory experiment with woody debris of European beech, Sessile oak, Norway spruce in three decay stages (fresh (DC-1), penetrable with a knife (DC-3), breakable with fingers (DC-5)) was carried out over a period of 380 days. Quantity and quality of DOC in leachates as well as CO_2 production were measured in regular intervals. To test the influence of an easily available C source on DOC and CO_2 production, additional woody debris samples were treated with a 600 mM glucose solution. The pH, humification index and specific ultra-violet absorption of leachates were measured to describe DOC.

Woody debris lost between 1 and 15% of its initial C within 380 days. DOC contributed 3-54% to the total C loss. Total C loss increased in the order spruce<oak<beech. At early decay stages, DOC contributed most to C loss of oak. At DC-5, DOC contribution from beech and oak are of similar range. DOC and CO_2 production generally increased with decay class. The pH values of leachates ranged between 4.18 and 5.61 and were lowest for oak and for samples at DC-5 of all tree species. Humification indices and specific UV absorption of leachates increased with decay class. The addition of glucose did not influence the quantity and quality of leached DOC or CO_2 production. Our results suggest that CO_2 production is the main path of woody debris decay, but DOC leaching is relevant as input to the soil especially at later decay stages of oak and beech.

Keywords: woody debris, tree species, CO_2 production, DOC, glucose, wood decay, humification index

Introduction

Coarse woody debris can account for up to 23% of carbon (C) in above ground litter (Prescott & Laiho 2002). It thus plays an important role in the C cycle of forest ecosystems, though the fate of C in the course of woody debris decay and its influence on the C pool of the soil are subject to speculations (Trumbore & Harden 1997, Strukelj et al. 2012). The decay of woody debris takes place through biological and chemical fragmentation, mineralization and leaching. Fragmentation and leaching represent C fluxes to the soil (Harmon et al. 1986). Basidiomycetes, commonly separated in white rot fungi and brown rot fungi, are strongly involved in the decay of woody debris and respire much of the C pool (Käärik 1974, Swift 1977). Chambers et al. (2001) estimate that respiration accounts for 76% of the total C loss from woody debris in the tropics over the whole decomposition period. Leaching of DOC is another important path in the decay of woody debris (Harmon et al. 1986). Decomposition products (Spears et al. 2003) or exudates from wood decomposing fungi (Fransson et al. 2004) induce changes in the characteristics of the mineral soil (Klinka et al. 1995). Several studies have been effectuated to measure respiration rates from woody debris (e.g., Chen et al. 2000, Chambers et al. 2001, Herrmann & Bauhus 2008) or DOC loss from woody debris (e.g., Spears et al. 2003, Hafner et al. 2005, Kuehne et al. 2008). We know of only one study that simultaneously measured both CO_2 and DOC production (Mattson et al. 1987). They found a CO_2:DOC ratio of 12:1, but tree species had no effect on the ratio.

The decay rate of woody debris depends on abiotic factors, like temperature and wood moisture, and biotic factors including wood characteristics (Harmon et al. 1986). Lignin content, N and P concentration, C:N ratio, wood density, dry matter content, wood pH and concentration of wood extractives are described as driving factors of wood decay (Weedon et al. 2009, Fréschet et al. 2012). These factors vary among common Central European tree species (Rock et al. 2008). DOC from woody debris is made up of a mixture of different substances including soluble decomposition products (e.g., Reid & Seifert 1982, Leisola et al. 1983, Song et al. 2012), wood extractives (e.g. Hillis 1987, Scalbert et al. 1988, Scheffer 1966), dead microbial cells (Zsolnay 2003) and fungal exudates (Fransson et al. 2004). The importance of DOC leaching is thought to increase with decay class due to greater surface area of fragmented woody debris (Harmon et al. 1986). The amount of water soluble compounds per mass unit wood of ground woody debris, however, decreases (Wilhelm 1976, Yano et al. 2005) or remains constant (Rajala et al. 2012) with increasing decay class.

As analyses for specific substances in DOM are sophisticated, different proxies have been proposed as explaining parameters for decay stages and their implications for environmental processes. The pH values of water extracts were found to predict leaf litter decomposability in a subarctic flora (Cornelissen et al. 2006) and to correlate with decomposition rates of woody debris of different tree species (Fréschet et al. 2012). The pH values of mineral soil underneath logs were reduced (Klinka et al. 1995, Krzyszowska-Waitkus 2006). Further proxy parameters are the humificiation indices (HIX) and the specific ultraviolet absorbance (SUVA) that are correlated with the complexity and the aromaticity of the DOC solution (Weishaar et al. 2003). DOC with high HIX and SUVA values seems to contribute more to C accumulation in the mineral soil than DOC with low values (Don & Kalbitz, 2005).

Non-structural carbohydrates (NSC) are common constituents of heart- and sapwood and represent easily available C sources for microorganisms. The concentration of NSC can be relatively high in fresh woody debris, but as in plant litter its concentration decreases rapidly by microbial consumption (Berg, 2000). With rising decay of hemicelluloses and celluloses, other easily available C sources arise in woody debris mainly through the activity of exoenzymes. To our knowledge, the influence of additional C sources on the decay of woody debris at different decay stages has not been studied yet. External C sources could be of relevance for the decay of woody debris because throughfall represents a considerable input of easily available C under natural decay conditions in forest ecosystems (van Hees et al. 2005). The effects of glucose addition on the decay of synthetic or isolated cellulose, lignin or lignocellulose were investigated in several studies using pure cultures of fungi. The availability of glucose decreases the amount of leachates and influences the quality of lignin decay products (Leisola et al. 1984). Glucose can stimulate or repress the decomposition of cellulose by white and brown rot fungi (Highley 1980, Highley 1987, Ritschkoff et al 1995). Under laboratory conditions the glucose content of wood increases during enzymatic hydrolysis during the initial decomposition step when up to 12% of the biomass is transformed to glucose (Giles et al. 2011). The presence of other decaying microorganisms might prevent the increase of soluble sugar concentrations (Giles et al. 2012).

The goal of our study was to investigate the C loss of woody debris of common European tree species at different decay stages through DOC and CO_2 production at constant temperature under laboratory conditions. The following hypotheses were tested: (1) DOC and CO_2 production are different for European beech, Sessile oak and Norway spruce (2) DOC and CO_2 production increase with increasing decay class, (3) humification and complexity of DOC increase while pH of leachates decrease with increasing decay class. Further, we tested the addition of glucose on DOC and CO_2 production.

Materials and methods

Study sites and sample preparation

The woody debris samples used in the incubation experiment originate from the forest sites Rohrberg (49°54’ N 009°26’ E) (European beech (*Fagus sylvatica L.*)), Ludwigshain (49°55’ N 011°48’ E) (Sessile oak (*Quercus petraea (Matt.) Liebl.*)) and Grübel (49°07’ N 013°07’ E) (Norway spruce (*Picea abies L.*)). Mean annual precipitation ranges from 760–1200 mm a^{-1} and mean annual temperature from 3-8°C.

Table 3.1: Decay class (DC) characteristics of coarse woody debris (CWD).

Decay class	Characteristics
DC-1	Recently dead, bark intact, small twigs and leafs, no visible signs of decomposition
DC-2	Bark mostly remaining, no leafs, wood not penetrable by a knife
DC-3	Bark mostly missing, wood partly penetrable with knife, visible discoloration
DC-4	No bark, wood completely penetrable with knife, deformation and discoloration
DC-5	Wood soft, breakable with fingers, advanced humification

All woody debris samples were taken in 2010 and attributed to decay classes following the criteria in Table 3.1. All samples of decay class 1 (DC-1) were sawn off in 2010 as part of thinning procedures. Woody debris of decay class 3 (DC-3) and decay class 5 (DC-5) resulted from natural mortality and decayed under field conditions until sampling. One wood slice per tree species and decay class from logs were saw off or a sample collected in case of loose woody debris. Samples of DC-1 and DC-3 were cut into cubes with 3 cm length and dry weight of 10-15 g. Cubes without bark and constituting of heartwood only were chosen. Material of DC-5 was gently sieved and pieces >2 mm were used for the incubation. Density of woody debris was determined from volume measurements by water displacement (Table 3.2). Samples were wrapped in foil to prevent water from soaking into the samples. C and N concentrations of ground subsamples from each sampled tree were measured with a Vario Max CN element analyser (Elementar Analysensysteme GmbH, Hanau, Germany) (Table 3.2). All woody debris samples were dried at 60°C for mass determination and subsequently rewetted by immersion in deionised water for 24h. The wet samples were preincubated on forest floor material of the same tree species at 30°C for 10 days to inoculate all samples to wood decaying organisms.

Table 3.2: Initial sample characteristics.

Tree species	Decay class	Density [g cm^{-3}]	Gravimetric water content [%]	C content [%]	N content [%]
Beech	DC-1	0.67	50	48	0.19
	DC-3	0.36	160	49	0.16
	DC-5	0.22	640	50	0.58
Oak	DC-1	0.65	40	48	0.14
	DC-3	0.47	60	49	0.17
	DC-5	0.08	370	49	0.73
Spruce	DC-1	0.36	90	50	0.01
	DC-3	0.37	80	50	0.01
	DC-5	0.17	540	53	0.50

Incubation and analysis

Twelve samples per decay class and tree species were incubated on Whatman ® VACUFLO vacuum filtration units in 1 l airtight glass jars at 15°C in a dark climate chamber for 380 days. Between measurements, the jars were kept open and parafilm was used to protect the woody debris samples from drying while enabling oxygen supply.

DOC was leached from woody debris every week by applying 25 ml of artificial rain with a pH of 6 and following composition: 1.0 µmol l^{-1} $MnCl_2$, 9.0 µmol l^{-1} $MgCl_2$, 1.5 $µmol^{-1}$ K_3PO_4, 0. 2 µmol l^{-1} $FeSO_4$, 1.0 µmol l^{-1} $Al(NO_3)_3.H_2O$, 99.1 µmol l^{-1} CaS, 87.1 µmol l^{-1} NH_4NO_3, 20.0 µmol l^{-1} K_2SO_4, 18.0 µmol l^{-1} NaCl, 16.0 µmol l^{-1} Na_2SO_4. The solution was applied in two steps of 15 and 10 ml and left to interact with woody debris for 5-10 min before being filtrated through a glass fiber prefilter (Schleicher & Schuell GF92) and a 45 µm cellulose acetate membrane filter (Whatman OE67). DOC samples were frozen at -18°C. A composite DOC sample of 4-16 weeks with increasing periodic intervals as the experiment advanced was created for each woody debris sample. DOC was measured as non-purgable organic C (NPOC) with a multi N/C 2100 analyzer (analytikjena) by the Analytical Chemistry of the Bayreuth Center of Ecology and Environmental Research (BayCEER). The pH values were measured with a WTW pH315i sensor. Emission of DOC samples between 254 and 500 nm were recorded on a SFM 25 spectrometer (BIO-TEK Instruments). The humification index (HIX) was calculated according to Zsolnay et al. (1999) by dividing the lower quarter (300-345 nm) by the upper quarter (435-480 nm). UV absorption was measured with a UV spectrometer (UV-1800 SHIMADZU) at a concentration of 10 mg l^{-1}. Specific ultraviolet absorbance ($SUVA_{254}$) was calculated by dividing the absorbance at 254 nm by the DOC concentration and multiplying it by 100 (Weishaar et al. 2003). HIX and $SUVA_{254}$ measured on the pooled samples of the first measurement period (days 1-28) and the last measurement period (days 270-380).

Respiration rates were measured on a weekly basis, starting on the day after the DOC leaching. They were calculated from the linear increase in CO_2 in the glass jars from the difference of two CO_2 concentration measurements with a 24h time interval. CO_2 concentration was measured as CH_4 with a gaschromatograph (SRI 8610C) equipped with a flame ionization detector. Gas samples (30 µl) were taken from the headspace of the jars and then injected with a 50 µl syringe (Hamilton 1805 RN 50 µl BBL, needles: Hamilton ga2Gs/51mm). CO_2 standards with the concentrations 380 ppm, 600 ppm, 1000 ppm, 3000 ppm and 10000 ppm were used for calibration. The mean precision of CO_2 measurement ranges from 4% (10000 ppm) to 8% (380 ppm).

After 8 weeks, half the samples (n= 6 per tree species and decay class) were treated with 2 ml of a glucose solution per week with a concentration of 600 mg C l^{-1} directly before the 24h CO_2 measurement interval. The glucose-C concentration corresponds approximately to the maximum concentration of DOC in throughfall of Bavarian forests.

Statistical analysis

We analyzed the effects of tree species and decay class on cumulative DOC and CO_2 production, pH-value, HIX and $SUVA_{254}$ using non-parametric linear regression analysis. Differences between glucose and control were tested with Student's t-test with a significance level of $p<0.05$. All statistical analysis was done with R 2.9.2 (R Development Core Team 2009).

Results

Tree species and decay class effects on CO_2 production

The mean cumulative CO_2 production of all tree species and decay stages varied between 1 and 9% of the initial C over 380 days (Table 3.3). In case of spruce, differences in CO_2 production were rather small (1-3%) among the decay stages. The linear regression showed differences between tree species and decay class and combinations thereof ($R^2 = 0.82$, $p<0.001$) Differences between decay classes are more important than between tree species (Table 3.4). For beech and spruce, CO_2 production increased with decay class, while oak had a distinct pattern. In contrast to the other tree species, DC-3 of oak produced less CO_2 than DC-1.

Regardless of tree species, we measured relatively constant CO_2 production rates for DC-5 over the course of the incubation (Fig. 3.1). In contrast, CO_2 production of DC-1 and DC-3 were generally highest in the first weeks and decreased thereafter. In particular, DC-3 of Norway spruce exhibited a strong dynamic: 50% of the CO_2 production occurred in the first 100 days of the experiment and remained then at a low and constant level.

Tree species and decay class effects on DOC production

Mean cumulative DOC production accumulated to 0.1 and 1.5% of the initial C (Table 3.3). Differences in DOC production among the three decay stages were very small for spruce (0.36-0.61) and greatest for beech (0.11-1.56). The effect of tree species and decay class on DOC production were significant ($R^2=0.85$, $p<0.001$). The order of cumulative DOC production depended on the decay class (Table 3.3): DC-5 always had the highest DOC production rates and DC-1 had the lowest production rates, except for oak. The differences for DC-3 among the tree species were small.

Table 3.3: Results of regression analysis of tree species and decay class effects in comparison to oak at DC-1 for total C loss, cumulative DOC and CO_2 production, mean humification index (HIX), mean specific ultra-violet absorption ($SUVA_{254}$) and mean pH values.

		Oak - DC-1	Beech	Spruce	DC-3	DC-5	Beech - DC-3	Spruce - DC-3	Beech - DC-5	Spruce - DC-5
Total C-loss	factor	3.16 (0.43)	-1.50 (0.61)	-0.87 (0.61)	-1.34 (0.61)	7.32 (0.61)	2.68 (0.86)	-5.36 (0.86)	4.48 (0.86)	1.21 (0.86)
	t-value	7.38	-2.49	-1.43	-2.21	12.09	3.13	-6.26	5.24	1.42
	p-value	<0.001	0.01	0.16	0.03	<0.001	0.002	<0.001	<0.001	0.16
Cumulative CO2 loss	factor	2.37 (0.40)	-1.08 (0.56)	-0.19 (0.56)	-1.03 (0.56)	6.66 (0.56)	2.24 (0.79)	-4.96 (0.79)	3.91 (0.79)	0.42 (0.79)
	t-value	6.0	-1.9	-0.3	-1.8	11.9	2.8	-6.3	4.9	0.5
	p-value	<0.001	0.06	0.73	0.07	<0.001	0.006	<0.001	<0.001	0.59
Cumulative DOC loss	factor	0.79 (0.06)	-0.43 (0.08)	-0.67 (0.08)	-0.30 (0.08)	0.66 (0.08)	0.44 (0.11)	-0.41 (0.11)	0.57 (0.11)	0.79 (0.11)
	t-value	14.0	-5.3	-8.4	-3.8	8.2	3.9	-3.6	5.1	7.0
	p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
HIX	factor	5.33 (0.30)	-1.61 (0.42)	-1.05 (0.42)	2.58 (0.42)	3.53 (0.42)	-5.03 (0.59)	-1.78 (0.59)	-2.29 (0.59)	2.22 (0.59)
	t-value	18.0	-3.8	-2.5	6.2	8.4	-8.5	-3.0	-3.9	3.8
	p-value	<0.001	<0.001	0.014	<0.001	<0.001	<0.001	0.003	<0.001	<0.001
$SUVA_{254}$	factor	0.35 (0.01)	-0.09 (0.02)	-0.15 (0.02)	-0.04 (0.02)	-0.04 (0.02)	-0.06 (0.02)	0.03 (0.02)	0.02 (0.02)	0.15 (0.02)
	t-value	31.4	-5.4	-9.2	-2.3	-2.8	-2.6	1.2	0.7	6.5
	p-value	<0.001	<0.001	<0.001	0.02	0.006	0.01	0.24	0.47	<0.001
pH	factor	4.54 (0.05)	0.82 (0.08)	1.36 (0.08)	0.03 (0.08)	0.05 (0.08)	-0.66 (0.11)	-0.96 (0.11)	-0.37 (0.11)	-1.26 (0.11)
	t-value	83.8	10.8	17.7	0.4	0.7	-6.1	-8.8	-3.4	-11.7
	p-value	<0.001	<0.001	<0.001	0.68	0.50	<0.001	<0.001	<0.001	<0.001

Table 3.4: Mean (± standard deviation) of DOC concentration, C loss as DOC in % initial C, pH (geometrical mean), humification index (HIX) and specific ultra-violet absorption ($SUVA_{254}$) from CWD leachates and cumulative C loss as CO_2 and DOC of three tree species and three decay stages.

Tree species	Decay class	DOC [mg C l^{-1}]	pH	HIX	SUVA [l mg^{-1} m^{-1}]	Cum. C as CO_2 [%]	Cum. C as DOC [%]
Beech	DC-1	14.7 (4.4)	5.61	4.28 (1.70)	2.49 (1.59)	2.18 (0.20)	0.11 (0.02)
	DC-3	23.2 (2.8)	5.44	4.58 (0.74)	2.34 (0.57)	5.05 (0.45)	0.38 (0.11)
	DC-5	37.6 (5.4)	4.52	10.03 (2.01)	3.95 (0.25)	9.26 (0.78)	1.56 (0.31)
Oak	DC-1	91.8 (18.5)	4.26	5.33 (2.86)	4.47 (0.65)	2.37 (0.44)	0.79 (0.21)
	DC-3	49.5 (6.2)	4.39	7.91 (1.29)	3.85 (0.44)	1.33 (0.18)	0.48 (0.06)
	DC-5	39.4 (9.9)	4.36	8.86 (1.58)	3.93 (0.47)	9.03 (0.49)	1.45 (0.33)
Spruce	DC-1	22.8 (3.9)	5.27	3.72 (0.59)	3.28 (0.64)	1.29 (0.13)	0.36 (0.09)
	DC-3	47.4 (5.9)	4.63	1.27 (0.65)	1.88 (0.91)	2.50 (0.19)	0.49 (0.20)
	DC-5	19.2 (2.6)	4.18	5.47 (0.85)	3.23 (0.70)	3.00 (0.16)	0.61 (0.18)

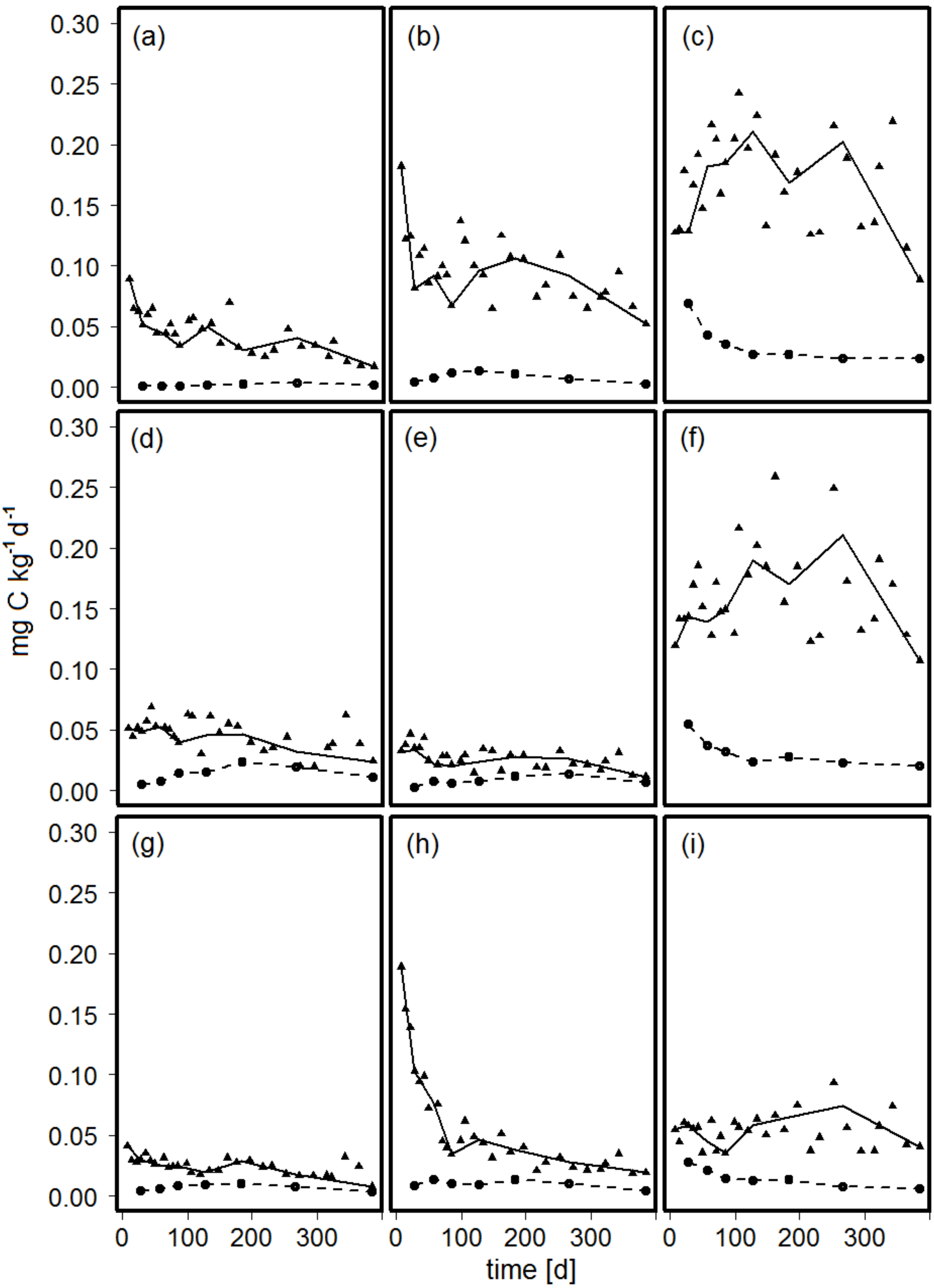

Fig. 3.1: Weekly C loss as CO2 and as DOC for the samples (a) beech DC-1, (b) beech DC-3, (c) beech DC-5, (d) oak DC-1, (e) oak DC-3, (f) oak DC-5, (g) spruce DC-1, (h) spruce DC-3, (i) spruce DC-5

Mean DOC concentrations ranged between 14.7 and 91.8 mg l^{-1} (Table 3.3). The dynamics were similar for all tree species of the same decay class: DOC concentrations of DC-1 and DC-3 peaked between days 90 and 270 and decreased thereafter (Fig. 3.2). The DOC concentrations of DC-5 strongly decreased during the first 100-150 days whereas the changes were small in the remaining time.

The relative contribution of DOC leaching to total C loss was tree species dependant and varied between 3 and 54% in single samples. In average, it was most important for oak at DC-3 (27%) and DC-1 (25%) and was least important for beech at DC-3 (5%) and DC-1 (7%) (Table 3.4). The ratio of DOC to CO_2 production fluctuated over the duration of incubation and revealed different patterns among the decay stages. For DC-1 and DC-3, the relative importance of DOC production increased during the first 200-300 days and decreased thereafter. The cumulative CO_2 and DOC production were not correlated for DC-1 and DC-3. In terms of DC-5, the relative C loss by DOC leaching dropped in the beginning and leveled off in the remaining time. The correlation between C loss via DOC leaching and CO_2 production of DC-5 was positive and significant (adjusted R^2=0.84, $p<0.001$, $y=0.25+0.13x$).

Qualitative DOC parameters

Mean pH values of leachates ranged between 4.18 and 5.61, indicating mainly decreasing pH values compared to the applied solution (pH 6.0) (Table 3.4). The decrease in pH was strongest for DC-5 of all tree species (Fig. 3.2b). Increasing pH values >6.0 were only measured in single samples of beech leachates of DC-1 and DC-3. The linear regression analysis revealed significant effects (R^2=0.88, $p<0.001$) of tree species and decay class on pH values (Table 3.3). Differences between tree species and decay stages became greater during the incubation.

Average HIX and $SUVA_{254}$ values were 5.71 and 3.27 l mg^{-1} m^{-1}, respectively. We found significant influences of decay stages and tree species (Table 3.3). Both HIX and $SUVA_{254}$ values were generally greatest at DC-5. Differences in HIX between days 1-28 and days 270-380 were greater than differences in $SUVA_{254}$ (data not shown).

Of the qualitative DOC parameters, cumulative CO_2 production was better correlated with HIX between days 270-380 than days 1-28 (Table 3.5). Weak correlations were found between CO_2 production and $SUVA_{254}$ as well as pH values. Cumulative DOC production was positively correlated with pH values, HIX and SUVA (Table 3.5) in the initial (days 1-28) and final incubation period (days 270-380). The best correlation between DOC production and parameters was found with HIX between days 270-380.

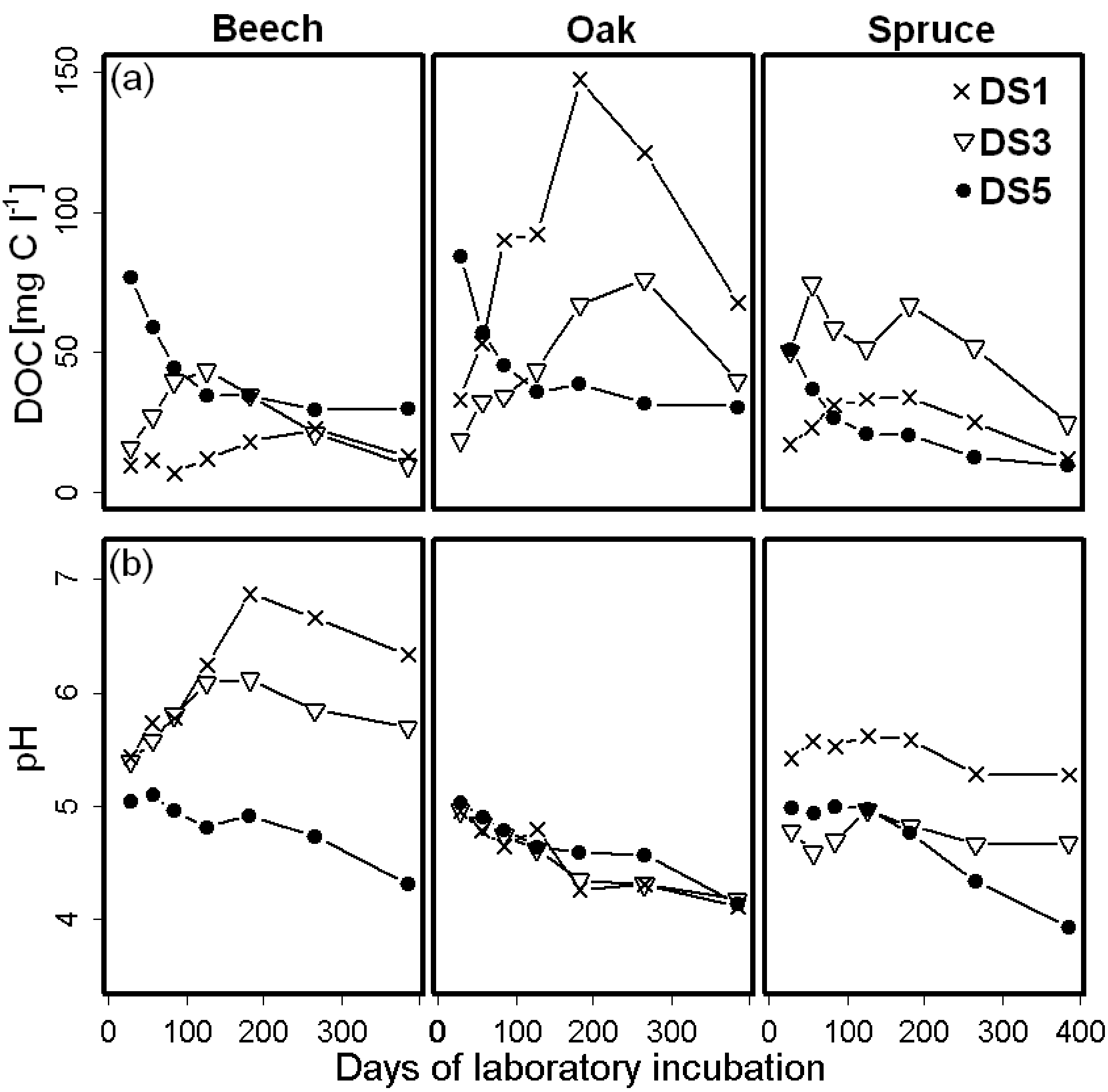

Fig. 3.2: Dynamics of (a) DOC concentrations and (b) pH values of extracts of decay class 1 (DC-1), decay class 3 (DC-3) and decay class 5 (DC-5) and three tree species over 380 days of incubation.

Effects of glucose addition on DOC and CO_2 production

The glucose added up to 56.4 mg C per woody debris unit which corresponded to 6% of the mean cumulative CO_2 or 28% of the mean cumulative DOC production during the 380 days of incubation. Despite the additional C source, glucose had no effect on CO_2 and DOC production of any tree species and decay class. Further, glucose addition had no significant effect on pH-value, HIX and $SUVA_{254}$ of leachates.

Table 3.5: Correlation between cumulative CO_2 and DOC production and mean humification index (HIX), specific ultra-violet absorption ($SUVA_{254}$) and pH value during the beginning (days 1-28) and the end of the incubation (days 270-380).

	Days 1-28			Days 270-380		
	Adjusted R^2	p-value	function	Adjusted R^2	p-value	function
CO_2 : HIX	0.00	0.47	y=0.32+0.01x	0.36	<0.001	y=-0.10+0.18x
CO_2 : $SUVA_{254}$	0.04	<0.05	y=0.48-0.43x	0.01	0.17	y=0.63+1.17x
CO_2 : ph	0.01	0.19	y=0.74-0.08x	0.05	<0.01	y=2.46-0.30x
DOC : HIX	0.28	<0.001	y=-0.02+0.02x	0.53	<0.001	y=-0.04+0.03x
DOC : $SUVA_{254}$	0.17	<0.001	y=-0.03+0.33x	0.15	<0.001	y=-0.02+0.46x
DOC : pH	0.03	<0.05	y=0.31-0.05x	0.25	<0.001	y=0.52-0.08x

Discussion

Tree species effects on total carbon loss, CO_2 and DOC production

We refer to total C loss as sum of cumulative CO_2 and DOC production during incubation as fragmentation was not relevant in our study. Given the dominance of CO_2 over DOC production, the linear regression analysis revealed similar results for cumulative CO_2 production and total C loss. Mean total C loss of 4.7% of the initial C within 380 days is higher than the mean annual C loss of 2.6% under field conditions calculated from radiocarbon dated woody debris logs of the same tree species (unpublished data). The elevated C loss under laboratory conditions can be attributed to different factors including temperature, moisture and sample size (Boddy, 1983). The incubation temperature is 7-10 K higher than mean annual temperatures at the study sites. Boddy (1983) found respiration rates from beech twigs to more than double between 5 and 15°C. For woody roots, Q_{10} values of 4 for the interval 5-10°C and of 2.4 for the interval 10-15°C have been found (Chen et al. 2000). Assuming these Q_{10} values to be similar for our investigated samples, C loss would be in the same order as in the field despite varying decomposition factors and woody debris composition.

On average, spruce had the smallest C loss while beech and oak had similar C losses, except for DC-3 (see discussion below). In a review, decay rate constants under field conditions including all decay stages were in the order beech>spruce>oak (Rock et al. 2008). The faster decay of oak in comparison to spruce in our incubation experiment might be due to the experimental setup that mixed inner and outer heartwood. While no differences in extractable contents for wood parts have been described for spruce and beech, inner heartwood of oak has lower contents of extractable substances than outer heartwood (Puech et al. 1999). Extractable substances contribute to the microbial resistance of wood (Scheffer & Cowling, 1966). Under natural conditions, inner heartwood of oak often decays before the complete tree death resulting in hollow snags (Ranius et al. 2009). The consideration of inner heartwood in this study might have led to an overestimation of decay rates of oak at DC-1 in comparison to natural decay processes. We expect this overestimation to be minor at more severe decay stages, when the largest portions of extractable substances have been leached from inner and outer heartwood.

In this study, DOC concentrations of 9 – 68 mg l^{-1} were lower compared to field measurements. Under European beech logs, DOC concentrations ranged between 11 and 115 mg l^{-1} (Kahl 2008, Kuehne 2008). In North American mixed broad-leaved stands, DOC concentrations varied between 76 and 180 mg l^{-1} (Mattson 1987, Hafner 2005) and in coniferous forests between 62 and 108 mg l^{-1} (Yavitt & Fahey 1985, Spears et al. 2003). Coniferous woody debris yields lower DOC concentrations than deciduous wood other than beech than European beech. The same order was found in our experiment as reported in literature. Different factors influence the release of DOC from woody debris. Differences in DOC leaching among tree species may result from different chemical and physical characteristics of woody debris as well as distinct fungal communities (Song et al. 2011). DNA sequences indicate that a wide variety of different fungi contribute to decay at different decay stages of woody debris (Rajala et al. 2012), reflecting the decline in resource quality. Wood of broad-leaved trees is commonly decomposed by fungi that cause white rot while wood of coniferous trees is mainly decomposed by brown rot fungi (Schmidt 2006). The great abundance of white rot fungi in broad-leaved wood is speculated to be responsible for elevated DOC concentration under broad-leaved logs as the decay products of lignin are water soluble (Kahl 2008). However, it does not explain the relatively low DOC concentrations under European beech logs. Initial concentrations of extractive substances in wood might control DOC leaching in the early phases of decay. The order of DOC concentration at DC-1 corresponded to the amount of extractable substances in fresh wood: broad-leaved wood generally contains more extractives than coniferous wood and European beech with fresh wood of oak containing up to 10% of extractable substances like tannins whereas spruce has a content of only 2.1% and beech contains 2.0% of extractable substances (Rowe 1979). We assume that the differences between tree species in DOC production decline with decay class as a result of missing extractives in older woody debris. The contribution of DOC to total C loss for oak and spruce was higher than in other studies, while the values for beech were in the same range. Mattson et al. (1987) found a CO_2:DOC ratio of 12:1 for woody debris after 6 years of decomposition. Spears et al. (2003) calculated that 5% of woody debris is released as DOC over the whole decomposition period leading to a CO_2:DOC ratio of 19:1. Due to the small sample size in comparison to logs, the surface:volume ratios in the incubation is increased in comparison to field conditions. This also increased the working surface of water leading to better leaching conditions (Harmon et al. 1986) and possibly an overestimation of the CO_2:DOC ratio of 6:1 in our study.

Decay class effects on DOC and CO_2 production

DOC leaching was always highest for DC-5. For DC-1 and DC-3, no consistent pattern was found for the three tree species. Our finding corresponds to the results of other studies. Kahl (2008) found no influence of decay class and time since death on DOC production from beech logs under field conditions. Kuehne et al. (2008) and Hafner et al. (2005) reported maximum DOC concentrations for the most heavily decayed woody debris. On the other hand, Spears et al. (2003) reported high variation for heavily decayed woody debris and lower DOC concentrations than for less decayed woody debris. In our study, the dynamics of DC-1 and DC-3 were marked by an early peak in CO_2 production and a later peak in DOC production. The delayed increase of DOC production during the incubation can partially be explained by an increase in moisture content of the woody debris sample (data not shown), that might have increased the diffusion for soluble products. An initial peak in respiration is typically found in litter decomposition studies and is explained by rapid consumption of easily available C sources during the initial phase of microbial decay (Berg, 2000). The sample preparation included cutting, which represents a form of physical fractionation that made new surfaces available for fungal colonization. On the other hand, fungal colonization of woody debris was restricted during the course of incubation because the woody debris had no contact to soil. High water contents could have limited the oxygen supply in the inner woody debris and thus the aerobic respiration of fungi. As woody debris of DC-5 constitutes of strongly fragmented material, sample preparation had likely minor influence on fungal colonization. The initial decrease of DOC concentration of DC-5 might be explained by a depletion of soluble decay products accumulated in the field prior to the incubation. The higher surface:volume ratio in the incubation might have favored DOC leaching in comparison to field conditions. Yavitt and Fahey (1985) also found an initial peak of DOC leaching from heavily decayed woody debris over the snow melt period. The significant correlation between DOC and CO_2 loss suggests that the extracted DOC mainly originates from decomposition processes rather than extractives. Our findings correspond with those of Klotzbücher et al. (2011) for leaf litter that a close correlation between DOC and CO_2 production only exists at later decay stages.

Qualitative DOC parameters

DOC characteristics gradually changed during the 380 days of incubation. The dynamics were most notable in the pH value of the extracts, pointing to an increase of hydrolysable organic groups. The influence of the decomposer community on the pH of woody debris was described with brown rot lowering the pH of woody debris to average values of 3.7 and white rot yielding more variable results (Koenigs, 1974). A negative correlation between woody debris pH and decay rates was described by Fréschet et al. (2012). Of the spectroscopic characteristics, HIX revealed the best correlation with C-loss. Lignin derived compounds have higher HIX values than other decomposition products (Don & Kalbitz, 2005). Hence, at high HIX values lignin decomposition controls DOC production during decomposition of leaf litter (Klotzbücher et al. 2011). The high HIX values of DC-5 as well as the good correlation with C loss suggest that lignin decomposition is the most important process at later decay stages. High HIX and $SUVA_{254}$ indicate increasing stability and perhaps increasing importance for C accumulation in the mineral soil (Don & Kalbitz, 2005). It also suggests that DOC from heavily decayed oak and beech woody debris could contribute more to C accumulation in soils than DOC of younger decay stages.

Effects of glucose on DOC and CO_2 production

We found no effects of glucose on the DOC and CO_2 production from CWD. To our knowledge, the effect of additional light C sources decomposition of CWD has not been studied so far. Few studies investigated the potential of C addition on the decay of isolated wood compounds by single fungal species. These cannot represent the diversity of the fungal community in CWD or the interactions of glucose with wood substrates in an arranged structure. Studies with soil showed that between 30 and 40% of glucose added to different substrate is immediately used for respiration and the remaining part is used for biomass growth (van Hees et al., 2005). Leisola et al. (1984) suggest that glucose inhibits the depolymerization of cellulose and result in a more effective usage of products of lignin decomposition. The lack of significant differences in any investigated parameter between control and treated samples indicates that glucose has no or only a slight effect on the decomposition of CWD. Thus, throughfall that contains easily decomposable substrates from canopy leaching has apparently no impact on decay of CWD.

Conclusions

Our study indicates that DOC and CO_2 production vary among the three tree species and among decay stages. Cumulative CO_2 production and DOC leaching per mass unit are highest for heavily decayed CWD. DOC concentrations in the leachates per volume of CWD, however, are often higher for less decayed CWD. CO_2 production is the most important pathway of C loss, but the production of DOC significantly contributes to the decay of CWD. In the initial decay stages, extractives seem to contribute to DOC production, while lignin derived compounds seem to be more important at later decay stages. Up to 25% of the C from oak CWD is lost as DOC. This makes oak the tree species with the largest potential to contribute to C input to the soil. Heavily decayed CWD produces more stable DOC, which might contribute more to the C accumulation in the soil. Further heavily decayed CWD also produces DOC with the lowest pH value, which might influence soil acidity more than DOC from less decayed CWD. The lack of significant effects from glucose addition suggests that easily available C input with throughfall does not affect CWD decay.

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Chapter 4

Carbon stocks and turnover of coarse woody debris and soil in three managed and unmanaged temperate forests

Carbon stocks and turnover of coarse woody debris and soil in three managed and unmanaged temperate forests.

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Abstract

Forest management may affect the carbon (C) stocks of coarse woody debris (CWD) and soil. CWD represents a short to middle term C sink in forest ecosystems, but the formation of soil organic carbon (SOC) from CWD is still subject to speculation. The effects of forest management on C stocks of CWD and soils were investigated in a Norway spruce and two European beech - Sessile oak forests located in different climatic and geological regions of Bavaria, Germany. In the unmanaged parts of the forests, wood was not harvested and CWD accumulated for about 40 to 100 years. C stocks of CWD, the forest floor and the mineral soil were inventoried. Turnover times (TTs) were calculated from radiocarbon signatures with a non-steady state model with three different C input pools for the forest floor and with a steady state model for the mineral soil. Above-ground CWD stocks amounted to 11 Mg C ha^{-1} in the unmanaged spruce forest and to 23-30 Mg C ha^{-1} in the unmanaged beech-oak forests, whereas CWD stocks were 4.2-5.6 Mg C ha^{-1} in the managed forests. The mean disappearance time of CWD from spruce and oak was longer (70 years) than of beech (30 years). Elevated CWD input did not affect the C stock of the forest floor and the mineral soil in the unmanaged forests, indicating that CWD has no or little potential for soil C sequestration. Elevated CWD input was compensated by faster turnover of organic C in the O_e horizon, indicating a stimulation of leaf litter decay. In the O_a horizon and the mineral soil, no consistent patterns of radiocarbon signatures were found in all three investigated forests, suggesting that ecosystem properties overshadow moderate forest management effects.

Keywords: soil organic carbon, turnover times, coarse woody debris, radiocarbon, forest floor turnover

Introduction

There is growing public and political interest in the carbon (C) sequestering potential of forest ecosystems. Forests contain 50% of the organic C in the terrestrial biosphere (Jandl et al. 2007) and therefore play an important role in the earth's climate. Management practices can impact the sequestration of C in forests (Ballard 2000), including the sequestration of C in coarse woody debris (CWD). In forests withdrawn from management, CWD stocks increase by <0.1 to 19 m^3 ha^{-1} a^{-1} (Vandekerkhove et al. 2009). CWD input contributes 3-24% to total above-ground litter in old growth forests (Laiho & Prescott 1999) and represents a short to middle term C stock in forest ecosystems (Laiho & Prescott 2004, Boulanger & Sirois 2006, Hagemann et al. 2009, Bradford et al. 2009). CWD of tree species differ in their decay (Rock et al. 2008) and thus in their potential as lasting C stocks.

CWD is incorporated in many soil and forest models, but only in a highly generalized form (Cramer et al. 2001, Parton et al. 1988, Tuomi et al. 2011). In soil models, C originating from CWD potentially contributes up to 10-60% of deep soil organic C stocks (Harden et al. 2000, Manies et al. 2005). Residues of CWD decomposition have the potential to accumulate in the mineral soil as lignin residues from woody debris can persist in the soil for decades to centuries (Arantes et al. 2012). However, an increase of C stocks in the soil due to CWD has not been reported so far.

The effects of forest management on soil C stock are hard to detect due to slow changes and high spatial variability (Schöning et al. 2006, Schrumpf et al. 2008, Homann et al. 2008). Forest management influences the C input to the soil, but it does not inevitably modify the stabilization of soil organic matter (SOM) (Jandl et al. 2007). SOM of the mineral soil is heterogeneous and is often divided into chemical or physical fractions with different stability and turnover times (TTs) (Trumbore 2000, Kögel-Knabner et al. 2008). In common procedures, SOM is fractionated in free particulate organic matter (fPOM), occluded particulate organic matter (oPOM) and mineral associated organic matter (MaOM). The fPOM fraction consists of visible plant residues (Wagai et al. 2008) from partly decomposed below-ground and above-ground litter. As an easily decomposable fraction with fast TT, it is often used as an early indicator for disturbances. Input of CWD as fragmented material would result in an increase of the fPOM fraction (Crow et al. 2007). The oPOM fraction contains highly fragmented plant debris (Wagai et al. 2008) and it is assumed to respond to disturbance within decades or centuries (Hedde et al. 2008, Don et al. 2009). The MaOM fraction has a low amount of plant-derived compounds and a high proportion of compounds derived from microbial cells (Wagai et al. 2008, Miltner et al. 2011). CWD has the potential to contribute to all fractions through dissolved organic carbon (DOC) production. An increase in DOC underneath CWD logs (Spears et al. 2003) has the potential to increase the soil organic carbon (SOC) stock as DOC leached from CWD has the same stability as background organic matter from other sources (Lajtha et al. 2005).

Only the fast turning C pools have the ability to sequester high amounts of C in a relatively short time period, whereas the recalcitrant C pool accumulated over thousands of years and turns over very slowly (Hahn 2004). Radiocarbon signatures have been used to calculate the TT of SOM or to detect changes in the SOM pools (Gaudinski et al. 2000, Torn et al. 1997). It thus represents a powerful tool to investigate the fate of C from CWD in the soil and to evaluate the impact of management changes on TT of SOM.

This study was conducted to evaluate the influence of management practices on the C sequestering potential of a forest in the time span of decades. The following aspects were investigated: (1) the C stocks of CWD in managed and unmanaged forests, (2) the management effect on the C stocks in the forest floor and the mineral soil and (3) the management effect on radiocarbon signature and the TT of organic C in the forest floor and mineral soil. A new model approach was employed to assess the TT of organic C in the forest floor with three different C input sources including fine woody debris (FWD), CWD, and organic material from the O_i horizon.

Material and methods

Study sites and general concept

Managed and adjacent unmanaged forests were compared at three different study sites in Bavaria, Germany: Ludwigshain, Rohrberg and Grübel. Each site represents a different geological region and different micrometeorological conditions. Further, different tree species (European beech, Sessile oak, Norway spruce) are dominant in each forest.

Grübel (49°07’ N 013°07’ E) is a 56.3 ha Norway spruce (*Picea abies* L.) forest reserve situated at 1250 m a.s.l. Mean average temperature is 3-4°C and mean annual precipitations are 1500 mm. The soil is a Podzol on gneiss with a highly variable forest floor. The pH-value is 3.1 in the upper 10 cm of the mineral soil and increases to 4.4 in 50-100 cm soil depth. The even aged forest is about 260 years old and has been protected since 1978. Above-ground timber biomass is about 450 m^3 ha^{-1} in the unmanaged forest and 500 m^3 ha^{-1} in the managed forest. Information of stand history is scarce; no thinning procedures took place in the past 20 years in the managed forest. In the unmanaged forest, single trees were cut due to bark beetle infestation. In most cases, the bark of the trees was removed and the logs were left in the forest.

Ludwigshain (49°55’ N 011°48’ E) consists of 2.4 ha unmanaged beech-oak forest situated at an altitude of 460 m a.s.l. Mean average temperature is 7-8°C, mean annual precipitations are 650-750 mm. The soil is a calcaric Luvisol and developed on Franconian Jura. Soil pH increases from 3.6 in the top 10 cm of the mineral soil to 6.8 in 50-100 cm soil depth. The forest has been protected since 1913, though high grade wood, especially oak, of trees that succumbed to natural mortality was removed until the mid-1960s. The mean tree age is 370 years, with oak trees of up to 470 years. In part of natural succession, dead oak trees were replaced by beech saplings, thereby increasing the natural dominance of beech. Currently about 30% of the living trees in the unmanaged forest are Sessile oaks (*Quercus petraea* (Mattuschka) Liebl.) and 70% are European beeches (*Fagus sylvatica* L.). Above-ground timber biomass is estimated at 350 m^3 ha^{-1}. The managed forest is a 125-year-old forest stand with 30 % European beech and 70 % Sessile oak. Above-ground timber biomass is 400 m^3 ha^{-1}. Historical sources indicate permanent usage of the site as forest since human colonization. Reliable forestry records are available for the past 20 years. The last thinning procedure was conducted 10 years prior to the study, when 337 m^3 wood ha^{-1} were removed.

Rohrberg (49°54’ N 009°26’ E) is a 9.9 ha unmanaged beech-oak forest located in the Hochspessart on Sandstone. The soil is a Cambisol with typical moder as dominant humus form. Soil pH values increase from 3.0 in the top 10 cm of the mineral soil to 4.0 in 50-100 cm soil depth. Mean average temperature is 7-8°C, mean annual precipitation is 950-1100 mm. The forest has been protected since 1928. Mean stand age is 550 years with up 840-year-old oak trees. As beech is becoming more dominant as part of natural succession, several dominant beech trees were cut in 2002 to maintain oaks. All cut beeches remained in the forest. Currently, above-ground timber biomass is 300 m^3 ha^{-1}, consisting of about 30% European beech and 70% Sessile oak. The site of the managed forest is separated in two parts with a 100-year-old beech forest and a 65-year-old oak forest. Average tree species distribution is 50 % European beech, 45 % Sessile oak and 5 % European larch (*Larix decidua* Mill.). Above-ground timber biomass is estimated to be 350 m^3 ha^{-1}. The last thinning procedure with harvest of 106 m^3 ha^{-1} wood took place three years prior to the study.

Above-ground coarse woody debris inventory

Within an area of 1 ha, above-ground woody debris, including logs, branches, snags and stumps with a diameter > 7 cm, was completely inventoried as CWD in 2010. Each piece of CWD was measured and attributed to a decay class (Table 4.1) following Goodburn & Lorimer (1998). CWD volumes were calculated from multiple measurements of length and diameters using volume formulas under the assumption that CWD pieces are regular cones or cylinders (Bebber & Thomas

2003). It is assumed that over- and underestimation of individual pieces levels out over the total stock.

Table 4.1: Decay class (DC) characteristics of coarse woody debris (CWD).

Decay class	Characteristics
1	Recently dead, bark intact, small twigs and leaves, no visible signs of decomposition
2	Bark mostly remaining, no leafs, wood not penetrable by a knife
3	Bark mostly missing, wood partly penetrable with knife, visible discoloration
4	No bark, wood completely penetrable with knife, deformation and discoloration
5	Wood soft, breakable with fingers, advanced humification

To investigate wood density and C concentration, samples were taken by drilling holes of known volume and by collecting all shavings. The shavings were dried at 60°C until mass constancy. Sub-samples were ground with a ball mill for further analysis. For conversion of CWD volumes to C stocks, site specific average wood densities and C concentrations were calculated for each tree species and decay class. The amount of C in a volume of CWD in kg C m^{-3} (hereafter C density) was used as a unit to compare the C loss from CWD. This unit considers changes in density and C concentration of CWD, but not loss of the initial wood volume. For calculation of CWD production and disappearance time, time of tree death was determined with radiocarbon analysis dendrochronological cross-dating (Krüger et al., in prep.).

Accumulation and disappearance time of coarse woody debris

CWD accumulation is calculated from CWD production and CWD loss. The decadal CWD production is estimated from time of tree death. In accordance to decay classes, the time of tree death distribution is extrapolated for the whole CWD stock. CWD stocks (m^3 ha^{-1}) with time of tree death of up to 20 years for beech and up to 40 years for oak and spruce were used for calculation of the decadal CWD production. To reconstruct CWD C production from age class distribution we assume that the initial C concentration and wood density correspond to undecomposed wood. Volume loss is assumed to play an inferior role in early stages of decay (Harmon et al. 1986).

Disappearance times are defined as the time period between death and decay of a tree or branch to fractions < 7 cm in diameter. Disappearance times are calculated from dated CWD logs and their C density. Yearly C losses from current C stocks are calculated assuming linear functions derived from the disappearance times.

Soil sampling

Within an area of 2 ha, 30 plots were measured at regular intervals in each of the three unmanaged and managed forests. At each plot, the forest floor was sampled with a quadratic sampler of 20 cm length. The forest floor was separated by horizon in O_i, O_e and O_a material. Fine woody debris (FWD), with a diameter of 0.2 - 7 cm, was separately collected as an additional component of the forest floor. The upper 0-10 cm of the mineral soil was sampled with a core cutter (10 cm height, 8.6 cm diameter). At the same plot, the soil was sampled up to 1 m depth with a percussion drill and separated by the depth intervals 10-20 cm, 20-50 cm and 50-100 cm. The samples were dried at 60°C until mass constancy. Samples were sieved (<2 mm), visible roots and stones sorted out and weighted. A sub-sample of the fine earth material was ground with a ball mill for C analysis. The bulk density was determined from additional samples taken with a core cutter and by correcting the samples taken by percussion drill for compression.

Density fractionation

For density fractionation, a pooled sample per soil depth and each managed and unmanaged forest was mixed from 30 sub-samples of equal dry mass. A procedure adapted from John et al. (2005) and Schulze et al. (2009) was used for density fractionation. Dry soil samples (<2 mm, 60°C) were dispersed in sodium polytungsten (TC-Tungsten Compounds SPT-0) solution at densities of 1.6 g cm^{-3} and 2.0 g cm^{-3}. In the first fractionation step, 10 g of soil and 40 ml of SPT with a density of 1.6 g cm^{-3} were shaken for 60 min. The solution was centrifuged at 5085 g for 15 min (Varifuge® 3.2 RS Heraeus SEPATECH). The supernatant with particles was filtered through a 0.4 µm pre-washed membrane filter (Isopore™ membrane filter HTTP04700, Millipore). In the second fractionation step, the pellet was treated with the same procedure with a 2.0 g cm^{-3} SPT solution. The supernatant with particles constitutes the oPOM fraction and the pellet contains the MaOM fraction. All fractions were washed with de-ionized water until the conductivity of the solution was <10 µS, subsequently dried at 60°C and ground with an agate mortar. Calcareous samples were treated with 0.6 mol HCl for 48 hours to remove all inorganic C.

Chemical analysis

C analysis were conducted by the Chemical Analytics of the BayCEER or in the laboratory of the Department of Soil Ecology at the University of Bayreuth with a CN analyser (Elementar Vario EL, Hanau, Germany). Calcareous soil samples were decalcified by fumigation with concentrated HCl prior to the C measurement. Soil pH was measured in a 0.01 $CaCl_2$ solution (soil:solution ratio 1:2.5) with a WTW pH315i sensor.

Radiocarbon signatures of forest floor, bulk mineral soil and density fractions were measured by accelerator mass spectrometry (AMS). Sub-samples of 0.8 mg C were combusted in sealed quartz tubes with CuO as oxidizer and silver wire for 2 hours at 900°C. The resulting CO_2 was cryogenically purified from water and non condensable compounds and converted to graphite targets using the modified sealed tube zinc reduction method described by Xu et al. (2007). The preparation of the samples took place at the Department of Soil Ecology at the University of Bayreuth. The radiocarbon signatures were measured by the Keck-CCAMS of the University of California, Irvine using an AMS with a precision of 2-3‰. Radiocarbon data are expressed as $\Delta^{14}C$, which is the per mil deviation from the $^{14}C/^{12}C$ ratio of oxalic acid standard in 1950. The sample $^{14}C/^{12}C$ ratio has been corrected to a $\delta^{13}C$ value of -25‰ to account for any mass dependent fractionation effects (Stuiver & Polach 1977).

Calculation of turnover time

The TT of C of each horizon or soil depth of the forest floor, mineral soil and density fraction was calculated from its radiocarbon signature. We used non-steady state models for the forest floor and a steady state model for the mineral soil. For the forest floor, input pools with different radiocarbon signatures were considered. We assume that all input to the O_i horizon corresponds to fresh leaf litter. The TT of C of the O_e horizon is estimated considering the input from the O_i horizon, FWD and CWD. For the estimation of the TT of C in the O_a horizon, inputs from the O_e horizon and root litter are considered. For the TT of C in the bulk samples of the mineral soil and the density fractions, a steady state model was used following Gaudinski et al. (2000). The radiocarbon signatures of the forest floor, FWD and the mineral soil were measured and the average radiocarbon signature of CWD stocks were estimated based on stand age and production time of CWD. For modern radiocarbon signatures, two TT are possible. The calculations are explained in detail in the Supporting information (S1).

Statistical analysis

All statistical analyses were performed with R 2.9.2 (R Development Core Team 2009) and Open Office Calc 3.4.0 with the implemented SCO Evolutionary Algorithm to solve non-linear equations. Differences in C stocks between management forms were tested with a Student's t-test with a confidence interval of $p<0.05$. Two-way ANOVAs were conducted to test the differences between study sites.

Results

Carbon stocks of above-ground coarse woody debris

CWD accumulated to 64 (Grübel), 165 (Ludwigshain) and 132 (Rohrberg) $m^3 ha^{-1}$ in the unmanaged forests and to about 30 $m^3 ha^{-1}$ in the managed forest. This corresponded to CWD stocks of 11 to 30 Mg C ha^{-1} in the unmanaged forests and about 5 Mg C ha^{-1} in the managed forests (Table 4.2). CWD stocks in the unmanaged forests were thus 2-6 times higher than in managed forests. Irrespective of forest management and tree species, most C was generally stored as decay stage 2 and 3. Up to 10 % of the soil surface was covered with CWD in the unmanaged forests, whereas less than 1 % of the soil was covered by CWD in the managed forests.

The distribution of decay class (Table 4.2) was related to the pattern of age distribution in all forests (Fig. 4.1). Assuming that age distribution of CWD stocks corresponded to CWD production, mean annual CWD production ranged between 100 and 250 kg C ha^{-1} a^{-1} in the managed and between 230 and 1180 kg C ha^{-1} a^{-1} in the unmanaged forests on a decadal time scale (Table 4.3). The unmanged forest at Grübel had a relatively small production rate similar to the managed forest at Ludwigshain and Rohrberg. Ludwigshain and Rohrberg showed distinct tree species patterns (Fig. 4.1): at Ludwigshain, CWD production of oak and beech was in a similar range over the last decades whereas at Rohrberg CWD production of beech was more than five times higher than oak. Similar patterns but lower production rates were found in the unmanaged forests.

We found significant differences in C density of CWD between tree species, decay classes and study sites ($p<0.001$) (not shown). Despite the unequal distribution, CWD of beech or oak from Rohrberg and Ludwigshain were pooled to achieve a better representation of the decay classes. The correlation between C density of CWD and time since tree death was best represented by a linear function for beech (adjusted $R^2=0.61$, $p<0.01$, $y=279.1-8.6x$) and spruce (adjusted $R^2=0.57$, $p<0.001$, $y=242.4-3.5x$) (Fig. 4.2a, 4.2c) whereas no correlation was found for oak (Fig. 4.2b). Disappearance times of 30 years for beech and 70 years for spruce were estimated. The times of tree death of the dated oak CWD indicated that it can remain in forest for as long as spruce. For further calculations, a disappearance time of 70 years was assumed for oak CWD. Mean annual C loss of CWD, calculated from the disappearance time, ranged between 0.06 to 0.73 Mg C a^{-1} resulting in an annual accumulation of 0.04 – 0.51 Mg C a^{-1} (Table 4.3).

Table 4.2: Carbon stocks in three unmanaged and managed forests in the above-ground coarse woody debris (CWD) separated in decay class (DC), the forest floor including FWD and the mineral soil up to 1 m depth. Standard errors are given in parentheses.

Forest		DC1	DC2	DC3	DC4 [Mg C ha^{-1}]	DC5	Total CWD	Forest floor	Mineral soil
Grübel	managed	0.2	1.1	1.8	0.9	0.3	4.3	15.0 (1.2)	233 (16)
	unmanaged	0.4	3.0	5.8	1.9	0.2	11.3	15.1 (1.5)	262 (21)
Ludwigshain	managed	0.0	0.4	2.2	1.9	0.6	5.1	4.0 (0.9)	56 (5)
	unmanaged	0.7	14.3	10.3	3.6	1.2	30.4	4.1 (0.7)	48 (3)
Rohrberg	managed	0.0	2.6	1.8	0.9	0.3	5.6	8.0 (0.8)	115 (8)
	unmanaged	3.4	5.1	11.1	3.2	0.4	23.2	8.0 (0.7)	112 (7)

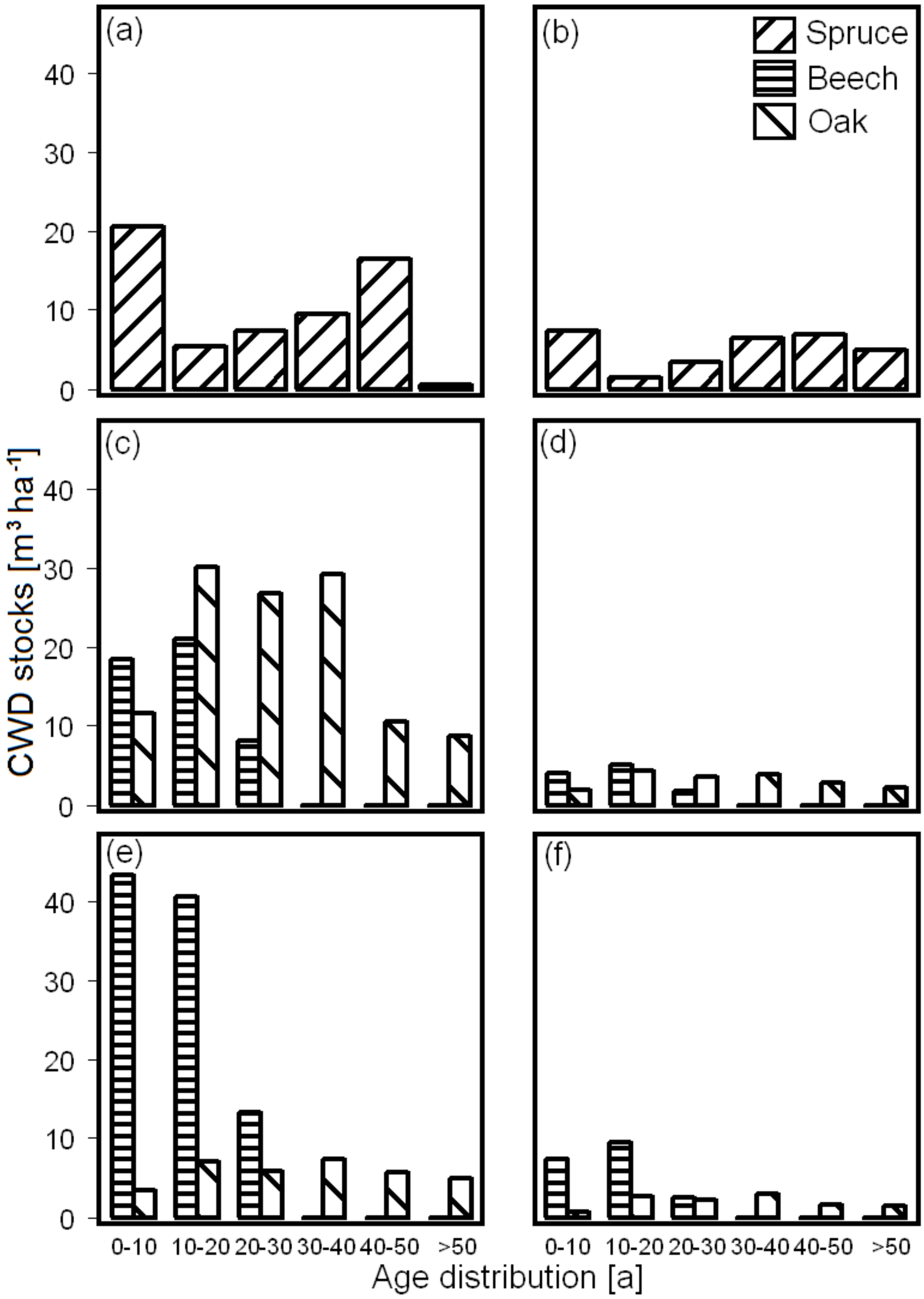

Fig. 4.1: Age distribution of coarse woody debris (CWD) in m³ per decade for each species for (a) unmanaged Grübel, (b) managed Grübel, (c) unmanaged Ludwigshain, (d) managed Ludwigshain, (e) unmanaged Rohrberg, (f) managed Rohrberg.

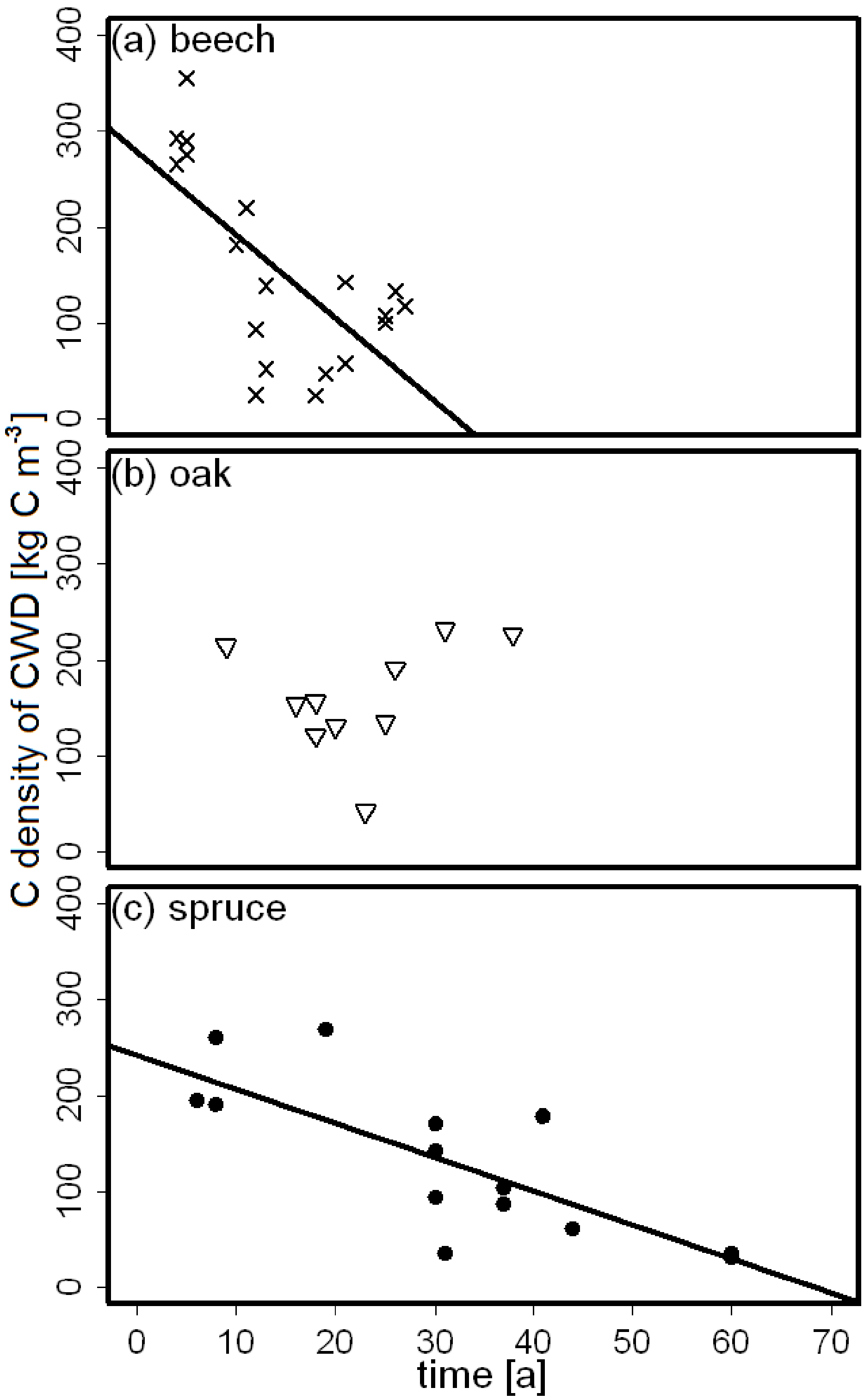

Fig. 4.2: Correlation between carbon density and time since tree death for lying logs with diameter >20 cm for the tree species (a) European beech, (b) Sessile oak and (c) Norway spruce.

Table 4.3: Model results for coarse woody debris production, loss and accumulation.

Forest		CWD production	CWD loss [kg C ha^{-1} a^{-1}]	CWD accumulation
Grübel	managed	100	60	40
	unmanaged	230	160	70
Ludwigshain	managed	200	100	100
	unmanaged	1080	570	510
Rohrberg	managed	250	130	120
	unmanaged	1180	730	450

Carbon stocks of forest floor and mineral soil

C stocks in the forest floor including FWD ranged from 4.0 to 15.1 Mg C ha^{-1} (Table 4.2). No significant differences between managed and unmanaged forests were found for any site. C stocks in the O_i horizon were slightly lower in the managed forest at Rohrberg and Ludwigshain and slightly higher at Grübel (Fig. 4.3). C stocks in the FWD ranged between 0.3-1.1 Mg C ha^{-1} and were higher in the managed than in the unmanaged forests (Fig. 4.3). The C stock of the forest floor were 6 times lower than the C stock of CWD in the unmanaged forest of Ludwigshain and Rohrberg, but of similar range in the unmanaged forest of Grübel.

In the mineral soil, the SOC concentration decreased from 3.5-17.6% at 0-10 cm to 0.2-1.1% at 50-100 cm soil depth. Differences in SOC concentration were greater among the study sites than between the management forms (Table 4.4).

The SOC stocks up to 100 cm depth accumulated to 48-262 Mg C ha^{-1} (Table 4.2). No significant differences between management forms were found. C Stocks were slightly lower in the unmanaged forests at Ludwigshain and at Rohrberg than in the corresponding managed forests. At Grübel, SOC stocks were slightly higher in the unmanaged than in the managed forest. C stocks in fine roots up to 1 m depth ranged from 3.4-13.4 Mg C ha^{-1} (data not shown).

The percentage of the total C stock in the fPOM decreased with soil depth from 20-70 % at 0-10 cm soil depth to 10-30 at 50-100 cm soil depth. The percentage of the total C stock in the MaOM increased from 5-40 % at 0-10 cm soil depth to 50-85 % at 50-100 cm soil depth (Fig. 4.4). The percentage of C in oPOM showed no consistent pattern. A two-way ANOVA revealed significant influences of forest sites on the distribution ($p<0.01$), but no effects of management. C stocks in the fPOM fractions were higher in the managed forests at Ludwigshain and Grübel and lower in the managed forest at Rohrberg (Fig. 4.4).

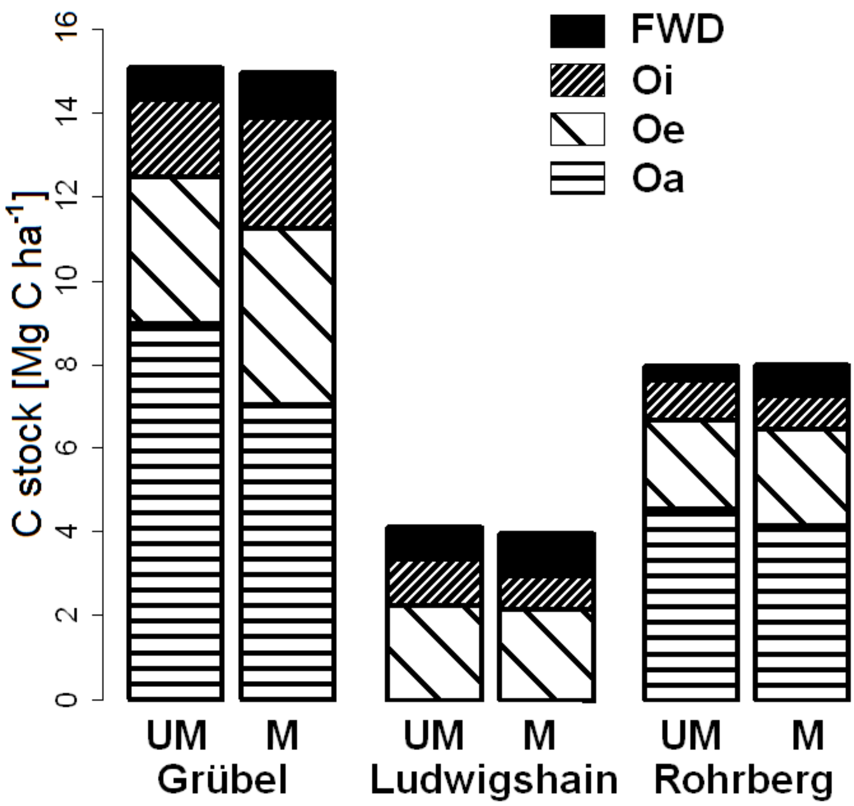

Fig. 4.3: Carbon stocks in forest floor in Mg C ha^{-1} for (a) unmanaged Grübel, (b) unmanaged Ludwigshain, (c) unmanaged Rohrberg, (d) managed Grübel, (e) managed Ludwigshain, (f) managed Rohrberg.

Turnover times of carbon in the forest floor

Radiocarbon signatures indicated mainly modern C in the O_i (40 – 82 ‰), O_e (65 – 137 ‰) horizons of all study sites and in the O_a (110 - 128 ‰) horizon at Rohrberg, but more pre-bomb C in the O_a (82 - 97 ‰) horizon at Grübel (Table 4.5). FWD had a radiocarbon signature of 126 - 154 ‰ indicating an age of 16-20 years since photosynthetic fixation. In the O_e horizons, radiocarbon signatures were consistently lower in the unmanaged than in the managed forests at all study sites. The difference was most pronounced in the combined O_e/O_a horizons at Ludwigshain.The TT of C in the O_e horizon was calculated assuming different scenarios of C input from the leaf litter in the O_i horizon, CWD and FWD (see Supporting Information S1).

Table 4.4: Soil characteristics, standard errors are given in parentheses.

	Grübel - unmanaged					Grübel - managed				
	Bulk density [g cm^{-3}]	Fine earth [%]	pH	SOC [%]	N [%]	Bulk density [g cm^{-3}]	Fine earth [%]	pH	SOC [%]	N [%]
O_i				50.1 (0.2)	1.56 (0.08)				50.2 (0.7)	1.73 (0.07)
O_e				46.7 (0.5)	2.17 (0.06)				45.8 (0.9)	2.20 (0.07)
O_a				41.9 (0.8)	2.25 (0.05)				39.4 (1.4)	2.14 (0.08)
0-10 cm	0.7	78	3.15	17.6 (2.0)	0.97 (0.12)	0.7	71	3.15	14.8 (1.5)	0.79 (0.08)
10-20 cm	1.1	56	3.42	8.5 (1.2)	0.46 (0.07)	1.1	69	3.38	6.9 (0.7)	0.35 (0.04)
20-50 cm	1.6	42	4	3.1 (0.3)	0.13 (0.01)	1.6	50	3.99	2.2 (0.2)	0.10 (0.01)
>50 cm	1.8	48	4.4	1.1 (0.1)	<0.05	1.8	47	4.42	0.8 (0.1)	<0.05

	Ludwigshain - unmanaged					Ludwigshain - managed				
	Bulk density [g cm^{-3}]	Fine earth [%]	pH	SOC [%]	N [%]	Bulk density [g cm^{-3}]	Fine earth [%]	pH	SOC [%]	N [%]
O_i				46.6 (0.3)	1.30 (0.03)				47.4 (0.2)	1.05 (0.02)
O_e/O_a				33.9 (1.5)	1.50 (0.05)				38.5 (0.7)	1.59 (0.04)
0-10 cm	1.0	64	3.59	3.8 (0.2)	0.20 (0.01)	1.0	81	3.72	3.5 (0.2)	0.18 (0.01)
10-20 cm	1.0	54	3.85	1.5 (0.1)	0.09 (0.00)	1.0	49	4.08	1.8 (0.2)	0.09 (0.01)
20-50 cm	1.2	36	4.25	0.7 (0.0)	0.06 (0.00)	1.2	39	6.28	0.7 (0.1)	0.06 (0.00)
>50 cm	1.7	22	6.75	0.3 (0.0)	0.04 (0.00)	1.7	38	6.88	0.3 (0.0)	0.04 (0.00)

	Rohrberg - unmanaged					Rohrberg - managed				
	Bulk density [g cm^{-3}]	Fine earth [%]	pH	SOC [%]	N [%]	Bulk density [g cm^{-3}]	Fine earth [%]	pH	SOC [%]	N [%]
O_i				47.2 (0.2)	1.62 (0.04)				47.7 (0.2)	1.38 (0.05)
O_e				43.2 (0.8)	1.99 (0.05)				42.5 (1.3)	1.80 (0.05)
O_a				33.3 (1.6)	1.72 (0.08)				37.9 (1.5)	1.80´(0.07)
0-10 cm	0.9	90	2.97	4.9 (0.3)	0.25 (0.01)	0.8	90	2.98	6.0 (0.5)	0.30 (0.03)
10-20 cm	1.0	84	3.3	3.3 (0.4)	0.16 (0.02)	1.0	77	3.29	2.8 (0.2)	0.13 (0.01)
20-50 cm	1.2	78	3.95	1.2 (0.1)	0.07 (0.01)	1.2	69	3.94	1.4 (0.1)	0.07 (0.00)
>50 cm	1.6	76	3.98	0.2 (0.0)	<0.05	1.6	71	3.91	0.2 (0.0)	<0.05

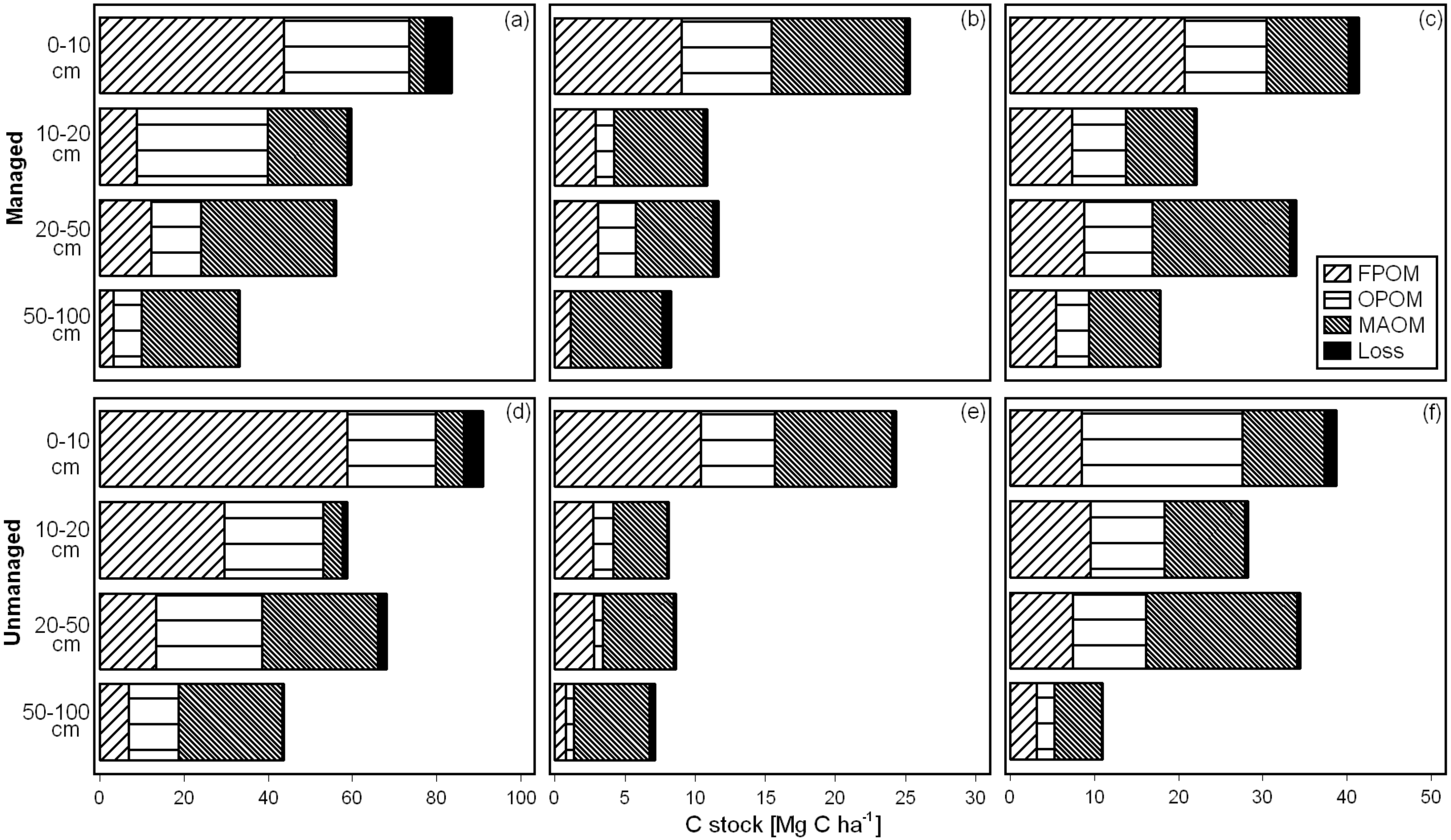

Fig. 4.4: Stocks of soil organic carbon in the three density fractions (fPOM, oPOM, MaOM) in four soil depths for three unmanaged and managed forests. "Loss" indicates the amount of soil organic lost during density fractionation for (a) unmanaged Grübel, (b) unmanaged Ludwigshain, (c) unmanaged Rohrberg, (d) managed Grübel, (e) managed Ludwigshain, (f) managed Rohrberg.

With fragmented leaf litter from the O_i horizon as single C input, TTs of C in the O_e horizon varied between 5.1 and 18.6 years. However, TTs of C in the O_e horizons were always shorter in the unmanaged forests than in the managed forests. The difference was smallest at Rohrberg (5.1 vs, 6.2 years) followed by Grübel (7.9 vs. 10.0 years) and Ludwigshain (5.1 vs. 18.6 years). The proportion of input to the O_e horizon from the O_i horizon (h_{Oi}) ranged between 10 and 40 %.
The simulated increase of CWD input (up to 10 % of CWD loss) resulted in longer TT of C in the O_e horizon irrespective of management and site (Fig. 4.5a-c). The sole exception was the managed forest Rohrberg, where the TT of C in the O_e horizon decreased from 6.2 to 5.6 years at a CWD input of 10 %. The increase of CWD input resulted in a bigger difference in TT of C in the O_e horizon in the unmanaged than in the managed forest (Fig. 4.5d-f). The increase was most important in the unmanaged Ludwigshain, where the TT of C in the O_e horizon increased from 5.1 to 10 years with an input of 10 % CWD (Fig. 4.5b). The uncertainty from the radiocarbon signature of CWD was slight. When the proportion of CWD input was less than 5 %, a variation of the radiocarbon signature of CWD resulted in a difference of TT of less than one year. An increased input of CWD resulted in a lower proportion of input from the O_i horizon (h_{Oi}). At equal H_{CWD} values or TT, the h_{Oi} values in the managed and unmanaged forests did not correspond. After consideration of FWD as input to the O_e horizon, the calculated TTs of C in the O_e horizon increased by 1.5 – 3.7 years.
Under all scenarios and at all study sites, TTs of the O_e horizon were faster in the unmanaged forests at the same CWD input than in managed forests. TTs of C In the O_a horizon ranged from 55-80 years. TTs of C in the O_a horizon in the unmanaged forests are faster at Grübel and slower at Rohrberg than in the managed forests.

Turnover times of carbon in the mineral soil

The radiocarbon signature of SOC in bulk soil decreased consistently with soil depth in all forests (Table 4.5). Accordingly, the TTs of SOC in bulk mineral soil range from 130-470 years in 0-10 cm depth to 740-3900 years in 50-100 cm depth (Table 4.5). Differences among the study sites were greater than between the management types. Similar to the bulk soil, radiocarbon signatures of density fractions generally decreased with soil depth in the order fPOM>oPOM>MaOM. TTs in the fPOM fraction were shorter (5-270 years) than in the oPOM (160-3600 years) and the MaOM fractions (125-4200 years) and decreased with soil depth. One exception is the fPOM fraction at Ludwigshain where radiocarbon signatures and TT remained almost constant with increasing depth at both the managed and unmanaged forests.

Table 4.5: Radiocarbon signatures of bulk soil and density fractions of three unmanaged and managed forests Grübel, Ludwigshain and Rohrberg. The turnover times expressed in years (given in parentheses) were calculated from radiocarbon signature with a steady state model.

	Grübel - unmanaged					Grübel - managed				
	Bulk	FPOM	OPOM [$\Delta^{14}C$‰]	MAOM	DOC	Bulk	FPOM	OPOM [$\Delta^{14}C$‰]	MAOM	DOC
O_i	73					82				
O_e	112					137				
O_a	97					82				
0-10 cm	11 (280)	13 (270)	-85 (900)	-152 (1450)	31 (200)	-25 (470)	36(190)	-77 (840)	-110 (1100)	34 (200)
10-20 cm	-113 (1120)	-61 (710)	-134 (1300)	-198 (1830)	-12 (390)	-124 (1210)	-32 (510)	-109 (1090)	-177 (1660)	-27 (480)
20-50 cm	-265 (2400)	-100 (1000)	-238 (2200)	-317 (2900)		-238 (2180)	-29 (495)	-254 (2320)	-328 (2950)	
>50 cm	-440 (3900)	-368 (3300)	-401 (3600)	-479 (4200)		-432 (3850)	-302 (2720)	-362 (3240)	-458 (4070)	

	Ludwigshain - unmanaged					Ludwigshain - managed				
	Bulk	FPOM	OPOM [$\Delta^{14}C$‰]	MAOM	DOC	Bulk	FPOM	OPOM [$\Delta^{14}C$‰]	MAOM	DOC
O_i	41					46				
O_e/O_a	65					134				
0-10 cm	37 (190)	61 (5/130)	41 (1/165)	65 (6/130)	92 (10/90)	45 (2/170)	64 (5/130)	44 (2/170)	32 (200)	101 (11/80)
10-20 cm	-2 (340)	38 (190)	-60 (710)	-46 (610)	38 (190)	-5 (350)	16 (260)	-26 (470)	-48 (620)	63 (5/130)
20-50 cm	-58 (690)	98 (11/80)	-59 (710)	-115 (1150)		-82 (880)	27 (220)	-46 (610)	-135 (1300)	
>50 cm	-95 (980)	113 (170)	-107 (1070)	-294 (2650)		-116 (1150)	84 (9/100)	-175 (1640)	-278 (2530)	

	Rohrberg - unmanaged					Rohrberg - managed				
	Bulk	FPOM	OPOM [$\Delta^{14}C$‰]	MAOM	DOC	Bulk	FPOM	OPOM [$\Delta^{14}C$‰]	MAOM	DOC
O_i	46					39.6				
O_e	70					78.9				
O_a	110					127.7				
0-10 cm	24 (230)	77 (8/100)	4 (310)	-7 (370)	78 (8/100)	62.0 (5/130)	121.6 (15/60)	46.8 (2/160)	34.1 (200)	102.8 (11/80)
10-20 cm	-28.6 (290)	47.7 (2/160)	8.5 (290)	-11.6 (390)	57.1 (4/140)	35.7 (190)	70.5 (7/120)	11.7 (280)	-11.3 (390)	86.5 (9/90)
20-50 cm	-43.2 (590)	23.1 (230)	-37.5 (550)	-59.2 (700)		-42.4 (580)	33.2 (200)	-244.2 (2230)	-33.3 (520)	
>50 cm	-126.6 (1240)	14.4 (260)	-123.4 (1210)	-185.1 (1730)		-63.9 (740)	31.7 (200)	-33.3 (520)	-130.4 (1270)	

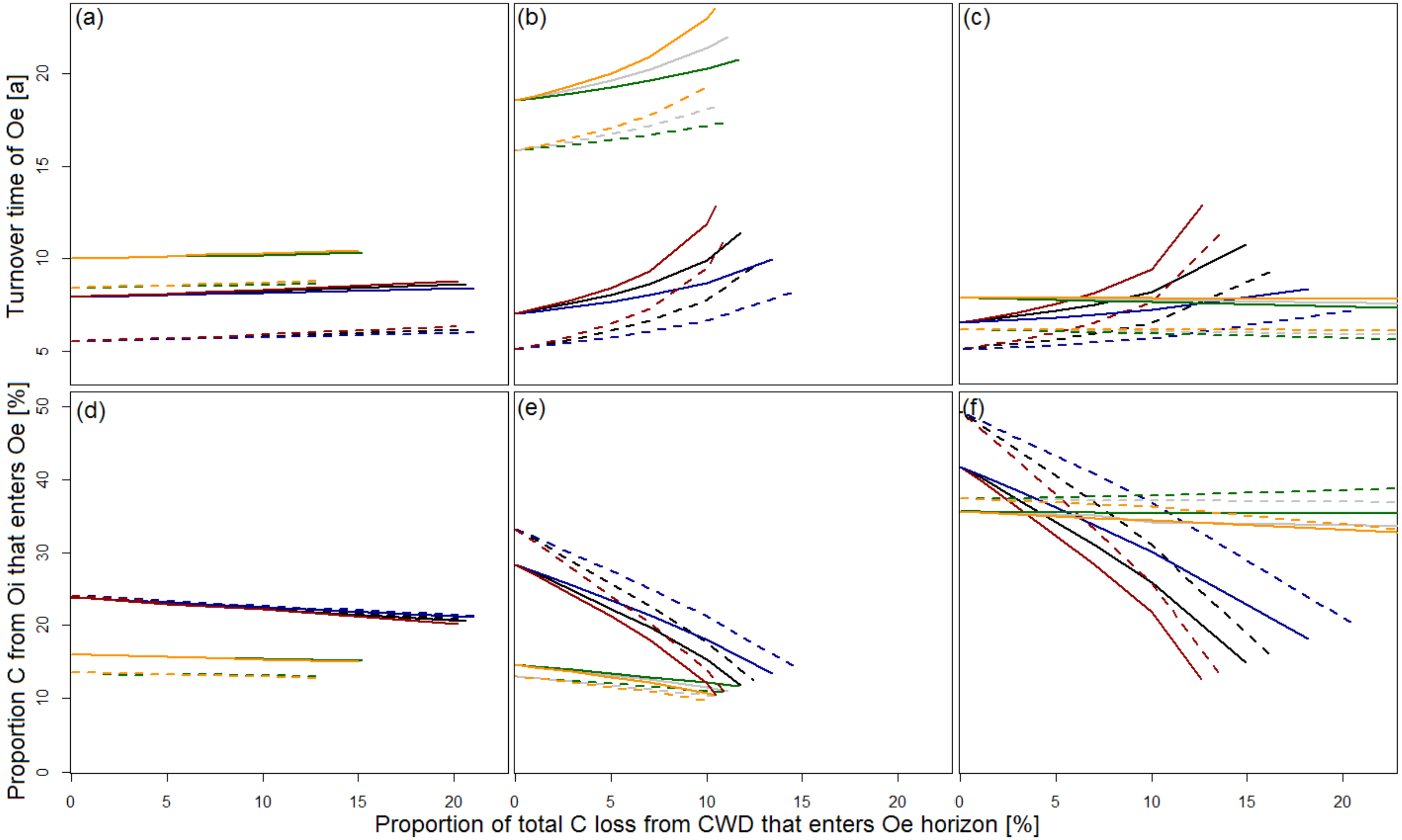

Fig. 4.5: Proportion of input to the Oe horizon from total C loss of the Oi horizon and from total coarse woody debris (CWD) loss in Grübel (a), Ludwigshain (b) and Rohrberg (c) and turnover time (TT) of the Oe horizon for proportion of input of total CWD loss in Grübel (d), Ludwigshain (e) and Rohrberg (f). The scenario with no consideration of fine woody debris (FWD) is shown in straight lines, the scenario with consideration of FWD is shown in dashed lines. Black/grey lines give mean radiocarbon signature of CWD (m_{CWD}), blue/green lines give the upper limit of radiocarbon signature of CWD (m_{CWD}+20 $\Delta^{14}C$ ‰) and red/orange lines the lower limit of radiocarbon signature of CWD (m_{CWD}-20 $\Delta^{14}C$ ‰) in the unmanaged and managed forests respectively.

In the fPOM and MaOM fractions of Grübel and Rohrberg, the radiocarbon signature were lower in the unmanaged forest than in the managed forest, but exhibited an opposite pattern at Ludwigshain. At all forest sites, radiocarbon signatures of the oPOM fraction were mostly lower in the unmanaged than the managed forest. Differences between management types were greatest in the fPOM fraction across all study sites and soil depths with a median difference of 20 ‰, whereas the median difference in the oPOM and the MaOM fraction was 11 ‰.

Discussion

Stocks and turnover of coarse woody debris

CWD stocks of 132 and 165 m^3 ha^{-1} in the unmanaged oak-beech forests at Rohrberg and Ludwigshain are in the same range as reported for European beech (50-200 m^3 ha^{-1}) and oak (70-160 m^3 ha^{-1}) forest reserves (Christensen et al. 2005). In the unmanaged spruce forest, the CWD stock of 64 m^3 corresponds to the CWD stocks (27-131 m^3 ha^{-1}) of subalpine spruce forests withdrawn from management (Motta et al. 2010, Holeksa 2001). The calculated accumulation rate of CWD of 2.8 m^3 ha^{-1} a^{-1} in the unmanaged beech-oak forests is at the lower end of the scale reported by Vandekerkhove et al. (2009) of 0.1 – 19 m^3 ha^{-1} a^{-1}, but above the median value of 1.6 m^3 ha^{-1} a^{-1}. In the spruce forest, the accumulation rate is smaller, possibly because of the younger age structure of the forest in comparison to the older beech-oak forests. CWD stocks of 30 m^3 ha^{-1} in all managed forests are higher than those reported for managed forests (about 6 m^3 ha^{-1}) in Germany (Baritz et al. 2000) or for mixed forests (21.5 m^3 ha^{-1}) in Switzerland (Weggler et al. 2012). CWD stocks are currently increasing in managed forests due to management measures in Bavaria (oral communication), though the accumulation rate is still smaller than in the unmanaged forests.
Disappearance times of CWD in the order beech < spruce < oak correspond to values in other forests of central Europe (Rock et al. 2008). The high variability in disappearance time can be attributed to the variation in abiotic and biotic factors that affect CWD on a punctual scale. The variability is greater when CWD is partially in contact with the soil due to different colonization by wood decomposing fungi. Despite the variability, a correlation between time since tree death and C density was found for beech and spruce CWD. The lack for CWD of oak can be attributed to a high variability in its wood chemistry (Puech et al. 1999), partial dieback of stem and branches while new tissue is being formed (Ranius et al. 2009). Further, decay of logs and snags are different, highlighting that TT of logs depend on whether it originated from a fallen snag or living tree. The old age of individual trees with high C densities suggests that oak CWD has the potential to remain for many decades in forests. This makes oak a suitable tree species to increase CWD stocks in

forests. Despite lower production rates than beech, oak can contribute more to total CWD stocks in unmanaged and managed forests. Despite lower C stocks, the high proportion of beech CWD (75 %) at Rohrberg resulted in higher C losses compared to Ludwigshain. At Grübel, CWD production is smaller than in the other investigated forests, however, as spruce decays within a similar time than oak, the forest has the potential to accumulate high amounts of C in its CWD stocks. Relatively low temperatures likely slow down the decay of CWD at Grübel, suggesting that not only the quality of spruce CWD impacts its disappearance time but also climatic conditions. Q_{10} values of 2.7-3.4 for CWD decomposition (Yatskov et al. 2003) would result in disappearance times that are about 50 % longer given the difference in annual mean temperatures of 4 K between Grübel and the beech-oak forests.

Carbon stocks of the forest floor and mineral soil

C stocks of FWD in the forest floor are higher in the managed forests than in the unmanaged forests at all study sites. The C stocks of FWD are in the same range or higher than mean FWD C stocks of 2.5 to 4.0 Mg ha^{-1} described in forests in the U.S (Woodall & Liknes 2008). In the managed forests, the input and stock of FWD depends on the management procedures and the time period since the last thinning (Vávřová et al. 2009). As thinning procedures are conducted in regular intervals, a sinus function was found suitable to model the changes of FWD production.

Forest management did not affect the C stock of the O horizons. The lack of significant differences between management forms indicates that CWD is either insignificant for the formation of organic matter or management affects other factors (see below) which counterbalance the C input by CWD.

The lack of significant differences in the C stock of the O_i horizon underpins that mortality of single trees and differences in tree age have minor influence on litter production of the study sites. The unmanaged forests at Ludwigshain and Rohrberg have even slightly higher C stocks in the O_i horizon, suggesting similar litterfall in managed and unmanaged forests. Minor differences in the C stocks of the O_e or O_a horizons between the management forms can be attributed to natural variability of the forest floor or incomplete separation of genetic horizons. Our results demonstrate that CWD has no or little potential to increase the C stock of the forest floor although the O_e horizons contained considerable portions of FWD and CWD. The imprint of FWD and CWD is further discernible through the radiocarbon signature and TT of the O_e horizons (see below).

The SOC stocks in the mineral soil of our study sites were in the range of similar forests surveyed in the Bavarian Soil Inventory (Wiesmeier et al. 2012). At Grübel, parts of the site consist of poorly drained soils resulting in very high C stocks of 250 Mg C ha^{-1}.

Differences between study sites are greater than between management forms. This indicates that management had none or minor importance in comparison to tree species and abiotic factors. Our study supports findings by Kahl et al. (2013) that C stocks of the mineral soil are not influenced by the presence of CWD.

Radiocarbon signatures and carbon turnover in the forest floor

Forest management has more effect on the forest floor than on the mineral soil (DeGryze et al. 2004). Differences in radiocarbon signatures between management forms were notable for the O_e and O_a horizons. In the O_i horizons, differences in radiocarbon signatures are within measurement uncertainty.

Many modeling approaches do not consider input to the O_e horizon other than O_i material (e.g., Gaudinski et al. 2000, Schulze et al. 2009) though low radiocarbon signatures of the O_e horizon have been attributed to the presence of CWD (Trumbore & Harden 1996). We found that consideration of CWD input can increase the calculated TT of the O_e horizon by up to 5 years. Consideration of FWD input resulted in an increase of the calculated TT by up to 4 years. This modeling approach displays large uncertainties in the calculated TTs at different C inputs of different radiocarbon signature. A C loss from the CWD stock by fragmentation of up to 5 % was assumed as respiration and DOC leaching make up a the C loss of up to 95 % (Chen et al. 2000, Olajuyigbe et al. 2012). We found that even a CWD input to the O_e horizon of 10 % of the annual C loss from CWD is not sufficient to explain the differences in radiocarbon signatures between the managed and unmanaged forests. Hence, the lower radiocarbon signatures of the O_e horizons in the unmanaged forests can be attributed to faster decay of leaf litter.

CWD has the capacity to modify a range of soil characteristics including the heterogeneity of organic compounds (Strukelj et al. 2012), the pH value (Klinka et al. 1995) and the microbial community of the soil (Rajala et al. 2012). A high abundances of CWD can increase the size of the fungal community in the soil and result in a shift of the fungal:bacterial ratio (Brant et al. 2006). This leads to a better utilization of phenol and oxalate in contrast to bacterially dominated communities with low capacity to degrade such compounds (Brant et al. 2006). The promotion of the fungal community by CWD input might result in faster TTs of the O_e horizon in the unmanaged forests.

The influence of CWD on the radiocarbon signature and TT of the O_a horizon at Grübel and Rohrberg seems to be of minor importance. It is likely that CWD almost completely decays in the O_e horizon and thus contributes little to the buildup of the O_a horizon. TTs of 55-80 years in the O_a

horizon are relatively slow and correspond to about half or twice the period since forest protection at Rohrberg and Grübel, respectively. The time since a relevant additional CWD stock has accumulated might not have been sufficient to induce significant effects on the decomposition processes in the O_a horizon.

Radiocarbon signatures and carbon turnover in the mineral soil

Positive radiocarbon signatures of the bulk soil were only found in 0-10 cm soil depth, pointing to large inputs of modern C. In greater soil depths, negative radiocarbon signatures display the dominance of pre-bomb C. The lowest radiocarbon signatures were found at Grübel, indicating older C in the spruce forest than in the two beech-oak forests.

In the mineral soil, we estimated TT of bulk SOC of 130-3900 years. This corresponds to or is slightly higher than previous studies that describe TT of SOC between 25 and 3570 years in temperate forests (Perruchoud 1999, Hakkenberg 2009, Schulze et al. 2009). Given its distinct climatic conditions conditions, Grübel has very long TT in the deep soil depths. The radiocarbon signatures of the bulk soil up to 10-20 cm indicates significant inputs of modern C at Ludwigshain and Rohrberg. In our study, inputs of modern C correspond to CWD inputs since management change. This means that the method is suitable to identify differences due to human impact.

Differences between management forms were smaller than among the study sites, indicating that site conditions and tree species have more influence on TTs than forest management. As the differences remain constant with depth, other factors overshadow forest management effects or management equally affects all soil depths through below-ground litter input.

The fPOM, oPOM and MaOM fractions represent C pools with different TT, degrees of degradation and humification (Baisden et al. 2002, John et al. 2005). At Grübel, TT in all density fractions and soil depths were at least 200 years. This makes management influences within decades improbable. At Ludwigshain and Rohrberg, TT of the fPOM fraction is shorter than 250 years at all soil depth, suggesting that elevated CWD input could potentially increase the TT at these study sites. While the patterns are consistent across soil depths, they do not correspond on both study sites. They can thus not be attributed to a management change. An elevated CWD input does thus not affect C stocks of the soil within time periods of decades.

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Supplemental Information

This appendix describes the calculation of the turnover time (TT) of the organic horizons and the mineral soil with non-steady state and steady state models. For all calculations, we used radiocarbon data originating from dendrochronologically dated wood samples published by Stuiver et al. (1998) and atmospheric radiocarbon data after 1959 published by Levin et al. (2008). The data cover the time period between 1510 and 2009. For calculation of the radiocarbon signature of coarse woody debris (CWD) that necessitate older radiocarbon data, the average radiocarbon signatures between 1510 and 1520 is used.

All radiocarbon signatures are expressed as Fraction modern (Fm) for calculation. Fm is calculated from measured $\Delta^{14}C$ ‰ with the following conversion:

$$Fm = 1 + \frac{\Delta^{14}C\,‰}{1000} \qquad (1)$$

where $\Delta^{14}C$ ‰ is the ‰ from the $^{14}C/^{12}C$ ratio of oxalic standard in 1950. The samples were corrected to a $\delta^{13}C$ value of -25 ‰ to account for mass-dependent fractionation effects (Stuiver & Polach, 1977).

Radiocarbon signature of coarse woody debris

The radiocarbon signature of each tree ring corresponds to the radiocarbon signature of the atmosphere of the year it was formed (Cain & Suess 1976). Calculations of the radiocarbon signature of CWD are based on the assumption that biomass growth is constant each year (Sievänen et al. 2000). The radiocarbon signature of an individual piece of CWD (Fm_{iCWD}) of the year 2009 can be calculated by integrating the radiocarbon signature of the atmosphere Fm_{atm} in each year t for the interval between time of sapling and time of tree death under consideration of radioactive decay in relation to 2009 divided by the duration of the interval calculated from the time of sapling ($t_{sapling}$) and time of tree death (t_{death}) in years (a). For ^{14}C, a half-time of 8267 years is assumed.

$$Fm_{iCWD}(2010) = \frac{\sum_{t_{sapling}}^{t_{death}} Fm_{atm}(t) * \left(1 - \frac{2009 - t}{8267}\right)}{t_{death} - t_{sapling}} \qquad (2)$$

To simplify the model, the CWD stocks are grouped by time of death per decades. Time of sapling is derived from mean tree age. A mean radiocarbon signature for the total CWD stock of a forest (Fm_{tCWD}) is calculated in dependance of the C stock (S_{iCWD}) of each group. S_{iCWD} is derived from the age distribution of current CWD stocks (see Fig. 4.1). The radiocarbon signature of the CWD stock is calculated for the time period between 1910 and 2009 with the following formula:

$$Fm_{tCWD}(2009)=\frac{\sum Fm_{iCWD}(2009)*S_{iCWD}(2009)}{\sum S_{iCWD}(2009)} \qquad (3)$$

We calculated three different radiocarbon signatures to estimate the sensibility of the model resulting from under- or over-estimation of the radiocarbon signature of CWD. To this end 0.02 was added/substracted from all $Fm_{tCWD}(t)$ values without consideration of the calendar year. An average uncertainty of 0.02 was calculated by varying the mean tree age and the CWD production rates.

Calculations of radiocarbon signatures of CWD range between 1.006 and 1.045 for the unmanaged forests and between 1.045 and 1.135 for the managed forest in 2009 (Fig. 4.S.1). Differences are mainly due to the stand age rather than the time of tree death of CWD or the disappearance times of CWD. This results in differences in radiocarbon signatures between unmanaged and managed forests at Ludwigshain and Rohrberg. Radiocarbon signatures of CWD are not different between managed and unmanaged forests at Grübel as the mean tree age is similar.

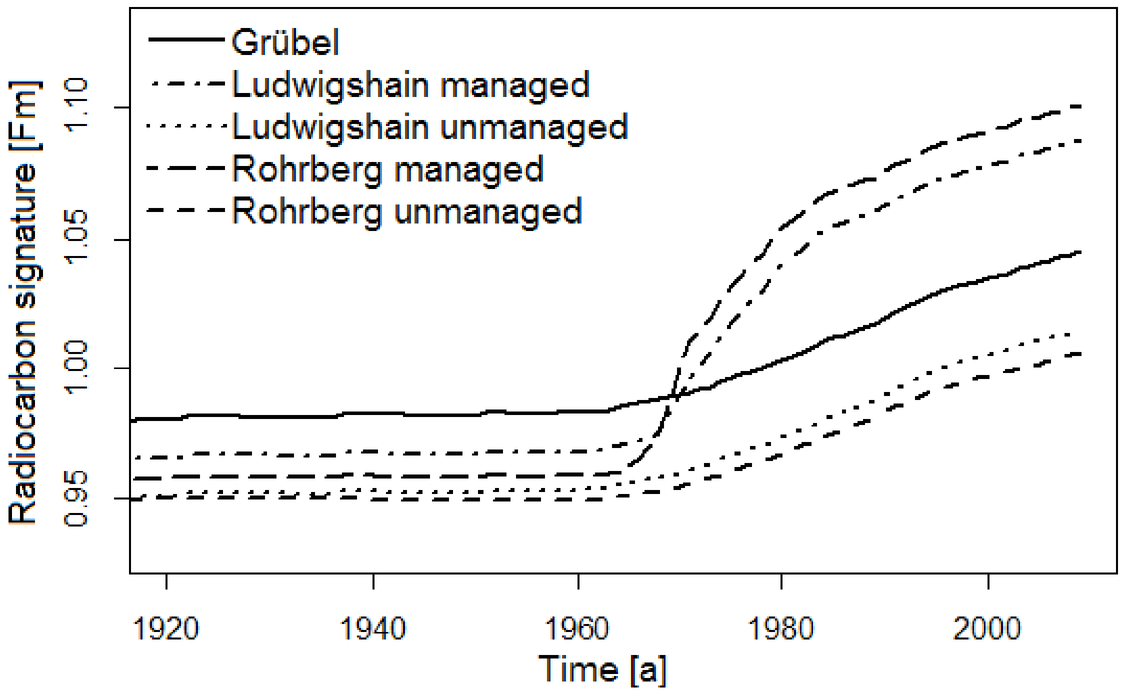

Figure 4.S.1: $\Delta^{14}C$ signature in ‰ of total coarse woody debris in the unmanaged and managed forests Grübel, Ludwigshain and Rohrberg.

Radiocarbon signature and turnover of carbon in the O_i horizon

As no data on past leaf litter input is available, we assume it to be produced at a constant rate and have applied a steady state model to calculate the TT. Fresh leaf litter of beech and oak from the year 2011 had a radiocarbon signature of 32.8 ± 9 ‰, which was close to the signature of the atmosphere in the year 2010. Leaf litter input to the O_i horizon thus has a lag period (lp) of one year. For Norway spruce a lag period (lp) of 6 years was assumed (Schulze et al. 2009). $Fm_{Oi}(t)$, the modern fraction of the Oi horizon in the year t was calculated as follows:

$$Fm_{Oi}(t) = k_{Oi} * Fm_{atm}(t - lp) + (1 - \frac{1}{TT_{Oi}} - \frac{1}{8267}) * Fm_{Oi}(t-1) \tag{4}$$

where TT_{Oi} is the turnover time of the O_i horizon, and Fm_{atm}(t-lg) is the radiocarbon signature of fresh leaf litter.

Radiocarbon signature, inputs and stocks of fine woody debris

A sinus function was used to model the regular increase and decrease in FWD input (I_{FWD}) in a year t resulting in an oscillating FWD input. For each managed forest, the year of the thinning procedure was determined from forest records. The dimensionless variables x and y were used to fit the sinus function in such way, that it had a maximum in the year of the last management procedure and that intervals between maximums correspond to time periods that likely pass between years of higher FWD input. The value z related to the FWD input measured for 2010 and represents the amplitude of the sinus curve.

$$I_{FWD}(t) = \left| \sin\left(\frac{t}{x} + y\right) \right| * z \tag{5}$$

The decay of FWD is assumed to have a faster decay rate than CWD. According to CWD, a linear C loss of FWD is assumed. The radiocarbon signature of FWD for the year 2010 was measured of one mixed sample per study site. Radiocarbon signatures for previous years are modeled by assuming a TT and a lag period of 8 years. The C stock of FWD in a year t ($S_{FWD}(t)$) can be calculated by combining the input ($I_{FWD}(t)$) to and the loss ($L_{FWD}(t)$) from the C stock:

$$S_{FWD}(t) = S_{FWD}(t-1) + I_{FWD}(t) - L_{FWD}(t) \tag{6}$$

where the C loss from FWD is calculated as follows

$$L_{FWD}(t)=\frac{S_{FWD}(t)}{8} \quad . \tag{7}$$

Turnover of carbon in the O_e horizon (Grübel and Rohrberg) and the mixed Oe/Oa horizon (Ludwigshain)

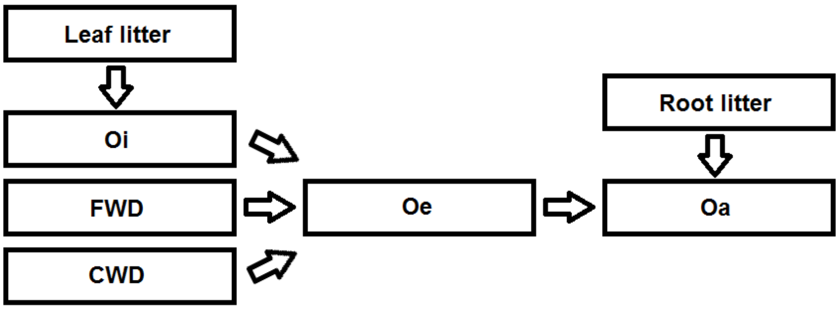

Figure 4.S.2: Carbon input model for the organic layer.

For the O_e horizon, three different input pools are considered: material from the O_i horizon, fine woody debris (FWD) and coarse woody debris (CWD) (Fig.4.S.2). The model calculates the C stock of the O_e horizon in the year t ($S_{Oe}(t)$) and the radiocarbon signature of the O_e horizon ($Fm_{Oe}(t)$) separately for the same TT (TT_{Oe}). For each input pool, L(t) is the total C loss and the value h is the proportion of the total C loss that enters the O_e horizon.

$$S_{Oe}(t)=h_{Oi}*L_{Oi}(t)+h_{FWD}*L_{FWD}(t)+h_{CWD}*L_{CWD}(t)+S_{Oe}(t-1)*(1-\frac{1}{TT_{Oe}}) \tag{8}$$

$$\begin{aligned} Fm_{Oe}(t)=(&h_{Oi}*S_{Oi}(t)*Fm_{Oi}(t)+h_{FWD}*S_{FWD}(t)*Fm_{FWD}(t)+h_{CWD}*S_{CWD}(t)* \\ &*Fm_{CWD}(t)+S_{Oe}(t-1)*(1-\frac{1}{TT_{Oe}}*\frac{1}{8267}))\div S_{Oe}(t) \end{aligned} \tag{9}$$

The value h is constant over time. For input from FWD, two different scenarios are calculated: (1) no input from FWD (h_{FWD}=0) and (2) the proportion of input from FWD is equal to the proportion of input from the O_i horizon (h_{FWD}=h_{Oi}). For CWD input, several scenarios with h_{CWD} ranging from 0-10 % were calculated. Additionally, a data point where the proportion of C input from CWD and C input from the O_i horizon are equal was calculated (h_{CWD}=h_{Oi}).

Turnover of carbon in the O_a horizon (Grübel and Rohrberg)

The TT of the Oa horizon (TT_{Oa}) was calculated with a non-steady state model. Two input pools were identified: material from the O_e horizon and root litter. The C stock of the O_a horizon ($S_{Oa}(t)$) and the radiocarbon signature of the O_a horizon ($Fm_{Oa}(t)$) are calculated separately. The C stock in the roots ($S_r(t)$) was measured as a fraction of the O_a horizon in 2009 (Rohrberg) or 2010 (Grübel), but no radiocarbon signatures were measured. We assume that the radiocarbon signature of the roots (Fm_r) corresponds to the radiocarbon signature of the atmosphere (Fm_{atm}). Two scenarios are calculated: (1) no input from roots to the O_a horizon ($h_{Oa} = 0$) and (2) all C in roots goes into the O_a horizon ($h_{Oa} = 1$). The proportion of the C stock of the O_e horizon (S_{Oe}) that flows into the O_a horizon (h_{Oe}) is calculated following

$$S_{Oa}(t)=h_{Oe}*S_{Oe}(t)+h_r*S_r(t)+S_{Oa}(t-1)*(1-\frac{1}{TT_{Oa}}) \qquad (10)$$

$$Fm_{Oa}(t)=\frac{h_{Oe}*S_{Oe}(t)*Fm_{Oe}(t)+h_r*S_r(t)*Fm_r(t)+S_{Oa}(t-1)*(1-\frac{1}{TT_{Oa}}-\frac{1}{8267})}{S_{Oa}(t)} \qquad (11)$$

Turnover of carbon in the mineral soil

A steady state model was used following Gaudinski et al. (2000) to calculate the radiocarbon signature (Fm_{soil}) and the turnover time (TT_{Soil}) for the bulk samples of the mineral soil and the density fractions. The radiocarbon signature of the input corresponds to the radiocarbon signature of the atmosphere (Fm_{atm}). For modern radiocarbon signatures, two TT are possible.

$$Fm_{soil}(t)=k_{soil}*Fm_{atm}(t)+(1-\frac{1}{TT_{soil}}-\frac{1}{8267})*Fm_{soil}(t-1) \qquad (12)$$

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Declaration/Erklärung

I hereby declare that this doctoral thesis is entirely my own work, and that I did not use any sources or auxiliary means other than those referenced. Moreover, I declare that no parts of this thesis have previously been submitted for the purpose of obtaining a doctoral degree at any other scientific institution. I have not conclusively failed any doctoral examination procedure.

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig verfasst und nur die angegebenen Quellen und Hilfsmittel benutzt habe. Ich versichere, dass ich diese Arbeit an keiner anderen wissenschaftlichen Einrichtung zum Zwecke einer Promotion eingereicht habe. Ich habe noch kein Promotionsverfahren endgültig nicht bestanden.

Bayreuth, den 08.04.2013

Inken Krüger