LINKING LITTER DECOMPOSITION PROCESSES TO SOIL CARBON SEQUESTRATION IN NORWAY SPRUCE, DOUGLAS FIR AND EUROPEAN LARCH STANDS

(Der Einfluss von Streuzersetzungsprozessen auf die Speicherung von Bodenkohlenstoff in einem Fichten-, Douglasien- und Lärchenbestand)

Masterarbeit

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Abstract

Increasing forest disturbances as a result of climate change are threatening Norway spruce (*Picea abies*) stands across Europe. Due to higher drought tolerance and storm resistance, Douglas fir (*Pseudotsuga menziesii*) and European larch (*Larix decidua*) became of greater silvicultural importance. The potential impacts of these tree species on litter decomposition processes and forest soil carbon (C) sequestration remain, however, unclear. Therefore, this master thesis targets to (1) quantify C fluxes during the initial phase of litter decomposition, (2) answer if partitioning of litter C fluxes into mineralization to CO_2 by microbial respiration and leaching of dissolved organic C (DOC) is influenced by tree species and (3) connect decomposition processes and stand parameters to soil organic C stocks. Microbial respiration of CO_2 and leaching of DOC were measured along with mass loss and biochemical litter properties in a decomposition field study over the course of nine months. Measurements were conducted in neighboring Norway spruce, Douglas fir, and European larch stands located in the Vienna Woods. Carbon losses during litter decomposition were dominated by CO_2 mineralization which accounted for 95 to 98 % of the measured C fluxes from litter. Two to 5 % was leached as DOC from litter. Partitioning of C fluxes differed among tree species and could be related to differences in biochemical litter properties. Although litter of European larch showed lowest C losses from mineralization, it featured highest DOC leaching rates when compared to Norway spruce and Douglas fir. Higher DOC leaching rates were reflected in a higher sequestration potential for organic C in the mineral topsoil. This study provides a detailed view on litter decomposition processes and their implications on soil C storage and provides suggestions for further research.

Keywords: Litter decomposition, carbon partitioning, microbial respiration, leaching of dissolved organic carbon, soil organic carbon storage

Zusammenfassung

Titel: Der Einfluss von Streuzersetzungsprozessen auf die Speicherung von Bodenkohlenstoff in einem Fichten-, Douglasien- und Lärchenbestand

Durch die Zunahme Klimawandel bedingter Störungsereignisse sind insbesondere europäische Fichtenbestände (*Picea abies*) stark gefährdet. Baumarten mit höherer Störungstoleranz gegenüber Trockenstress und Windwurf rücken daher vermehrt in den waldbaulichen Fokus, dazu zählen beispielsweise Douglasie (*Pseudotsuga menziesii*) und Lärche (*Larix decidua*). Der Einfluss dieser Baumarten im Zuge ihrer Streuzersetzung auf die Kohlenstoffspeicherung im Waldboden wurde im Vergleich zur Fichte noch nicht untersucht und ist daher Gegenstand dieser Masterarbeit. Ziel war es, (1) die unterschiedlichen Kohlenstoffflüsse der betreffenden Baumarten während der Anfangsphase der Streuzersetzung zu quantifizieren. Es wurde weiters untersucht, (2) ob sich der zersetzungsbedingte Verlust von Kohlenstoff (C) aus der Nadelstreu hinsichtlich seiner Aufteilung in Mineralisation durch mikrobielle Respiration zu CO_2 und Auswaschung von gelöstem C (DOC) zwischen den Baumarten unterscheidet. Schließlich wurden (3) die Streuzersetzungsprozesse sowie die baumartenspezifischen Bestandeseigenschaften mit den jeweiligen Bodenkohlenstoffvorräten verknüpft. Mittels eines neunmonatigen Feldversuches im Wienerwald wurden Massenverlust, mikrobielle Respiration von CO_2 und die Auswaschung von DOC im Zuge des Streuabbaus in benachbarten Reinbeständen von Fichte, Douglasie und Lärche gemessen und zusätzlich biochemische Streuparameter ausgewertet. Mit einem Anteil von 95 bis 98 % an den gesamt gemessenen C-Flüssen während der Streuzersetzung wurde der Großteil des C im Zuge der Mineralisation an die Atmosphäre abgegeben, lediglich 2 bis 5 % wurden als DOC in den Boden ausgewaschen. Zurückzuführen auf deren unterschiedliche Zusammensetzung und Eigenschaften der Streu, unterschieden sich die untersuchten Baumarten hinsichtlich dieser Aufteilung: Lärche zeigte hierbei einen signifikant geringeren C-Verlust durch mikrobielle Respiration bei gleichzeitig signifikant höheren Auswaschungsraten im Vergleich zu Fichte und Douglasie. Die Ergebnisse deuten auf einen Zusammenhang zwischen vermehrter C-Auswaschung und höherem C-Speicherpotential im oberen Mineralboden hin. Diese Studie bietet einen detaillierten Einblick in Streuzersetzungsprozesse sowie deren Auswirkungen auf die C-Speicherung im Boden. Zudem werden weiterführende Fragestellungen in Hinblick auf diese Thematik aufgezeigt.

Schlagwörter: Streuzersetzung, Kohlenstoffflüsse, mikrobielle Respiration, C-Auswaschung, Kohlenstoffspeicherung im Boden

Index

1 Introduction

1.1 Litter decomposition and soil organic carbon stocks

Aboveground litter decomposition is a major process within the forest carbon (C) cycle (Batjes, 2014). It connects atmospheric and terrestrial C pools (Coûteaux et al., 1995, Houghton, 2007) and marks a primary process of soil organic matter (SOM) formation and the storage of C in soil (soil organic C, SOC; Cotrufo et al., 2013). Soils represent the largest terrestrial reservoir for organic C storing up to 2200 Pg C (Batjes, 2014, IPCC, 2014); this amount of C equals two to three times the amount held in the atmosphere (Batjes, 2014). Soils are considered to play an essential role in regulating the climate system by sequestering atmospheric carbon dioxide (CO_2) (Wiesmeier et al., 2019). Forest ecosystems are of particular importance as their soils store more than 40 % of the terrestrial organic C (IPCC, 2014). With hindsight to global climatic changes, information on how to maximize C stocks is urgently requested (Victoria et al., 2012, Wiesmeier et al., 2019) and the question whether and how soil C sequestration is related to litter decomposition has already received scientific attention (e. g. Huang et al., 2011, Prescott, 2010).

Litter decomposition is characterized by three interlinked processes: fragmentation, leaching of solubles and catabolism by decomposers (Cotrufo et al., 2010a, Swift et al., 1979). During these processes, litter biomass C is lost, either in the course of mineralization to CO_2 by microbial respiration or by translocation of organic matter into the soil (Rubino et al., 2010). The CO_2 emissions caused by microbial respiration account for one of the largest fluxes into the atmosphere (Houghton, 2007); the fraction of C being respired is effectively lost from the terrestrial C pool. In contrast, biomass C being transported into the soil by fragmentation (physical processes, e.g., via soil macrofauna) or leaching potentially contributes to SOM formation and consequent C sequestration (Cotrufo et al., 2015). The controlling factors driving this partitioning are, however, not fully understood (Soong et al., 2015). In addition, to understand the actual contribution of litter decomposition on SOC sequestration, a quantification of C partitioning has been demanded (Mueller et al., 2015, Rubino et al., 2007, Rubino et al., 2010, Soong et al., 2015).

As suggested by Cotrufo et al. (2015), there are two pathways leading to the formation of SOM that evolve from the three litter decomposition processes: In the dissolved pathway, soluble litter compounds are leached especially during the initial phase of decomposition into the mineral soil

whereas the physical pathway occurs mainly at later stages, describing the physical translocation (e.g.,, biotic perturbation) of litter fragments (particulate organic matter = POM) into the soil. Compounds of the dissolved pathway are suggested to be subsequently microbially processed or to form mineral-associated organic matter by adsorption to mineral surfaces; both ways that have been found to generate stable SOM (Cotrufo et al., 2013, Cotrufo et al., 2015, Lavallee et al., 2020).

It has been hypothesized that microbial derived products contribute more efficiently to stable SOM than directly plant derived compounds (Cotrufo et al., 2013, Mambelli et al., 2011). However, more recent findings report equal efficiency in stable SOM formation by particulate organic matter derived from high quality litter (Cotrufo et al., 2015) or an even higher efficiency by mineral associated organic matter derived from low quality litter (Córdova et al., 2018). In general, concerning the amounts and persistence of SOM, evidence suggests both are largely controlled by climate conditions, soil properties, substrate quality and decomposer activity (Amelung, 2014, Liang et al., 2017).

Litter decomposition has traditionally been investigated by means of litter bags and the determination of litter mass loss rates (Hobbie et al., 2006, Prescott, 2010). Although the limitations of litter bag studies are well known, it is still the most common method to study litter decay (Cotrufo et al., 2010b). The mesh bags prevent to a great extent fragmentation and its translocation by soil fauna, leading to a considerable underestimation of mass loss rates (Cotrufo et al., 2010a). Hence, it may not reflect the full potential of litter derived C actually contributing to SOM formation (Rubino et al., 2010). Another commonly used method to study litter decay is the determination of mineralization rates from microbial respiration (Ladegaard-Pedersen et al., 2005, McTiernan et al., 1997). The release of CO_2 during mineralization was assumed to correspond to litter mass loss, still dismissing to quantify the fraction that is directly transported into the soil, e.g., by fragmentation or leaching. This was due to the opinion, that mainly recalcitrant material – the stable remains from litter decay – would contribute significantly to SOM formation (Berg and McClaugherty, 2014, Cotrufo et al., 2015). Other studies have investigated litter decomposition by investigating dissolved organic carbon (DOC) fluxes into the soil (Cleveland et al., 2004, Tietema and Wessel, 1994). Dissolved organic C derived from initial litter decomposition stages has only recently been identified to be essential for long-term soil C sequestration (Cotrufo et al., 2015, Kalbitz and Kaiser, 2008, Magill and Aber, 2000, Rubino et al., 2010), and even more, if the plant derived substances undergo microbial processing (Bradford et al., 2013). Most of litter derived DOC was found to be retained within the upper layers of mineral soil (Kammer et al., 2012).

To date, only few studies have investigated C partitioning into CO_2 and DOC during litter decomposition *in-situ* (Huang et al., 2011, Tietema and Wessel, 1994). Results from the more common laboratory incubations (Kammer and Hagedorn, 2011, Lu et al., 2012, Soong et al., 2015) do provide useful insight on the topic but exclude environmental factors such as temperature, precipitation and exchange processes in nutrients and soil biota. Isotopic labelling studies allow precise conclusions obtained from field observations (Cotrufo et al., 2015, Kammer and Hagedorn, 2011, Kammer et al., 2012, Rubino et al., 2010), but are costly and laborious.

1.2 Factors determining litter decomposition

It is widely acknowledged that litter decomposition is influenced by several biotic and abiotic factors. These include chemical litter composition and the involved decomposer organisms as biotic, and environmental conditions as abiotic factors (Berg and McClaugherty, 2014, Coûteaux et al., 1995, Swift et al., 1979). Climate has been identified to largely influence decomposition on a global and a cross-regional (Cornwell et al., 2008, Coûteaux et al., 1995, Zhang et al., 2008) scale; even indirectly through altering litter chemical composition (Aerts, 1997). However, if environmental conditions are similar, e.g., on a more regional or local scale, chemical composition of litter dominates decomposition (Cotrufo et al., 2010a, Coûteaux et al., 1995). Nevertheless, the influence of climate on a microsite level is decisive for decomposition rates: here, temperature and moisture are the most influential drivers of litter decomposition affecting not only microbial community composition and abundance but also their activity (Bani et al., 2018, Manzoni et al., 2012, Prescott, 2010, Wang et al., 2019).

Chemical and physical litter properties are widely used to describe litter decomposition rates as function of litter quality. Litter has been classified to be of *high* or *low* quality, depending on how fast or slow it decomposes. High quality litter is thereby defined to be rich in nutrients and easily degradable carbohydrates, and has low concentrations of complex compounds such as lignin (Cotrufo et al., 2010a). Ratios like C to nitrogen (N), lignin to N (Melillo et al., 1982, Prescott, 2010) or the lignocellulose-index (LCI, = ratio of lignin to cellulose + hemicellulose; Moorhead et al., 2013) are common predictors of litter decomposability and are usually negatively correlated with litter mass loss rates. High contents of N are associated with rapid litter mass loss rates in early decay stages, but slowed litter mass loss rates in later decay stages (Berg, 2000). Aside from chemical properties, some

physical functional traits of leaves and litter have been proven suitable in estimating early decomposition. Traits such as specific leaf area, leaf toughness or water uptake may play a decisive role in DOC leaching dynamics and accessibility for decomposers (Zukswert and Prescott, 2017).

Decomposition has been studied for centuries, hence a myriad of concepts describing litter decomposition exist (Cotrufo et al., 2010a), yet new ones are still developed (e. g. Klotzbücher et al., 2011, Soong et al., 2015). However, constructing generalized principles on how decomposition occurs for various litter types and different environments remains a challenging task. Across concepts, it is acknowledged that the composition of litter changes throughout its degradation process and over time, its degradability declines: soluble and non-structural compounds (e.g., sugars, low molecular weight phenolics, certain nutrients like potassium) are promptly lost whereas structural and more complex components (e.g., cellulose, hemicellulose, lignin) take more time to decompose. Microorganisms like fungi and bacteria colonizing and growing into the litter decompose and metabolize its compounds and contribute to formation of new substances, e.g., by degradation of lignified structures. At the beginning of litter decomposition, mass loss occurs rapidly, and quantities of leached soluble compounds are high. In the course of decomposition, the proportion of structural and complex components in litter increases and mass loss tends to slow down (Berg and McClaugherty, 2014, Cotrufo et al., 2010a).

Although it is agreed that mass loss rates are substantially affected by lignin, its decomposition dynamics remain to be a matter of debate (Soong et al., 2015). A variety of concepts describing the decomposition of this polyphenolic macromolecular compound exist, e.g., it does not or only barely decompose during early stages and accumulates in litter residue (Berg and Staaf, 1980, Kalbitz et al., 2006). Contrastingly, its decomposition is proposed to occur primarily at initial stages, depending on C availability (Klotzbücher et al., 2011). Other theories, however, suggest it is degraded during all stages of decomposition (Preston et al., 2009a). Promising new approaches may soon reveal more insight on this matter by observing the succession of microbial communities and litter degrading enzymes along with changes in litter chemistry during decomposition (e. g. Margida et al., 2020, Schneider et al., 2012, Voříšková et al., 2011). To date, studies have also tried to associate the decomposition of recalcitrant substances like lignin to litter compounds that are more easily degradable, such as holocellulose (= cellulose + hemicellulose; e. g. Campbell et al., 2016, Moorhead et al., 2013), explaining the usage of LCI as a predictor for decomposition.

Decomposers like fungi and bacteria play a major part in litter decomposition, yet many aspects on how they alter underlying processes remain poorly understood (Bani et al., 2018). Fungi are, contrasting to bacteria, able to access new substrate (Bani et al., 2018), exchange N through hyphae (Hättenschwiler et al., 2005, Zeller et al., 2000) and contribute significantly to the breakdown of structural compounds via their enzyme production (Schneider et al., 2012). Decomposers may be specialized in degrading certain plant species (Ayres et al., 2009, Moorhead and Sinsabaugh, 2006) or may follow opportunistic strategies (Moorhead and Sinsabaugh, 2006). Moreover, specialized decomposers are also suggested to account for a faster decay when litter is decomposing close to its place of origin than elsewhere (homefield advantage, e. g. Ayres et al., 2009, Veen et al., 2015) As decomposition progresses, microbial communities have been observed to undergo successional changes (Moorhead and Sinsabaugh, 2006, Wang et al., 2019). A variety of concepts have been developed to describe the linkage between litter decomposition and the involved microbial processes (e. g. Campbell et al., 2016, Moorhead and Sinsabaugh, 2006, Moorhead et al., 2013) and dynamics of C use efficiency (Sinsabaugh et al., 2013, Manzoni et al., 2012, Manzoni, 2017). The latter describes the ratio for growth of microbial biomass per unit of substrate C uptake; carbon is utilized to generate microbial biomass rather than being respired if C use efficiency is high, whereas a low C use efficiency indicates a lower production of biomass with high losses of C into the atmosphere (Manzoni et al., 2012).

1.3 Tree species effects on litter decomposition and SOC stocks

Tree species specific differences in litter quality and decomposability have been extensively investigated and documented (e. g. Hobbie et al., 2006, Laganière et al., 2010, Preston et al., 2009b). Furthermore, studies have also engaged in identifying potential synergistic effects on decomposition rates by mixing litter of various species (Berger and Berger, 2014, Cuchietti et al., 2014, Hättenschwiler et al., 2005, Setiawan et al., 2016, Wang et al., 2019). However, information on species specific C partitioning into CO_2 and DOC during litter decomposition remains scarce (e. g. Rubino et al., 2007, Huang et al., 2011) and demands further research, especially by means of field studies.

Knowledge on how tree species selection influences SOC pools could help authorities to specifically target the uptake of atmospheric C via forest management (Jandl et al., 2007). In addition, a climate

induced shift in tree species composition in many areas is to be expected (Lexer et al., 2002, Seidl et al., 2011), requiring more detailed information to evaluate the upcoming consequences for the forest C cycle. Evidence suggests that SOC stocks are affected by tree species selection with potential increases in C storage as impactful as 200 – 500 % in the forest floor and 40 – 50 % in the top mineral SOC stocks; however, the underlying dynamics are not fully understood and tree species effects, especially in mineral soils, were found to be inconsistent (Vesterdal et al., 2013).

Forest floor and mineral SOC stocks for this study were investigated previously (Hechenblaikner, 2019), where tree species effects were suggested to result from discrepancies in litterfall input due to varying stand densities. Along with root litter, aboveground litter generates the main C input to SOC pools (Cotrufo et al., 2013, Vesterdal et al., 2013). Stand parameters such as tree productivity have been discussed to strongly affect SOC stocks besides litter chemistry and decomposition processes (e. g. Blaško et al., 2020, Gärdenäs, 1998, Hansson et al., 2011, Vesterdal et al., 2013).

A decline in Norway spruce (*Picea abies*) across Austrian forests has been observed (Russ, 2019), linked to ongoing pressure by increasing disturbances (Seidl et al., 2017). While Norway spruce still represents the dominant tree species (Russ, 2019), its suitability under future climatic scenarios is threatened, or rather dramatically, will no longer be given for low elevations (Lexer et al., 2002). In contrast, Douglas fir (*Pseudotsuga menziesii*) and European larch (*Larix decidua*) have received considerable attention in silviculture due to their comparatively higher suitability for prospective climatic conditions, i.e., coping with dry periods and storm resistance. Offering favorable wood properties, they represent a non-native and a native silvicultural alternative to Norway spruce (Brosinger and Baier, 2008, Ruhm et al., 2016a, Ruhm et al., 2016b, Schüler et al., 2017). Knowledge on decomposition of Douglas fir and European larch litter in comparison to Norway spruce litter remains still unclear and particularly for Austria no such studies are available.

1.4 Objectives and hypotheses

Here, early-stage decomposition of Norway spruce, Douglas fir and European larch litter was investigated in forest stands of the Vienna Woods over the course of 9 months. Litter decomposition dynamics were linked to SOC storage. Litter mass loss was determined using litter bags. Partitioning into CO_2 and DOC fluxes during litter decomposition was assessed by field and laboratory

measurements of microbial respiration- and DOC leaching rates. Additionally, biochemical litter properties and soil microclimate was measured. The objectives of the study were to (1) quantify the pathways of litter derived C fluxes during decomposition, (2) ascertain whether the C partitioning is influenced by tree species and (3) connect decomposition processes and stand parameters to SOC stocks. Based on earlier findings (Cotrufo et al., 2015, Kammer et al., 2012), it was hypothesized that (H1) litter properties are stronger predictors of C partitioning than environmental stand conditions, and (H2) litter types with high DOC leaching lead to larger SOC stocks in the mineral top soil.

2 Materials & Methods

2.1 Study site and experimental design

The study took place near Klausen-Leopoldsdorf in the Vienna Woods (Lower Austria, 48°04'38.7" N, 15°59'52.6" E). Natural woodland community is dominated by European beech (*Fagus sylvatica*) (Kilian et al., 1994). The altitude of the study site ranges from 460 to 540 meters above sea level (Land Niederösterreich, 2019). Mean annual precipitation from 2009 to 2018 was 848 mm and mean annual temperature was 9.8 °C (ZAMG, 2019). Exposition of the study site is south-east. The substrate for soil formation is Flysch, which consists mainly of marly clay and sandstone (Kilian et al., 1994). Soil types are dominated by Cambisols (IUSS Working Group WRB, 2006) and the main humus form is Mull (Zanella et al., 2019). Detailed information on soil and forest floor properties can be found in Table 1.

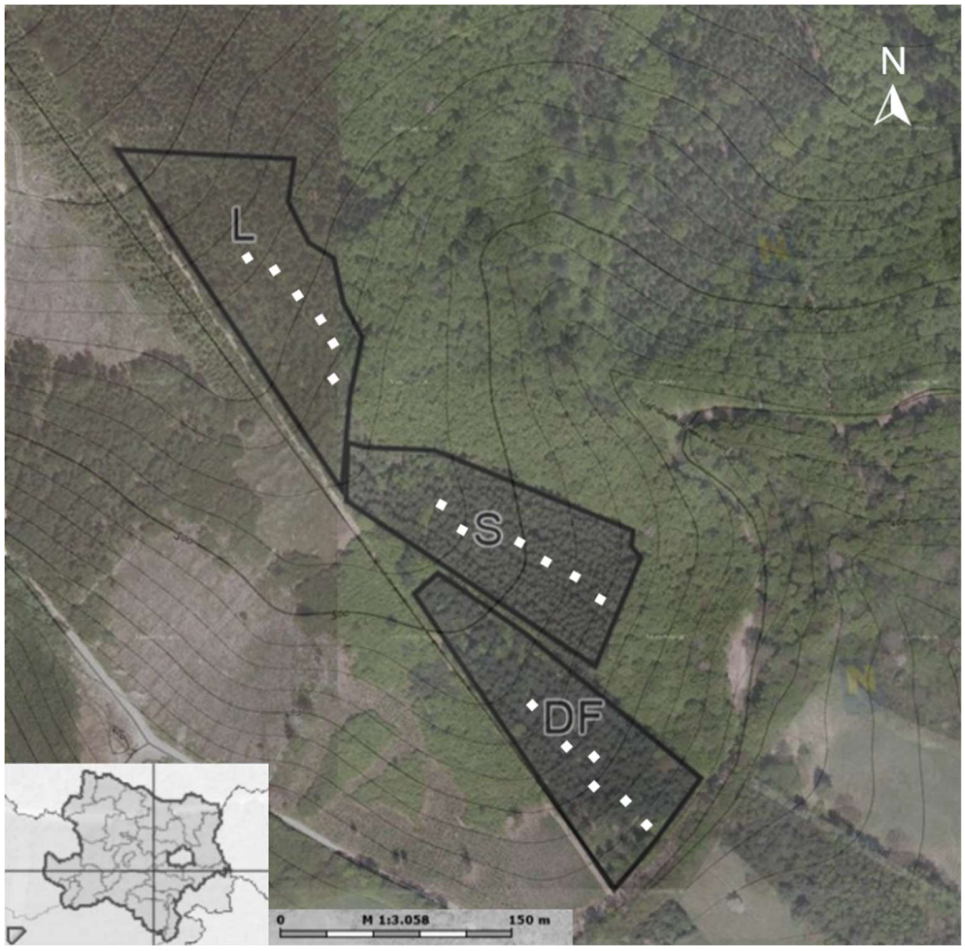

Figure 1. Map showing the location of the study site near Klausen-Leopoldsdorf, Lower Austria, with adjacent pure stands of Douglas fir (DF), Norway spruce (S) and European larch (L). Arrangement of plots is represented by white squares. Map created with NÖ Atlas (Land Niederösterreich, 2019).

Neighbouring pure stands of Norway spruce (*Picea abies*), Douglas fir (*Pseudotsuga menziesii*) and European larch (*Larix decidua*) were selected for the study (Figs. 1 and 2). The area covered by the stands is about 0.7 ha, 0.9 ha and 1.0 ha for Norway spruce (S), Douglas fir (DF) and European larch (L) respectively. Stands were established by planting and stand age was ~ 40 years in 2018. Owner of the site are the Austrian Federal Forests AG (ÖBf). Each stand was thinned once at a stand age of ~ 25 years. Harvesting intensities were species specific resulting in varying stand densities (Table 1). Within each stand, six plots (1.5 x 1.5 m) were established for further measurements (Figs. 1 and 3).

Table 1. Stand and soil parameters for the study site (Hechenblaikner, 2019). Given are mean values ± standard error of the mean. More detailed information can be found in Hechenblaikner (2019).

	Unit	*Norway spruce*	*Douglas fir*	*European larch*
Stand properties				
Density	n ha^{-1}	1103 ±85	806 ±112	679 ±42
DBH	cm	22.3 ±0.74	28.2 ±0.87	20.9 ±1.32
Height	m	21.2 ±0.62	23.6 ±0.85	17.8 ±1.54
Basal area	cm^2 ha^{-1}	45.5 ±2.50	50.9 ±6.83	26.6 ±1.19
Standing volume	m^3 ha^{-1}	464.9 ±29.60	627.6 ±101.03	238 ±13.53
Needle biomass	kg m^{-2}	2.3 ±0.13	1.6 ±0.22	0.3 ±0.01
Soil properties				
Carbon stocks				
$O_L + O_F$	g m^{-2}	692.2 ±62.17	476.1 ±46.40	308.5 ±48.66
0-10 cm	g m^{-2}	3162.6 ±363.71	2447.4 ±155.28	2401.6 ±141.89
10-20 cm	g m^{-2}	1467.3 ±231.71	2003.9 ±477.04	1554.8 ±213.77
20-30 cm	g m^{-2}	1013.3 ±107.07	977.4 ±117.26	927.2 ±83.87
Total	g m^{-2}	6335.3 ±527.53	5904.8 ±420.01	5192.1 ±370.71
Nitrogen stocks				
$O_L + O_F$	g m^{-2}	16.6 ±1.79	15.2 ±1.52	10.6 ±1.77
0-10 cm	g m^{-2}	184.4 ±33.78	178.1 ±14.85	167.4 ±16.06
10-20 cm	g m^{-2}	115.4 ±27.28	121.5 ±13.38	133.7 ±16.96
20-30 cm	g m^{-2}	92.7 ±13.78	80.5 ±14.25	94.6 ±12.19
Total	g m^{-2}	409.2 ±69.61	395.3 ±20.74	406.2 ±40.07
pH in $CaCl_2$				
0-2 cm		4.5 ±0.29	4.5 ±0.15	4.0 ±0.10

DBH = Diameter at breast height.

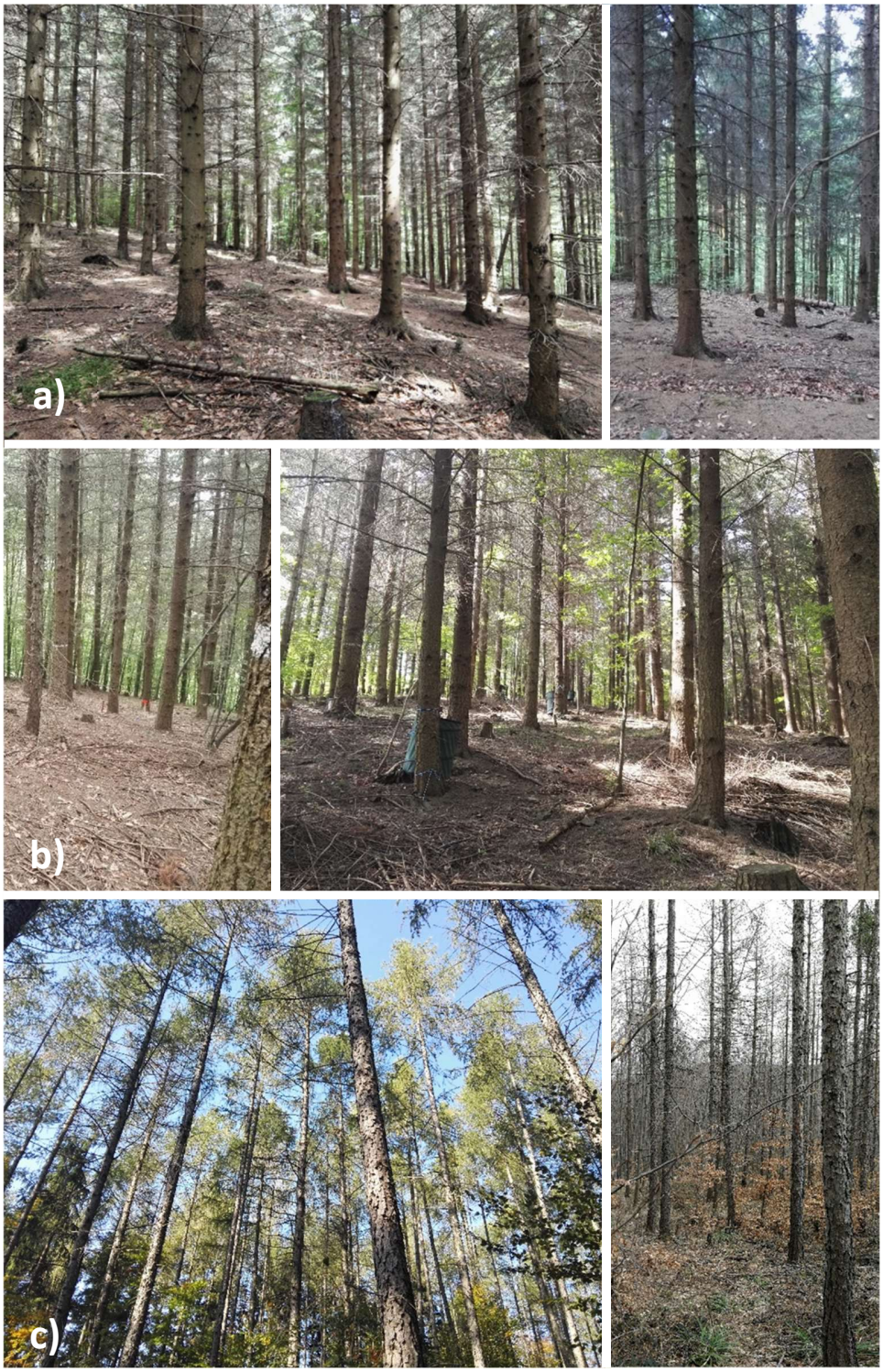

Figure 2. Impressions from the study site, whereas a) shows the Norway spruce (S) stand, b) the Douglas fir (DF) stand and c) the European larch (L) stand.

2.2 Litter preparation

Freshly fallen, intact needle litter was collected from the soil surface of each stand in March 2018, ~ 3 weeks prior to the begin of the study. In the laboratory, litter was carefully sorted by hand to remove needles with advanced signs of decomposition as well as small pieces of cones or twigs. Litter was mixed and dried at 30 °C to constant weight. Afterwards, subsamples were dried at 105 °C for 48 hours to calculate final litter dry mass. Litter dried at 30 °C was used for further field measurements and laboratory analyses.

2.3 Litter bag incubations

Litter bags were used to study litter mass loss and biochemical properties during the study period (Fig. 3). For that, polyethylene mesh bags (mesh size 1 mm) with an approximate size of 5 x 10 cm were filled with 2 g of dried litter (30 °C). Bags had a double layered bottom and were closed with stainless-steel staples (Berger and Berger, 2012). Two bags were installed at each plot (*home* litter, Fig. 3). To isolate the effect of litter quality and stand properties on litter decomposition a reciprocal litter transplant experiment (*away* litter) was conducted (Ayres et al., 2009, Veen et al., 2015). For that, two bags were filled with litter of the other tree species which were additionally installed at each plot. Thus, each plot contained two 2 g bags of S, DF, and L litter (Fig. 3). To study biochemical properties of litter, larger mesh bags (S 17 x 12 cm, DF 17 x 15 cm, L 17 x 18 cm) were filled with 12 g of dried litter. Three litter bags were installed at each plot. Both types of litter bags were fixed to the mineral soil (after removing the native litter layer) using stainless-steel pins. Loss of litter due to transport was negligible, with on average 0.004 g and 0.007 g for small and large bags, respectively. Installations were conducted between 16th and 19th of April 2018. Litter bags for the determination of mass loss were harvested in July and December 2018. Litter bags for biochemical analyses were harvested in April (one week after installation), July, and December 2018; the incubation of the first set of bags for one week should allow for a recovery of the microbial community following litter preparation (e.g., from drying). The litter bag harvests are referred to as *sampling dates* and mark the two *phases* of the experiment. In the laboratory, litter bags were opened and cleaned from non-needle litter material. Litter samples for mass loss determination (2 g bags) were dried (105 °C for 48 hours) and weighted afterwards (Berger and Berger, 2012). Litter samples for biochemical analyses (12 g bags) were analyzed for moisture content (1 g subsample dried at 105 °C for 48 hours) and were stored at 4 °C until further processing.

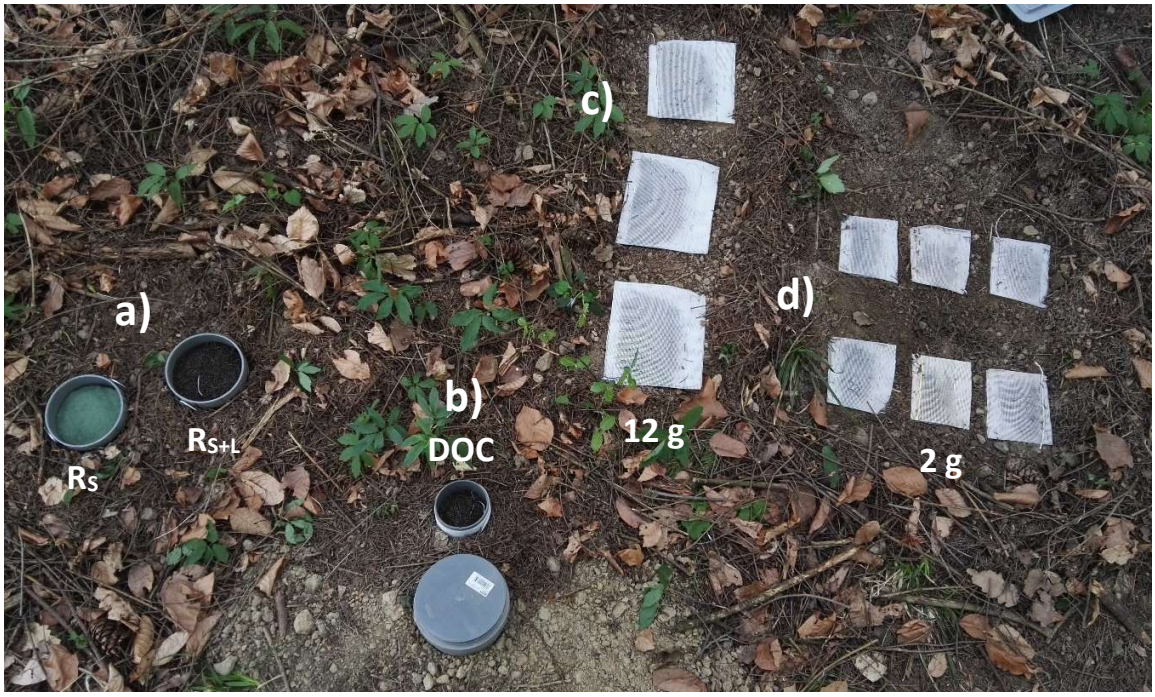

Figure 3. Plot design. a) Installations for measuring CO_2 efflux from mineral soil (R_S) and from mineral soil and added litter (R_{S+L}), b) lysimeters to evaluate litter leaching of dissolved organic carbon (DOC) from litter and c) litter bags for chemical analyses (12 g; sampling in April, July, December) and d) mass loss of litter (2 g; sampling in July and December)

2.4 Microbial respiration, soil climate, litterfall and needle biomass

For respiration measurements, each plot was equipped with two plastic collars (diameter: 10 cm, height: 7 cm; soil insertion depth: 3 cm) 2 weeks prior to first measurements (Fig. 3). Collars were installed ~ 20 cm apart. Prior to installation, native litter layers were gently removed. One collar per plot was then filled with a 1.5 cm layer of dried (30 °C) litter; to achieve an equal litter depth, different litter masses were used (S: 15 g, DF: 11 g, L: 6 g); between litter and mineral soil horizon, a polyethylene mesh (mesh size 1 mm) was installed to exclude soil fauna. Additionally, a mesh (mesh size 4 mm) was installed on top of the litter layer to exclude input from litter fall. The mineral soil inside the second collar was covered with a fleece material, to ensure a comparable microclimate inside the collars (Leitner et al., 2016). Respiration measurements were conducted using a portable infrared gas analyzer (EGM-4, PP Systems International, Inc. Amesbury, MA, USA; Fig. 4a) and a mobile respiration chamber (SRC-1, PP Systems International, Inc. Amesbury, MA, USA; Fig. 4a, b). By attaching the respiration chamber to the collars, the temporal increase of CO_2 was measured for a maximum of two minutes or until the concentration change inside the chamber exceeded 50

ppm. Collars of one plot were measured consecutively, starting with the collar containing the litter layer.

Figure 4. Set up for microbial respiration measurements; a) shows portable infrared gas analyzer (EGM-4, PP Systems International, Inc. Amesbury, MA, USA,; framed in white) and b) mobile respiration chamber (SRC-1, PP Systems International, Inc. Amesbury, MA, USA) attached to collar during measurement.

Along with the respiration measurements, soil temperature at 5 cm depth (including litter layer) of each plot was assessed by means of a handheld thermometer. Soil moisture between 0 - 7 cm (including litter layer) was measured via time domain reflectometry (Field Scout, Spectrum Technologies, Inc. Plainfield, IL, USA) and was expressed as volumetric soil water content (vol %). Litter moisture was determined gravimetrically (grav %). For that, litter was sampled randomly within each stand and dried at 105 °C for 48 hours in the laboratory. Measurements were conducted biweekly from April until December 2018. A complete measurement cycle took ~ 2 to 4 hours. To avoid a temporal sampling bias, the measurement order of the stands was changed regularly. To determine respiration from litter only (RL), respiration from mineral soil (RS) was subtracted from respiration from mineral soil and litter layer (RS+L). Respiration rates were corrected for differences in headspace volume of collars due to litter filling and for initial spatial differences between the collars. Data for aboveground litterfall was collected for a one-year cycle with three replicates of litter traps (55 x 39 cm, Fig. 5a) per stand. Litter traps were positioned close to the study plots. Needle biomass

for each stand was calculated by allometric equations based on tree DBH according to Forrester et al. (2017).

2.4.1 Forest floor C dynamics

Carbon dynamics of the forest floor incorporate mean residence time and mean turnover rate of the forest floor mass and the forest floor C. The mean residence time (T) in years and mean yearly turnover rate (R) for each stand were calculated according to Huang et al. (2011). Residence time is

$$T = \frac{O_L + O_F}{LF} \tag{2.01}$$

where $O_L + O_F$ represents the average standing forest floor mass in g m^{-2} and LF is the annual litterfall in g m^{-2}. Mean turnover rate (R) of forest floor mass in yr^{-1} is

$$R = \frac{1}{T} \tag{2.02}$$

Residence times and turnover rates for forest floor C were calculated according to forest floor mass, with average C contents per tree species obtained from the 12 g litter bag samplings in April.

Figure 5. Images showing a) litter trap and b) throughfall collector, both installed close to the plots with three replicates per stand.

2.5 Leaching of dissolved organic carbon and throughfall

Custom-made, zero-tension lysimeters were installed at each plot (Figs. 3 and 6), to measure leaching rates of DOC and dissolved nitrogen (DN) from litter into mineral soil due to percolating precipitation (Joergensen and Meyer, 1990). Lysimeters consisted of PVC collars (diameter 7.1 cm) with a double layered mesh bottom (mesh size 1 and 0.5 mm, respectively), placed on top of a plastic funnel. Dried litter (30 °C) was filled into collars; to achieve an equal litter depth, different litter masses were used (S: 7 g, DF: 5 g, L: 3 g). Collars were equipped with holes (diameter 1 cm) to allow microbial exchange between manipulated litter and native litter inside and outside the lysimeters. The holes were covered with a mesh (mesh size 1 mm). Precipitation passing through litter was collected in glass bottles (1 liter) which were placed in buried PVC pipes (Marley Deutschland GmbH, Wunstorf, Germany). A mesh (mesh size 4 mm) was installed on top of the lysimeter to exclude input from litter fall. Additionally, precipitation within stands (hereafter: throughfall) was collected at three plots per stand. Throughfall collectors consisted of a plastic funnel (diameter 12 cm) connected to a glass bottle (1 liter) by a silicon tube (Fig. 5b). The amount of litter leachate and throughfall was quantified and collected biweekly during respiration measurements. Leachate and throughfall samples were

subsequently pooled per stand; a subsample was brought to the laboratory where the samples were filtered (Whatman® Grade 589/2, Ashless Filter Paper) and frozen until further analysis. Litter leachate and throughfall was analyzed for DOC and DN content using a Shimadzu TOC-L analyzer (Shimadzu Corp., Kyoto, Japan). In the case lysimeters were corrupted (e.g., clogged tubes, leakage), leachate rates were estimated by means of linear regression models, predicting percolation through litter as a function of throughfall.

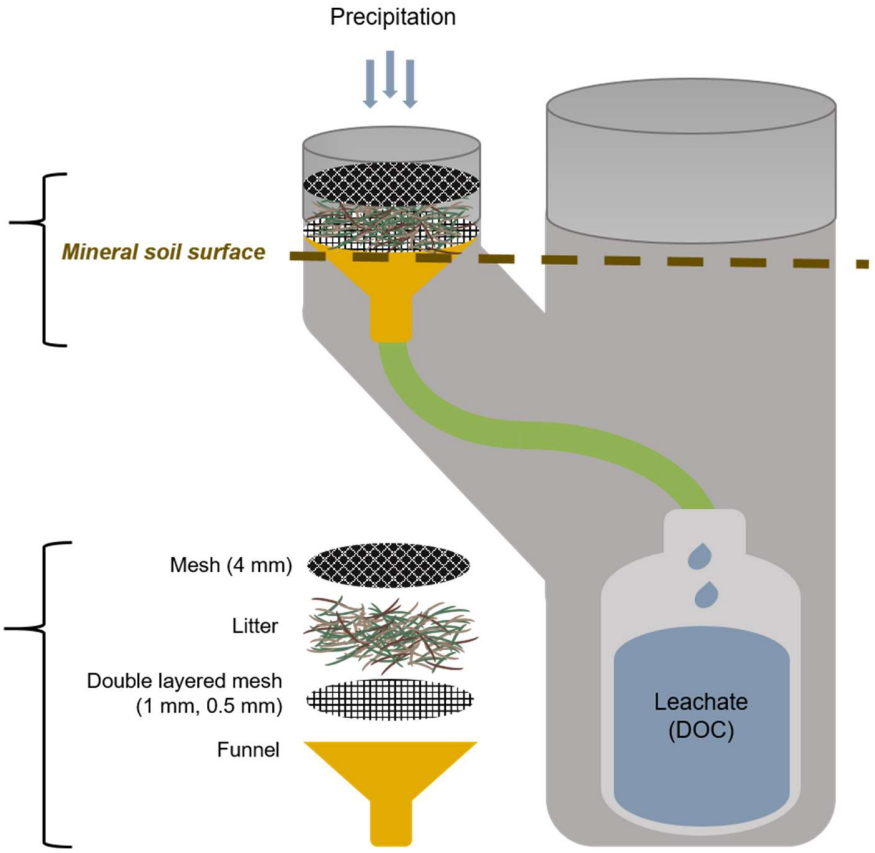

Figure 6. Illustration of lysimeters used to determine leaching of dissolved organic C (DOC) from litter. Broken line represents mineral soil surface. Zoomed area shows set-up inside the collar with the litter among the mesh material placed on top of the funnel.

2.6 Microbial respiration under standardized conditions

For measurements of litter mineralization to CO_2 by microbial respiration under controlled laboratory conditions, harvested litter from 12 g bags was filled into steel cylinders (Eijkelkamp Soil & Water, Giesbeek, The Netherlands). All samples were brought to a gravimetric water content of 120 % using deionized water. Prior to measurements samples were stored at 4 °C for one day to equilibrate. The CO_2 efflux from microbial respiration was measured by placing the cylinders in 2-liter plastic containers inside an incubator (Fig. 8). The containers were connected to an infrared gas analyzer via tubing (SBA-4, PP Systems International Inc., Amesbury, MA, USA). Inert tissues dampened with deionized water were put into the containers to reduce evaporation from the litter samples. In this dynamic closed-chamber system (Pumpanen et al., 2010), one container is measured at a time while the remaining containers are disconnected from the infrared gas analyzer and ventilated to avoid accumulation of CO_2 inside the containers. The concentration of CO_2 was recorded every 10 seconds, with a total of 6 minutes sampling time per container.

Figure 7. Containers inside the a) incubator connected to infrared gas analyzer (SBA-4, PP Systems International Inc., Amesbury, MA, USA) measuring microbial respiration via dynamic closed-chamber system (Pumpanen et al., 2010). Close up of b) container with liter sample

Due to insufficient gas mixing within the tubing and the headspace of the chambers, the first minute of recording was discarded. Microbial respiration was measured at 5 temperature steps (4, 10, 16, 22, and 28 °C). In total, one measurement cycle per temperature step took 7 hours. Between the temperature steps, samples were corrected for moisture losses. Per temperature step, respiration was measured three times per sample and a mean value was used for further analysis. A more detailed description of the measurement system can be found in Mayer et al. (2017). An exponential function was fitted to the data in order to determine standardized respiration rates at 15 °C (Mayer et al., 2017).

2.7 Analysis of carbon, nitrogen, lignin, cellulose and hemicellulose

Total C and N content of litter was measured on dried 0.3 g subsamples with a TruSpec CN Analyzer (Leco Corp., St Joseph, MI, USA). The content of lignin, cellulose and hemicellulose of the litter was characterized by neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL) analysis based on the van Soest procedure (Van Soest et al., 1991, Van Soest, 1963) and according to the ANKOM Analytical Methods (Gesellschaft für Analysentechnik HLS, 2014a, Gesellschaft für Analysentechnik HLS, 2014b, ANKOM Technology, 2016). Acid detergent lignin was used as a proxy to determine the fraction of lignin. The fraction of hemicellulose was calculated as the difference of NDF and ADF , and cellulose was determined as the difference of ADF and ADL. All values are given as percentage of organic matter based on dry mass and are corrected for ash-content. Lignocellulose Index (*LCI*) was calculated according to Soong et al. (2015),

$$LCI = \frac{L}{L + (C + HC)} \tag{2.03}$$

with *L*, *C* and *HC* representing the litter fractions of lignin, cellulose and hemicellulose. Analyses were conducted using the ANKOM 200 Fiber Analyzer (ANKOM Technology, Macedon, NY, USA) at the Institute of Animal Nutrition, Livestock Products and Nutrition Physiology (TTE) at the University of Natural Resources and Life Sciences, Vienna. A more detailed description of the analysis for ADL, ADF and NDF can be found in the Supplements.

2.8 Microbial biomass and extractable carbon and nitrogen

Fumigation extraction method (Vance et al., 1987, Witt et al., 2000) was used to determine microbial biomass C (MicC) and N (MicN) of litter samples (from 12 g litter bags). Two sets of 1 g subsamples were prepared for each sample; one set was fumigated with 40 ml of ethanol free chloroform for 24 hours. The second set served as control set and was not fumigated. Subsamples were extracted in 25 ml of 0.5 M K2SO4 and shaken in a rotary shaker for 2 hours. Extracts were filtered (Whatman® Grade 589/2, Ashless Filter Paper) and frozen until they were analyzed for total extractable C (TEC) and total extractable N (TEN) using a Shimadzu TOC-L (Shimadzu Corp., Kyoto, Japan). Microbial biomass C and microbial biomass N were calculated as the difference of the fumigated and the non-fumigated TEC and TEN values, respectively. A correction of MicC and MicN was made via efficiency factors of 0.45 (Vance et al., 1987) and 0.54 (Brookes et al., 1985), respectively.

2.9 Statistical Analysis

Statistical analysis and plots were made using *R* and *R Studio* (R Core Team, 2019) in the version R-3.6.1. Level of significance was determined as a p value < 0.05.

2.9.1 Mass loss

Mass loss of litter was evaluated as the difference between initial weight of litter dry mass and its respective weight on the sampling dates (July 24th and December 8th). To test for significant differences between mass loss of litter type, one-way analyses of variance (ANOVA) were performed followed by Tukey's HSD test as post-hoc test. Assumptions for ANOVA (i.e., homogeneity of variances and normality of residuals) were verified visually prior to analysis and by means of Bartlett's test and Shapiro Wilk's test. In case the assumptions of ANOVA were not met, Kruskal-Wallis test by ranks and pairwise Wilcoxon test as post-hoc test were used. To determinate significant effects of the litter translocation experiment, a two-way ANOVA with litter mass loss as dependent, and litter type and stand as independent variables were used. Testing also included an interaction effect of litter type and stand type. Tukey's HSD tests were used as post-hoc test.

2.9.2 Microbial respiration, DOC leaching, throughfall DOC and SOC stocks

To determine the amount of C lost by microbial respiration, average respiration rates were calculated for every sampling plot and phase. These rates were then multiplied by the number of days of the respective phase (88 days for phase 1, 137 days for phase 2). To receive the cumulated C for the entire duration of the experiment, phase 1 and phase 2 were summed up. Values for leaching of DOC from litter and for the C input via throughfall (hereafter: throughfall DOC) were summed up per plot and phase. To correct for differences in stand structure, SOC stocks (0 – 10 cm mineral soil) were normalized to stand density (i.e., number of trees), basal area and annual litterfall of each stand. Differences between stands and litter type were tested by means of one-way ANOVA followed by Tukey's HSD post-hoc test. Prior to analysis, assumptions for homogeneity of variances and normality of residuals were verified visually and by means of Bartlett's test and Shapiro Wilk's test, respectively. In case the assumptions for ANOVA were not met, a log transformation was applied. If assumptions were still not met, a Kruskal-Wallis test by ranks and a pairwise Wilcoxon test was performed. Cumulative C sums from respiration and leaching were tested for differences between litter type for each phase and in total. The experimental phases are in accordance with that of the litter mass loss experiment and mark their respective sampling dates.

2.9.3 Soil microclimate

To detect differences between stands regarding soil temperature and soil moisture, a nested linear mixed effect model was used (Pinheiro and Bates, 2000). Assumptions like homogeneity of variances and normality of residuals were controlled visually prior to analysis. Models were fitted with the *lme* function of the *nlme* package by Pinheiro et al. (2019) in *R* (R Core Team, 2019). Stand type was assigned as fixed effect. To account for the repeated and nested measurement structure, sampling plots were assigned random effects and were nested within stand type and sampling date. The model was fitted by restricted maximum log likelihood. A constant variance function structure of type *varIdent* was added whenever it helped to improve model fit (Pinheiro and Bates, 2000). Testing for the individual stand type effects was done by means of Tukey's HSD test using the *Multcompview* package (Piepho, 2004) in *R*. Throughfall sums for each stand and phase were tested by one-way ANOVA followed by Tukey's HSD test.

2.9.4 Effects of soil temperature and -moisture on microbial respiration

Effects of soil temperature and soil moisture on microbial respiration were tested by means of a linear mixed effects model (Pinheiro and Bates, 2000). The *lme* function of the *nlme* package (Pinheiro et al., 2019) in *R* (R Core Team, 2019) with a restricted maximum log-likelihood method was used to

fit the model. Different arrangements of random and fixed effects (i.e. model parameter selection) were tested by means of ANOVA and the best model was selected based on the *Akaike's Information Criterion* (AIC), the *Bayesian Information Criterion* (BIC) and log likelihood tests (Pinheiro and Bates, 2000). The best model explained microbial respiration as a function of temperature and moisture and their interaction with stand type, which were assigned fixed effects. Plots were assigned random effects, to account for a repeated measurement structure. The inclusion of a random slope per plot did not improve the model fit. An exponential relationship between microbial respiration and temperature was linearized by log transformation prior to analysis. Model goodness of fit was assessed by *marginal* R^2 and *conditional* R^2 using the *MuMIn* package (Bartoń, 2013).

2.9.5 Biochemical properties of litter

One-way ANOVA was used to test for differences in biochemical litter properties. Assumptions of homogeneity of variance and normality of residuals were tested visually and by using Bartlett's test and Shapiro-Wilk's test, respectively. As a post-hoc test, Tukey's HSD was performed. In case the assumptions for ANOVA were not met, data were log transformed. If assumptions were still not met, a Kruskal-Wallis rank sum test followed by pairwise Wilcoxon test as a post-hoc test was performed.

3 Results

3.1 Litter mass loss

During phase 1 of the study, mass loss of *home* litter was 7.9 ± 0.63 (mean ± SE), 6.6 ± 1.18 and 4.4 ± 0.64 % for S, DF and L, respectively (Fig 8). Mass loss did not differ significantly between litter types. However, there was a tendency of slower decomposition in L litter (*p* value = 0.083).

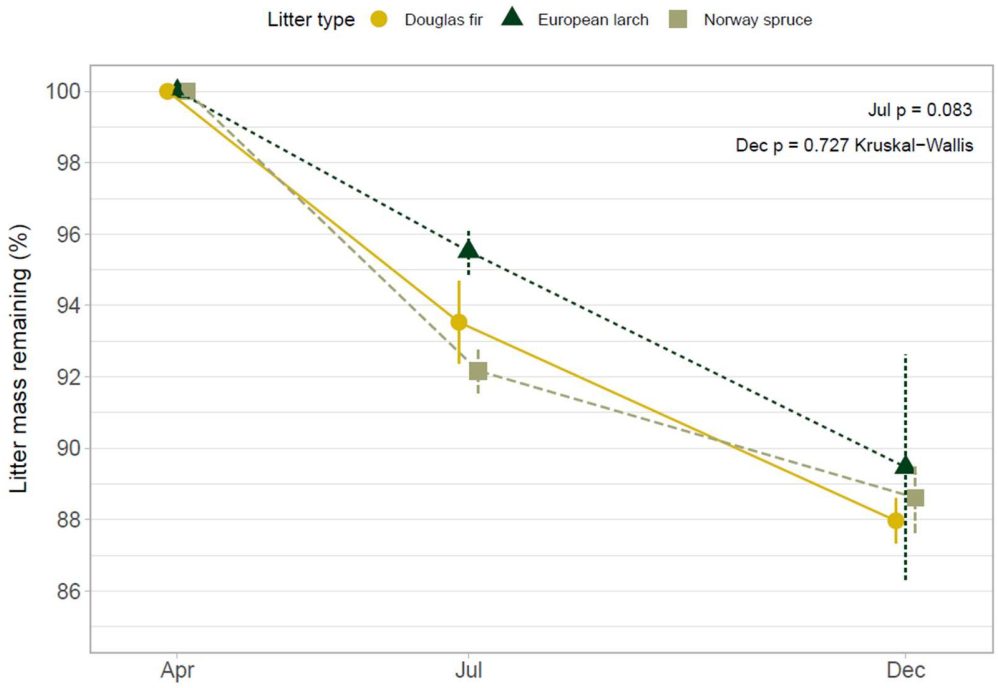

Figure 8. Litter mass remaining from decomposition of Norway spruce, Douglas fir and European larch litter in their respective stands of origin (home litter) after 14 (July) and 34 weeks (December) of incubation. Litter bags were filled with 2 g of dried litter (30 °C), ANOVA and Tukey's HSD post-hoc test were used to determine differences between litter types. Number of litter bags per stand and sampling date: n = 6.

For the second sampling in December (phase 1 + 2), mass loss was highest for DF with 12.2 ± 0.66, followed by S 11.4 ± 0.99 and L 10.4 ± 3.16 % (Fig. 8). Again, differences between species were not significant. Mass loss of S was found to level off after phase 1 (Fig. 8). Correspondingly, average C loss from the litter bag experiment was highest for DF, followed by S, and was lowest for L litter with 114.6 ± 27.99, 107.8 ± 8.18 and 94.0 ± 7.09 of mg C g^{-1} DM of litter, respectively.

In the reciprocal litter transplant experiment (*away* litter), highest mass loss after phase 1 (April) of the study was observed for litter incubated in the L stand, with an average of 8.2 ± 0.80 % for all litter types (Fig. 9b). Litter that was decomposed in the S and DF stand displayed lower mass loss, with 6.9 ± 0.61 and 6.7 ± 0.68 %, respectively (Fig. 9a, c). Litter of DF and S incubated in the L stand had particularly high mass loss with 10.2 ± 0.92 for DF and 10.0 ± 0.98 % for S (Fig. 9b). DF litter mass loss was also significantly enhanced in the L (10.2 ± 0.92 %) stand compared to the S (9.0 ± 0.62 %) and DF stand (6.6 ± 1.2 %). Mass loss of L litter (4.7 ± 0.52 %) was consistently lower among all stands, followed by S (8.5 ± 0.55 %) and DF litter (8.6 ± 0.62 %). After phase 1, for none of the litter types the mass loss was found to be higher when incubated in *home* than *away*.

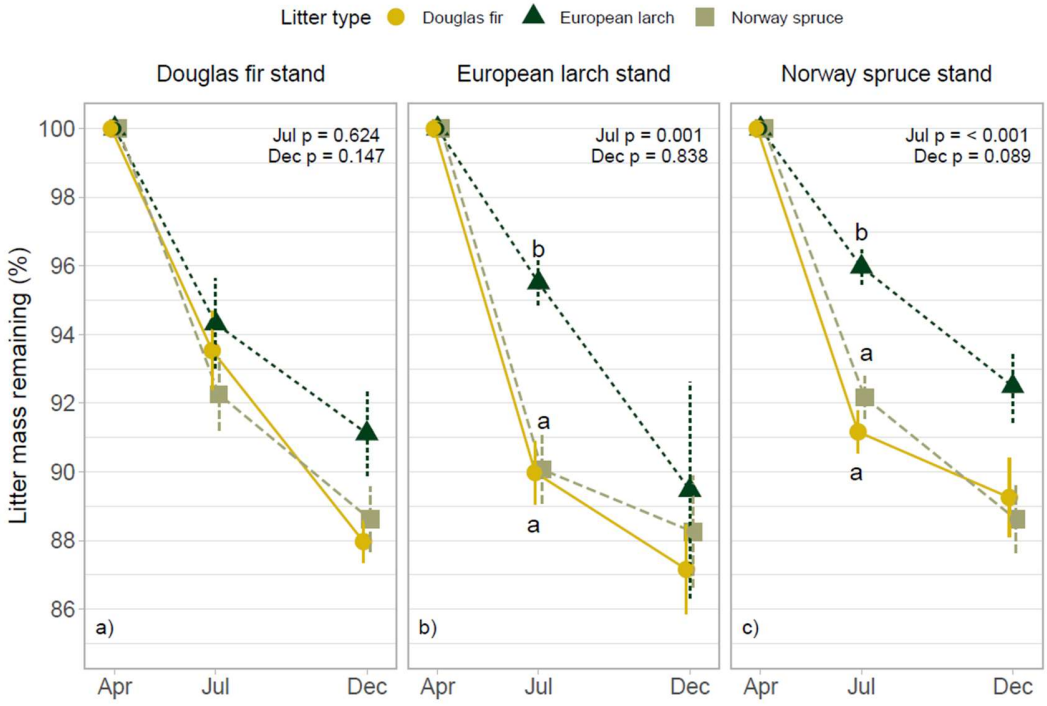

Figure 9. Litter mass remaining from decomposition of Norway spruce, Douglas fir and European larch litter in a litter translocation experiment after 14 (July) and 34 weeks (December) of incubation. Litter bags of each litter type were incubated in the a) Douglas fir stand, b) the European larch stand and c) the Norway spruce stand. ANOVA and Tukey's HSD post-hoc test were used to determine differences between litter types. Different letters indicate significant differences between litter type. Number of litter bags per stand and sampling date: n = 6.

After phase 2 (December) of the study, average mass loss of all litter types was again found to be highest in the L stand (Fig. 9b), with 11.8 ± 1.22, followed by DF (10.8 ± 0.64 %) and S (9.9 ± 0.71 %). No significant differences in mass loss between litter types per stand were found; however, a

tendency (*p* value = 0.09) towards slower decomposition of L litter was noticed in the S stand (Fig. 9c). Higher mass loss in *home* than *away* decomposition in December was only found for L litter (Fig. 9b).

Mass loss of S and DF litter was clearly levelling off in phase 2 in the L and S stands, while litter decay for L remains rather constant (Fig. 9b, c). This, however, does not apply for litter decomposition in the DF stand, where mass loss was generally reduced for all litter types but remained rather constant (Fig. 9a).

3.2 Microbial respiration

In phase 1 of the study, total sums of microbial respiration from litter were significantly lower in L when compared to S and DF (Table 2). In phase 2, no significant differences in microbial respiration could be observed between stands. Respiration was found to decline in DF after phase 1, while rates remained stable for S litter. Larch litter showed an increase in respiration in phase 2. Highest respiration rates were found in S. Overall, total C loss from microbial respiration was estimated at 171.1 (± 11.68), 142.3 (± 8.18) and 119.2 (± 5.05) mg C g^{-1} DM for S, DF and L respectively; significant differences were observed between S and L.

Table 2. Cumulative C loss from microbial respiration (mg C g^{-1} DM litter) in Douglas fir, Norway spruce and European larch stands for two phases of the study. Given are mean values ± standard error of the mean. When assumptions of ANOVA were not met, data were log-transformed. Tukey's HSD test was used as a post-hoc test. Letters indicate significant differences between stands, whereas *a* represents the lowest mean.

	Douglas fir	*Norway spruce*	*European larch*	*p* value
Phase 1				
Apr 24 – Jul 27	74.1 ±4.83 b	86.0 ±8.27 b	45.5 ±3.70 a	<0.001
Phase 2				
Jul 27 – Dec 8	68.2 ±9.01	85.1 ±10.59	73.6 ±7.20	0.423
Total				
Apr 24 – Dec 8	142.3 ±8.18 ab	171.1 ±11.68 b	119.2 ±5.05 a	0.040

Microbial respiration rates, with the exception of L in phase 1, principally followed the seasonal patterns in soil temperature and soil moisture (Fig. 10). This was also confirmed by means of the linear mixed effects model, where respiration was modelled as a function of soil temperature, soil

moisture, stand type and the interaction of soil climate and stand type; both, temperature and moisture were found to be positively related to respiration. Estimated model coefficients are shown in Table 3. The model explained 45 % of variation in microbial respiration between stands, and 51 % by including variation at plot level. Comparing L to DF reveals a significant stand effect on litter respiration; moreover, the relationship between respiration and soil climate variables was significantly different among these stands. No such differences were found when comparing DF and S.

Table 3. Summary statistics of a linear mixed effects model describing CO_2 efflux from microbial respiration (mg C g^{-1} DM d^{-1}) explained as a function of soil temperature (° C), soil moisture (vol %) and their interactions with stand type. Given are the estimated model coefficients, standard errors (SE) and p values of fixed effects, standard deviation (SD) of the random effects, and model goodness of fit (n = 254).

Coefficient	Estimates	SE	*p* value
Fixed effects			
Intercept (Douglas fir)	-0.66	0.12	0.00
Soil temperature (Douglas fir)	0.06	0.01	0.00
Soil moisture (Douglas fir)	0.03	0.00	0.00
Norway spruce	0.14	0.17	0.42
European larch	0.60	0.17	0.00
Norway spruce:soil temperature	-0.01	0.01	0.60
European larch:soil temperature	-0.03	0.01	0.00
Norway spruce:soil moisture	-0.00	0.01	0.78
European larch:soil moisture	-0.02	0.01	0.00
Random effects			
SD intercept		0.08	
SD residual error		0.23	
Goodness of fit			
Marginal R^2		0.45	
Conditional R^2		0.51	

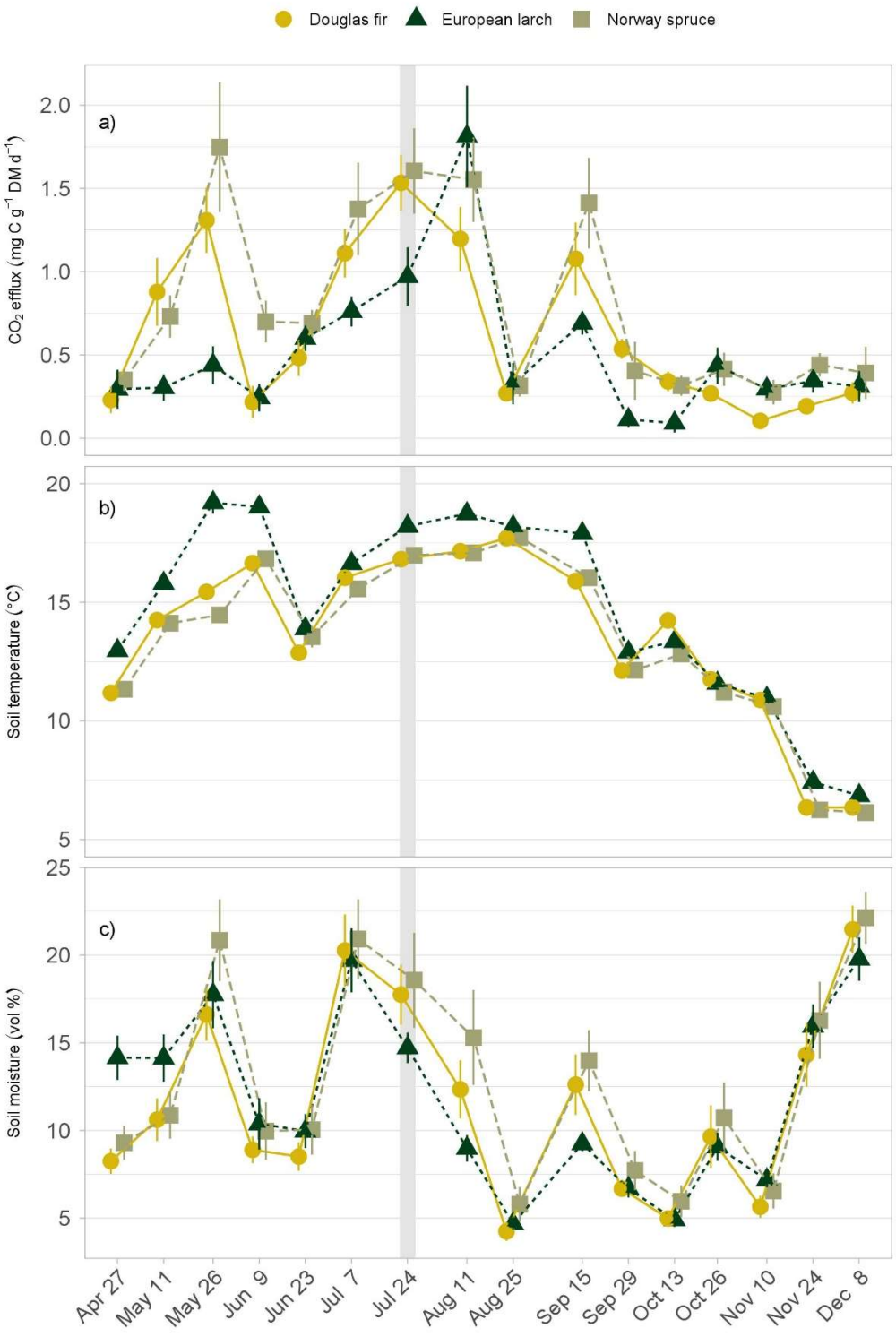

Figure 10. Average microbial respiration a), soil temperature in 5 cm depth b) and soil moisture content c) measured in Douglas fir, European larch, and Norway spruce stands from biweekly samplings. Given are mean values ± standard error of the mean. Beginning of phase 2 of the study period is marked by grey vertical line.

3.3 Litter leaching and throughfall DOC

Litter Leaching rates of DOC were insignificant between stands during phase 1 of the study (Table 4). In the second phase and in total, DOC leaching rates were found to be highest in L, followed by DF and S. Total sums of DOC leached from litter were 6.5 ± 0.76, 4.6 ± 0.29 and 3.4 ± 0.38 mg C g^{-1} DM for L, DF and S respectively. Compared to phase 1, DOC leaching in DF and S decreased in phase 2, while it kept rather constant in L.

Throughfall DOC was observed to be significantly higher in L than in DF and S (Table 4). This applies to both phases and matches with the higher amounts of throughfall measured in the L stand (Table 6). In general, input of throughfall DOC was related to throughfall dynamics. Less input was therefore observed in phase 2, which is in accordance with the lower precipitation rate for this period. In total, average sums for throughfall DOC were 8.5 ± 0.12, 3.7 ± 0.66 and 3.1 ± 0.30 mg C g^{-1} DM in L, DF, and S, respectively. The DOC input by throughfall for L was higher than the measured litter leaching of DOC (Table 4).

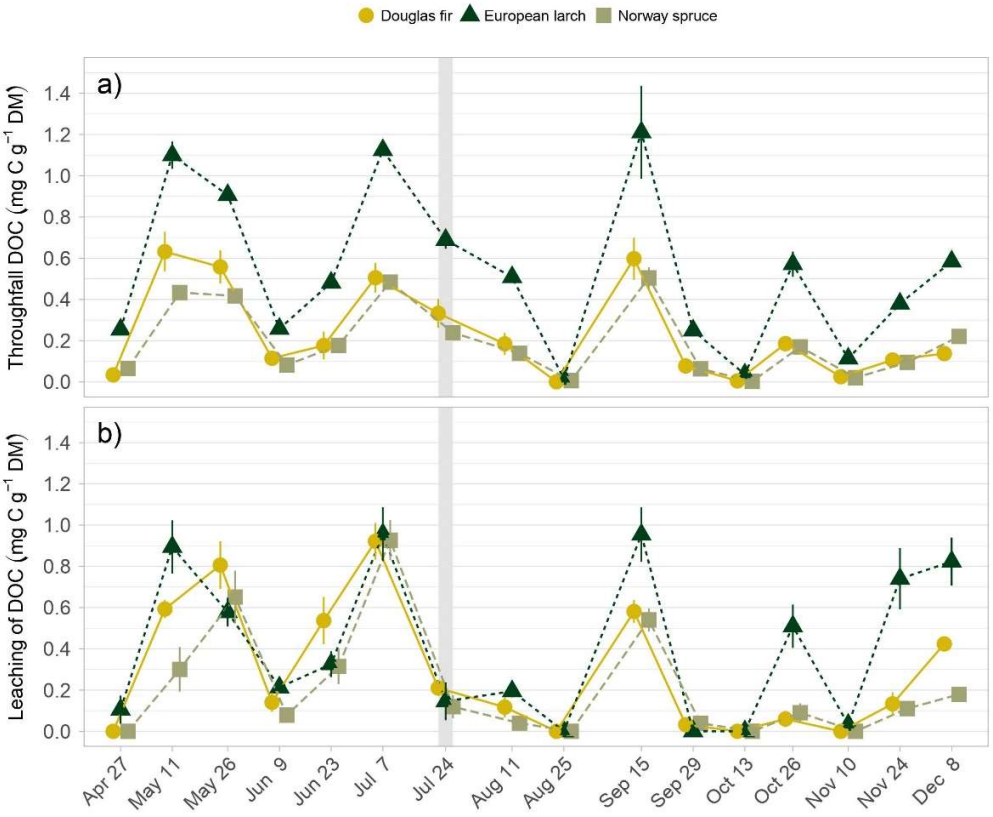

Figure 11. Average input rates of throughfall derived dissolved organic carbon (DOC) a) and litter leaching of dissolved organic carbon b) from biweekly samplings in European larch, Douglas fir and Norway spruce stands. Given are mean values ± standard error of the mean. Beginning of phase 2 is marked by grey vertical line.

Table 4. Litter leaching of dissolved organic carbon (DOC) and throughfall DOC in mg C g^{-1} DM litter. Given are mean values and ± standard error of the mean for two phases (Phase 1 = April 27 – July 24, Phase 2 = July 24 – December 8) of the study and in total. When assumptions of ANOVA were not met, data were log-transformed. Tukey's HSD test was used as a post-hoc test. Letters indicate significant differences between stands; *a* represents the lowest mean.

	Phase 1				Phase 2				Total			
	DF	*S*	*L*	*p* value	*DF*	*S*	*L*	*p* value	*DF*	*S*	*L*	*p* value
leaching	3.2 ±0.34	2.4 ±0.28	3.2 ±0.32	0.135	1.4 ±0.10 a	1.0 ±0.12 a	3.3 ±0.46 b	< 0.001	4.6 ±0.29 a	3.4 ±0.38 a	6.5 ±0.76 b	0.002
throughfall	2.4 ±0.42 a	1.9 ±0.15 a	4.8 ±0.13 b	< 0.001	1.3 ±0.24 a	1.2 ±0.15 a	3.7 ±0.14 b	< 0.001	3.7 ±0.66 a	3.1 ±0.30 a	8.5 ±0.12 b	< 0.001

DF = Douglas fir, *S* = Norway spruce, *L* = European larch.

3.4 Soil microclimate and throughfall

Soil temperature showed a clear seasonal pattern, with warmest temperatures in spring and summer months (Table 5). Throughout the study, soil temperature was found to be significantly elevated in L when compared to DF and S. No differences were found between DF and S. Average soil temperature was 14.6 ± 0.40, 13.5 ± 0.35 and 13.3 ± 0.36 °C in L, S and DF, respectively. The observed mean temperature in the L stand compared to DF and S was found to be around 1.2 °C warmer.

Soil moisture did not differ between stands in phase 1 of the study (Table 5). In phase 2, soil moisture was significantly lower in L when compared to S but did not differ significantly from DF. Higher soil moisture was generally observed in phase 1. Average soil moisture throughout the study was 11.7 ± 0.56, 11.4 ± 0.61 and 12.8 ± 0.69 vol % in L, DF and S, respectively.

In phase 1, differences in litter moisture were not significantly different between stands, but a trend for moister L litter was present (Table 5). In phase 2, litter moisture content of L was found to be significantly above DF and S. No differences were found between DF and S. The seasonal pattern in litter moisture content was similar to that of soil moisture content, with higher values observed in phase 1. Throughout the study, average litter moisture was highest in L with 44.4 ± 4.65 grav %, followed by S with 33.5 ± 3.44 and DF 32.8 ± 3.50 grav %.

Throughfall was found to be significantly different between L and DF, with highest amounts in L (Table 6). More throughfall was observed for the time between April and July. Total throughfall was on average 1608.1 ± 8.22, 1375.7 ± 41.8 and 909.5 ± 52.5 l m^{-2} in L, S and DF, respectively.

Table 5. Average (mean ± standard error) soil temperature (°C) in 5 cm depth, soil moisture in 0-7 cm depth (vol %) and moisture content of the litter layer (grav %) in Norway spruce, Douglas fir and European larch stands for different phases of the study. Different letters indicate significant differences between stands. Repeated measure ANOVA with mixed model structure was used to test for differences between stands. Letters indicate significant differences; *a* represents the lowest mean. Respective p values can be found in the supplements (Table 11)

	Temperature			Soil moisture			Litter moisture		
	Norway spruce	*Douglas fir*	*European larch*	*Norway spruce*	*Douglas fir*	*European larch*	*Norway spruce*	*Douglas fir*	*European larch*
Phase 1									
Apr 24 – Jul 27	14.7 ±0.30 a	14.8 ±0.31 a	16.5 ±0.37 b	14.4 ±1.03	13.0 ±0.87	14.4 ±0.71	39.2 ±4.64	38.1 ±3.96	47.7 ±7.43
Phase 2									
Jul 27 – Dec 8	12.2 ±0.55 a	12.5 ±0.55 a	13.1 ±0.58 b	11.6 ±0.90 b	10.2 ±0.83 ab	9.6 ±0.70 a	29.7 ±4.58 a	29.3 ±5.03 a	42.1 ±6.21 b
Total									
Apr 24 – Dec 8	13.3 ±0.36 a	13.5 ±0.35 a	14.6 ±0.40 b	12.8 ±0.69	11.4 ±0.61	11.7 ±0.56	33.5 ±3.44 a	32.8 ±3.50 a	44.4 ±4.65 b

Table 6. Throughfall (l m^{-2}) in Norway spruce, Douglas fir and European larch stands for different phases of the study. Given are mean values ± standard error of the mean. One-way ANOVA was performed to test for significant differences. Tukey's HSD was used as a post-hoc test. Letters indicate significant differences whereas *a* represents the lowest mean; p values can be found in the supplements (Table 11).

	Norway spruce	*Douglas fir*	*European larch*
Phase 1			
Apr 24 – Jul 27	811.4 ±20.63 ab	558.8 ±31.42 a	944.8 ±8.26 b
Phase 2			
Jul 27 – Dec 8	534.3 ±21.15 ab	350.7 ±21.30 a	663.2 ±9.71 b
Total			
Apr 24 – Dec 8	1375.7 ±41.77 ab	909.5 ±52.53 a	1608.1 ±8.22 b

3.5 Biochemical properties of litter

Biochemical properties of litter were analyzed after one week (April 2018), 14 weeks (July 2018) and 34 weeks (December 2018) of litter bag incubation in the field and are given in Table 7.

For the first sampling date, significant differences between total C and total N content of all litter types were found. The C:N ratio in the beginning of the incubation in April was significantly narrower for DF and was 58.3 ± 0.56, 51.8 ± 0.92 and 33.2 ± 0.24 for L, S and DF, respectively. Carbon content of the litter was decreasing with time of incubation, while N content increased. The litter C:N ratio throughout the study therefore converged for all species, resulting in 41.5 ± 0.42 for S, 39.8 ± 0.84 for L and 27.7 ± 0.39 for DF litter in December 2018.

Content of TEC increased for DF and L throughout the study period, with strongest increase found in L litter, showing significantly higher concentrations in December. Total extractable C was found to remain stable in S until July but increased considerably afterwards. Total extractable N was significantly higher for DF litter in April, then declined for all species in July and accumulated again by December, where no significant differences between species were found. Microbial biomass C was significantly different for all litter types in the beginning and showed an increase from April to July. In December, significant differences between species in MicC content had vanished and showed a further increase for S, a clear decline for DF and remained stable for L litter. Initial MicN was found to be significantly higher in DF litter when compared to S and L litter. An increase in MicN was observed among all species in July, and a further increase in MicN was recognized in S and L litter in December whereas MicN declined in DF.

Table 7. Biochemical properties of Norway spruce, Douglas fir, and European larch litter, measured at 3 sampling dates in 2018. Given are mean values and ± standard error of the mean. Equivalents for cellulose-, hemicellulose- and lignin fractions were conducted according to van Soest procedure (1991, 1963) for the first sampling date only. R_{15} represents litter respiration rate at a temperature of 15 °C. One-way ANOVA was performed to test for significance followed by Tukey's HSD as a post-hoc test. When assumptions for ANOVA were not met, data were log-transformed. When assumptions were still not met, a Kruskal-Wallis rank sum test followed by pairwise Wilcoxon as a post-hoc test was performed. Letters indicate significant differences; *a* represents the lowest mean.

		April 24			July 27			December 8		
	Unit	*Norway spruce*	*Douglas fir*	*European larch*	*Norway spruce*	*Douglas fir*	*European larch*	*Norway spruce*	*Douglas fir*	*European larch*
Total C content	mg g^{-1} DM	536.1 ± 1.47 a	551.9 ± 1.13 b	557.2 ± 1.22 c	523.2 ±4.02	520.7 ±11.1	512.1 ±17.0	518.4 ±8.60	511.3 ±12.30	501.7 ±7.09
Total N content	mg g^{-1} DM	10.4 ± 0.18 b	16.7 ± 0.11 c	9.56 ± 0.10 a	11.3 ±0.11 a	17.3 ±0.32 b	10.9 ±0.32 a	12.5 ±0.27 a	18.4 ± 0.30 b	12.6 ±0.39 a
C : N ratio	-	51.8 ± 0.92 b	33.2 ± 0.24 a	58.3 ± 0.56 b	46.3 ±0.37 b	30.1 ±0.46 a	47.0 ±1.41 b	41.5 ±0.42 b	27.7 ± 0.39 a	39.8 ±0.84 b
Total E1tractable C	mg g^{-1} DM	0.9 ± 0.04 b	1.0 ± 0.03 b	0.8 ± 0.02 a	0.9 ±0.04 ab	1.1 ±0.12 b	0.8 ±0.05 a	1.7 ±0.12 a	1.7 ± 0.04 a	2.2 ±0.17 b
Total E1tractable N	mg g^{-1} DM	0.2 ± 0.01 a	0.3 ± 0.01 b	0.2 ± 0.00 a	0.1 ±0.00 a	0.2 ±0.01 c	0.1 ±0.01 b	0.3 ±0.02	0.4 ± 0.02	0.4 ±0.04
Microbial C	mg g^{-1} DM	2.8 ± 0.32 a	5.4 ± 0.14 c	4.0 ± 0.39 b	7.3 ±0.67 a	13.0 ±0.60 b	10.4 ±1.22 ab	10.9 ±0.51	8.7 ± 0.54	10.0 ±0.82
Microbial N	mg g^{-1} DM	0.4 ± 0.04 a	0.9 ± 0.04 b	0.6 ± 0.05 a	0.9 ±0.08 a	1.6 ±0.08 b	1.1 ±0.14 a	1.5 ±0.11	1.3 ± 0.07	1.3 ±0.04
MicC : MicN ratio	-	7.1 ± 0.46 b	6.5 ± 0.37 a	7.2 ± 0.33 b	8.5 ±0.34 a	8.2 ±0.33 a	9.7 ±0.81 b	7.4 ±0.71	6.5 ± 0.48	7.4 ±1.46
R_{15}	mg C g^{-1} DM d^{-1}	1.2 ± 0.08 b	1.1 ± 0.07 b	0.6 ± 0.05 a	0.9 ±0.04 b	1.0 ±0.07 b	0.6 ±0.05 a	0.7 ±0.03	0.7 ± 0.02	0.7 ±0.07
Cellulose[a] content	mg g^{-1} DM	244.7 ±13.42	200.9 ±17.42	225.7 ±15.85						
Hemicellulose[b] content	mg g^{-1} DM	65.7 ± 5.85	80.27 ±11.05	69.9 ±21.65						
Lignin[c] content	mg g^{-1} DM	308.7 ±14.35 a	378.5 ±11.44 b	408.4 ±16.30 b						
Lignin : N ratio	-	29.8 ± 1.28 b	22.8 ± 0.61 a	42.7 ± 1.59 c						
Lignocellulose Inde1	-	0.50 ± 0.02 a	0.57 ± 0.02 ab	0.58 ± 0.02 b						

C = Carbon. *N* = Nitrogen. *DM* = litter dry mass, *MicC* = Microbial carbon, *MicN* = Microbial nitrogen.
[a] acid-detergent fibre – acid-detergent lignin, in % of DM, ash-corrected.
[b] neutral-detergent fibre – acid-detergent fibre, in % of DM, ash-corrected.
[c] acid-detergent lignin, in % of DM, ash-corrected. Ash contents = *S* 8.4 ± 0.22 %, *DF* 8.1 ± 0.06 %, *L* 5.6 ± 0.08 %.

The ratio of MicC to MicN also illustrates this development over time, where higher values indicate higher contents of TEN. For the sampling in December, MicC:MicN ratios were 7.4 ± 1.46, 7.4 ± 0.71 and 6.5 ± 0.48 for L, S and DF respectively, and did not show significant differences between litter types.

Standardized respiration rates at 15 °C from laboratory incubations were 0.6 ± 0.05, 1.1 ± 0.07 and 1.2 ± 0.08 mg C g^{-1} DM d^{-1} for L, DF, and S in April and declined slightly in July; for both sampling dates, R_{15} values were significantly lower in L than in DF and S. Respiration rates for December sampling were similar among tree species. The lower respiration rates observed for L kept almost constant during the complete study period, while those of S and DF were steadily declining.

Cellulose, hemicellulose and lignin measurements were only conducted for the first sampling date in April 2018. Significant differences were found for initial lignin content, being significantly lower for S (30.9 ± 1.44 %) than for DF (37.9 ± 1.14 %) and L (40.8 ± 1.63 %). Also, Lignin:N ratios showed significant differences between litter types, with lowest values for DF (22.8 ± 1.28 %) followed by S (29.8 ± 1.28 %) and highest values for L litter (42.7 ± 1.59 %).

3.6 Soil organic C stocks and forest floor C dynamics

Data for SOC stocks and forest floor mass C for each stand are listed in Table 1. In a depth of 0 to 10 cm, C stocks appear to be highest for S with 3162.6 ± 363.71 g m^{-2}, while DF and especially L demonstrate lower SOC stocks with 2447.4 ± 155.28 and 2401.6 ± 141.89 g m^{-2}, respectively.

However, stand structure needs to be considered when comparing the SOC stocks as it is linked to the potential C input of the respective stand. Stand density and basal area (Table 1) varied among species. Annual aboveground litterfall was found to increase according to stand density and needle biomass (Table 1) and was on average 115.4 ± 4.62, 261.4 ± 9.38 and 304.6 ± 16.26 g DM m^{-2} for L, DF and S, respectively. Basal area however is not related to litterfall (DF > S > L) but is representative for productivity of aboveground biomass.

Soil OC stocks were normalized to stand parameters, by dividing mineral SOC stocks from 0-10 cm depth by annual litterfall, stand density and basal area. This revealed that relative to litterfall, SOC stocks were highest for the L stand and significantly differed from S and DF, with 20.8 ± 1.23, 10.4

± 1.19 and 9.4 ± 0.59 kg C kg^{-1} litterfall, respectively (Fig. 12). Accounting for the variation in productivity, basal area normalized stocks were also found to be L > S > DF, and significantly higher for L than for DF with 903.8 ± 60.90, 703.2 ± 78.56 and 520.2 ± 65.18 kg C m-2 for L, DF and S, respectively (Fig. 13).

Carbon stocks normalized to stand density did not differ significantly and were 36.4 ± 3.90 for L, 32.5 ± 3.57 for DF, and 29.6 ± 3.93 for S kg C per tree (Fig. 14).

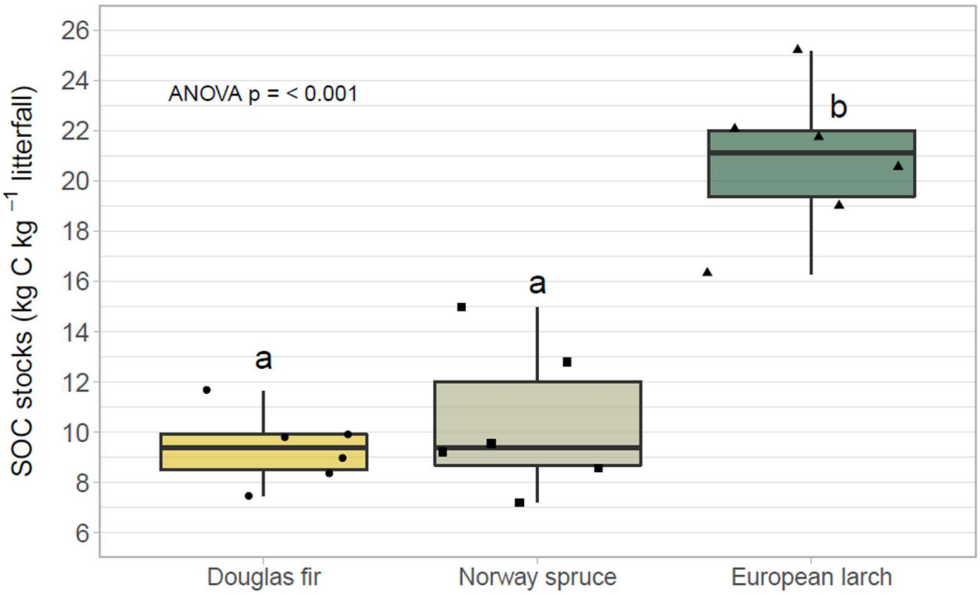

Figure 12. Soil organic carbon (SOC) stocks (kg m^{-2}) in 0-10 cm mineral soil depth normalized to annual litterfall (kg m^{-2}) measured in Douglas fir, Norway spruce, and European larch stands. Differences between stands were tested by means of one-way ANOVA and Tukey's post-hoc test. Different letters indicate significant differences between stands.

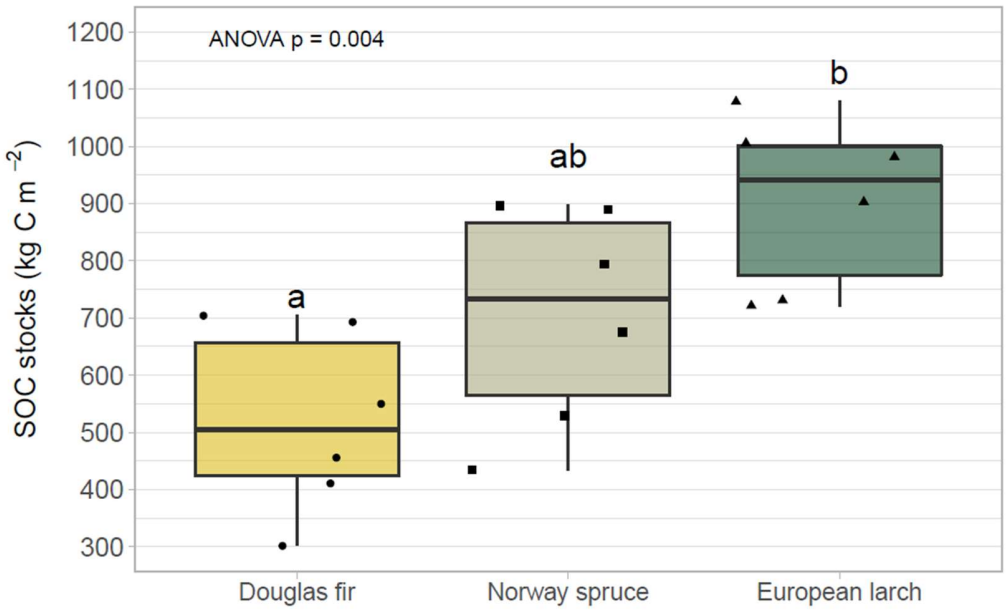

Figure 13. Soil organic carbon (SOC) stocks (kg C ha^{-1}) in 0-10 cm mineral soil depth normalized to basal area in m^{-2} ha^{-1} measured in Douglas fir, Norway spruce, and European larch stands. Differences between stands were tested by means of one-way ANOVA and Tukey's post-hoc test. Different letters indicate significant differences between stands.

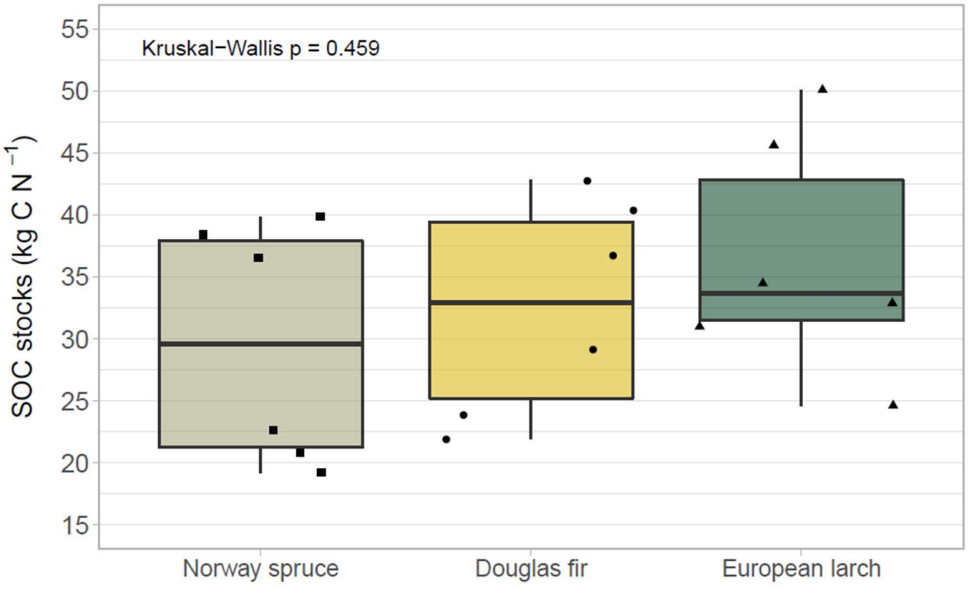

Figure 14. Soil organic carbon (SOC) stocks (kg C ha^{-1}) in 0-10 cm mineral soil depth normalized to stand density (N ha^{-1}) measured in Douglas fir, Norway spruce, and European larch stands. To test for differences between stands, a Kruskal-Wallis rank sum test was performed.

Mean residence times for forest floor mass shown in Table 8 were found to be highest for the L stand, followed by S and DF. Consequently, C stored in the average forest floor mass for L remains in the litter layer for more almost 5 years, followed by S with 4.2 ± 0.38 and DF with 3.3 ±0.32 years.

Mean turnover rates demonstrate corresponding values; DF turns over roughly one third of its forest floor mass per year, whereas and S and L are turning over only one fifth of its average standing litter layer per year. Turnover rates of forest floor C are similar across species and show a turnover of 30 % of C stored in the forest floor.

Table 8. Residence times and turnover rates of the average standing forest floor mass (O_L + O_F, g m^{-2}) and forest floor C (g m^{-2}) in Norway spruce, Douglas fir and European larch stands. Values were calculated according to Huang et al. (2011). Given are mean values in years ± standard error of the mean.

	Unit	*Norway spruce*	*Douglas fir*	*European larch*
Residence time				
Forest floor mass	yr	4.7 ±0.39	3.7 ±0.38	5.6 ±0.93
Forest floor C	yr	4.2 ±0.38	3.3 ±0.32	4.8 ±0.76
Turnover rate				
Forest floor mass	yr^{-1}	0.2 ±0.02	0.3 ±0.03	0.2 ±0.04
Forest floor C	yr^{-1}	0.3 ±0.02	0.3 ±0.03	0.3 ±0.05

O_L = Humus litter layer, O_F = Humus fermentation layer.

4 Discussion

In this study, litter decomposition and its relation to SOC storage was investigated for S, L and DF stands in the Vienna Woods. Decomposition processes were studied *in situ* using litter bags, CO_2 measurements and lysimeters and were related to litter biochemical- and microclimatic parameters.

4.1 Litter Mass loss

The litter bag experiment revealed notably differences in mass loss rates and mass loss dynamics between the investigated tree species. Larch litter was found to decompose substantially slower but contrasting to S and DF did not show retarding mass loss rates in the second phase of the experiment (Fig. 8). Moreover, L litter also exhibited the highest overall decline in total C contents (Table 7). Differences in mass loss between DF and S were marginal, with a slightly higher loss for DF of less than 1 % when compared to S. Over the course of 9 months, the average mass loss for all litter types was 10.8 % (Fig. 8).

The mass loss of *home* litter indicated an overall slower litter decomposition for L compared to S and DF litter, respectively (Fig. 8). The high variance of L after phase 2, however, mitigated the statistical decisiveness: Two samples had to be cleaned thoroughly from large amounts of mineral soil inside the litter bags, which presumably led to additional mass loss. Hence, it might be that decomposition of L litter after phase 2 is slightly overestimated.

Litter chemical composition showed significant differences between species and may have largely controlled mass loss: The high lignin content and wide C:N ratios found in L litter are associated with slow decomposition and would classify this litter to be of *low quality* (Cotrufo et al., 2010a, Melillo et al., 1982, Prescott, 2010). Litter quality, especially litter lignin content, was also rendered an important factor controlling decomposition during a common garden experiment by Hobbie et al. (2006), where a similar pattern in mass loss was found for DF, S, and L litter (DF > S > L).

For the investigated litter types, the lignin:N ratios were found to correspond to litter mass loss rates, which is in accordance to Melillo et al. (1982). Contrary to findings from previous studies (e.g. Preston et al., 2009b, Soong et al., 2015), the LCI, however, only partly corresponded to mass loss

rates in this study; namely when N contents in litter were initially low: Spruce litter had the lowest LCI (0.50) and showed a rather high mass loss, whereas a low mass loss at a correspondingly high LCI (0.58) was found in L. Despite an LCI similar to that of L litter (0.57), the highest mass loss was found in the N-rich DF. This suggests the availability of N to be a more important controlling factor for decomposition dynamics in this study than the initial content of lignin and holocellulose. This agrees to the findings of Voříšková et al. (2011), who reported N rather than lignin to be the main factor determining the growth of a lignin decomposing fungi hence controlling mass loss.

Total extractable N contents were declining for all litter types from April to July, whereas total N did not change for DF or slightly increased for S and L, respectively (Table 7). Nitrogen concentrations are known to increase during litter decomposition (Berg and McClaugherty, 2014); they can also increase due to N incorporation from external sources, such as throughfall or microorganisms (Pei et al., 2019, Zeller et al., 2000). Like total N, MicN increased for all species in July, implying N immobilization by incorporation of extractable N into microbial biomass (Table 7). An increase in MicN was found to continue for S and L after July, whereas DF showed a decrease in MicN.

How litter chemistry and N contents in detail affect decomposition and C use efficiency remains difficult to estimate; especially in field studies, relationships were found to vary considerably: Microbial community composition and succession as well as enzyme activity may determine many aspects of decomposition (Moorhead and Sinsabaugh, 2006, Voříšková et al., 2011). On the contrary, findings from Cleveland et al. (2014) suggest microbial community composition to be less important for litter decomposition than are litter quality and climate.

The reciprocal litter translocation experiment (*away* litter) was conducted to distinguish between the influence of stand properties (e.g., climate) and litter quality on litter decomposition. Interestingly, a tendency (p value = 0.09) for enhanced decomposition of L litter when incubated in the DF stand was observed after phase 1, even though the overall mass loss for all litters was weakest in the DF stand (Fig. 9a). It is assumed that primarily site-specific conditions, such as the decomposer community along with the slightly higher soil pH values (Table 1) are responsible for the increased decomposition of L litter in the DF stand (Laganière et al., 2010); as microclimate was observed to be similar in the S stand (Fig. 9b, c and Table 5) where no acceleration in mass loss for L litter was observed. The unexpected acceleration in mass loss for L may also be linked to litter mixture effects: Non-additive effects occur when litter mixtures influence each other in their decomposition. Such effects include the fungal transfer of nutrients between litter types, promoting or inhibiting microbial activity by

certain litter compounds or the positive reaction of soil biota to increased resource diversity (Hättenschwiler et al., 2005). Given the substantial difference in N contents between DF and L, fungal transfer from DF to L litter could have led to enhanced decomposition. Such non-additive effects however strongly depend on litter species, their chemistry, and presumably nutrient availability of soils - therefore mixing effects are hardly generalizable (Cuchietti et al., 2014, Setiawan et al., 2016). In addition, Wang et al. (2019) reported effects of litter mixture to mainly be related to litter pH (H_2O) and C contents, which are vital drivers of microbial community structure. Initial C contents differed significantly between DF and L litter (Table 7); litter pH was not evaluated in this study but was retrieved from other publications and indeed shows quite a discrepancy between DF (pH = 5.5; Cárcamo et al., 2000) and L (pH = 4.8; Wang et al., 2019). However, litter pH and initial C contents also varied between L and S (pH = 5.4; Priha and Smolander, 1997), where no acceleration for L in the S stand was observed, which indicates a more dominant influence of litter N than litter pH or C content.

Mass loss for DF and S litter decomposing in the L stand was found to be highly accelerated in phase 1 (p value = 0.003) and at least a tendency to be enhanced (p value = 0.089) for phase 2 (Fig. 9b). This may be primarily due to microclimatic conditions in the L stand, which showed higher soil temperatures and throughfall rates than D and S stands (Tables 5 and 6). Warmer and moister conditions are known to promote microbial activity and hence accelerate decomposition (Aerts, 1997, Bani et al., 2018, Hobbie et al., 2006).

The decomposability of litter generally decreases over time, resulting in retardation of mass loss rates. This is due to changes in the chemical composition, as easily degradable compounds become depleted and structural components are proportionally enriched (Cotrufo et al., 2010a): A clear decline in mass loss after phase 1 was observed for S litter in *home* (Fig. 8) and *away* (Fig. 9a, b, c), and therefore presumably related to its chemical composition. The retardation in mass loss for DF was evident when incubated *away* (Fig. 9b, c), but only weakly pronounced in *home*. Hence, negative litter mixture effects (e.g., on decomposer community) may also be plausible.

According to the home field advantage hypothesis, litter decay occurs fastest at the site of litter origin due to specialized decomposer organisms (Ayres et al., 2009, Veen et al., 2015). Here, findings provide no evidence for this hypothesis, as mass loss was not found to be highest at *home* sites. Yet, home field advantage is also possible to occur in the opposite direction, i.e., faster decomposition when incubated *away* than at *home*, as observed in this study; this effect strongly depends on how

much litter quality and plant community from *home* and *away* sites differ (Veen et al., 2015), which partly applies to results of this study (e.g., DF and S litter incubated in the L stand). However, since the data set consists of six replicates per stand and sampling date and the decomposition duration was less than one year, it may not be sufficient for definitive conclusions concerning home field advantage. As previously mentioned for *home* litter, a slight overestimation in mass loss for two L samples is likely; the very same samples are part of the litter transplant experiment (*away* litter, Fig. 9b) and hence are also affected.

Results of the reciprocal litter transplant experiment also approve slower decomposition for L litter and further suggest chemical litter composition rather than site conditions to be a stronger control for decay, as L litter demonstrated the lowest mass loss regardless of the stand it was incubated in (Fig. 9). Nevertheless, decomposing *away* litter in the L stand showed that site conditions such as microclimate or litter mixture effects can have notable influence on mass loss rates. Litter mixture effects and their influence on decomposition remain to be a matter of further investigation due to an anticipated increase in mixed stands in European forests.

A comparison of litter chemical composition data with other studies investigating the same species needs to be treated with caution. Litter chemical composition is influenced by environmental conditions (Aerts, 1997, Berg and McClaugherty, 2014) and also varies depending on what time during the year the leaves or needles were harvested from the branch or for how long they have been on the ground prior to analysis (Berg and McClaugherty, 2014). Moreover, a variety of methods exists to assess litter composition and therefore hinder the comparison of studies. This holds true especially for the determination of lignin, where a variety of techniques (e.g., Klason lignin, infrared reflectance spectroscopy) yielding different results is used (Berg and McClaugherty, 2014, Margida et al., 2020). The van Soest procedure (Van Soest, 1963, Van Soest et al., 1991) used in this study is well established, however the results for ADL also comprise compounds other than lignin, hence slightly overestimating true values. Furthermore, lignin contents were found to be highly variable even within the same species (Berg and McClaugherty, 2014). Nevertheless, Hobbie et al. (2006) reported similar results for litter structural compounds, although the lignin contents ranking L > DF > S where overall lower. However, measured values for lignin, cellulose and hemicellulose from this study may even slightly underestimate true values. This is due to a loss in sample material, which characterized as blank bags appearing heavier after the extraction process. Samples were ground too fine at preparation and hence some material got lost from the filter bags during analysis. Also total N contents, and accordingly, C:N ratio from Hobbie et al. (2006) were diverging from results of this study and showed

different rankings from low to high values, e.g., N contents of DF were found to be much lower and correspondingly, C:N ratio was higher than for S and L. Berg and McClaugherty (2014) reported total N to range between 0.2 and 3.0 % in woody litters, which is consistent with results here (Table 7). Higher lignin and N contents though may indicate that litter samples were already in a more advanced stage of decomposition than expected, which cannot be ruled out entirely.

By means of isotopic labelling, 19 % (Cotrufo et al., 2015) and even as much as roughly 60 % (Rubino et al., 2010) of the C that was lost during decomposition was found to enter the soil through fragmentation and leaching, stressing the importance in including these processes in litter decomposition studies. However, as fragmentation was not investigated in this study, this informational gap can be accounted for by results of the DOC leaching and SOC stocks. In addition, the investigated mass loss dynamics are in line with the calculated turnover and residence times of the forest floor (Table 8), which support findings concerning similar and faster decomposition rates for S and DF than L, provided that the system of litterfall and forest floor mass is in a steady state (Olson, 1963).

4.2 Microbial Respiration

Mineralization to CO_2 by microbial respiration was found to be the dominate pathway in C partitioning during litter decomposition, accounting for roughly 95 to 98 % of the measured C loss depending on species (Tables 2 and 4). Spruce exhibited the highest CO_2 release while L had significantly lower C losses into microbial respiration. Results demonstrate that microbial respiration partly differs between tree species: In phase 1, amounts of C lost from respiration were found to be significantly different for L than for S and DF litter. In phase 2, differences between species diminished. Corroborating the first hypothesis (H1), the results suggest chemical litter composition such as lignin, C and N contents along with microbial biomass dynamics to exert a more dominant influence on C partitioning into respiration than environmental stand conditions (i.e., temperature and moisture).

Temperature and moisture are known to be major drivers for mineralization to CO_2 by microbial respiration (Curtin et al., 2012, Reichstein and Beer, 2008). Here, roughly half of the variation in respiration was explained by temperature and moisture as shown by the linear mixed effects model.

(Table 3). This is in line with findings from measurements of forest soil respiration (e. g. Borken et al., 2002, Laganière et al., 2012). The dependency on temperature was found to decrease when soil moisture was low and hence limited microbial respiration (Mayer et al., 2014). A reduction in respiration rates was present during the sampling campaigns in June and August when soil moisture was low (Fig. 6).

According to the linear mixed effects model, microbial respiration did not differ between S and DF stands. Soil temperature between S and DF stands was found to be similar, and it is assumed that little variations of soil moisture were balanced by the stronger influence of temperature on respiration (Table 5, Fig. 6). Respiration modeled by temperature and soil moisture was significantly lower for L, although higher average soil temperatures were found in the L stand. Respiration further seemed to be somewhat decoupled from climatic influence during phase 1 (Fig. 10). Microbial respiration of L litter could have been restricted on many occasions due to the insufficient soil moisture, causing this decoupling. Surprisingly though, during phase 1, the higher soil temperatures did not seem to negatively affect average soil moisture in the L stand (Fig. 10, Table 5). Presumably, the greater amount of throughfall (Table. 6) in combination with substantially higher litter moisture (Fig. 15, Supplements) - which is related to a higher water uptake capacity of L litter (Zukswert and Prescott, 2017) - might have mitigated the temperature effect on soil moisture. Lower average soil moisture could only be found during phase 2 (Table 5). It is therefore suggested that moisture induced limitations on microbial respiration are not the determining factor for the decoupling and the overall lower microbial respiration rate in L litter.

This is also indicated by the respiration rates obtained from the laboratory incubations (Table 7). Under standardized conditions, the CO_2 release of L litter was substantially lower than of DF and S. Initial differences in respiration rates were found to converge throughout the study, resulting in similar laboratory respiration rates for all litter types by December. Contrasting to DF and S, microbial respiration of L did not decline but remain stable, even showing a slight increase in December.

According to Manzoni (2017), temperature and moisture influence decomposition by regulating microbial metabolic rates but do not affect whether C is used for growth or respiration. Instead, microbial processes and the efficiency by which C is metabolized, is suggested to be largely controlled by litter chemical composition. As shown by previous studies investigating C partitioning (e. g. Hagedorn and Machwitz, 2007, Huang et al., 2011), lignin contents, ratios of C:N and lignin:N

were found to be negatively correlated with mineralization of microbial respiration. This is consistent with results concerning L litter, and partly consistent with S and DF. The lowest lignin contents were found in S, which also showed highest overall C loss due to respiration. Both, C:N and lignin:N ratio were most favorable in DF litter, but CO_2 efflux was lower than that of S, especially in phase 2 (Tables 2).

These patterns though may be explained by including the observed temporal development of microbial biomass-, N- and C dynamics (Table 7): In DF litter, decomposition dynamics may be tightly linked to its high N contents (Berg, 2000) which promoted microbial growth (Pei et al., 2019, Voříšková et al., 2011) and led to initially high mass loss rates. A suggested high initial C use efficiency for N-richer litter supports this assumption (Manzoni, 2017). Microbial biomass of DF was highest among species in April and further increased until July (Table 7). By December, it was found to have substantially declined, which is in line with the reduction in mass loss and respiration rates for phase 2. The reduction in microbial biomass and along with it, reduced litter mass loss, is ascribed to the limitation of substrate availability for microbial growth: As decomposition progresses, easily degradable compounds have already been leached or utilized and C becomes limiting (Berg, 2000, Manzoni, 2017). In addition, N contents which positively affected degradation in the beginning delecerate decomposition at later stages, as N availability does interfere with the production of extracellular enzymes by fungal decomposers necessary to degrade lignin (Berg, 2000, Manzoni, 2017, Moorhead and Sinsabaugh, 2006). Moreover, N and lignin derived substances from later phases can form recalcitrant aromatic complexes, additionally retarding further degradation (Berg, 2000).

In contrast to DF, the microbial biomass of S litter was found to steadily increase throughout the study (Table 7), whereas mass loss declined after phase 1 (Fig. 8) and cumulative respiration rates (Table 2) were found to remain stable. It is assumed that also for S litter readily available C depleted over time, reducing the overall decomposition rate. However, initial total N was substantially lower in S litter (Table 7), explaining different effects on microbial activity: Microbial colonization and growth presumably happened at a slower pace than for DF, namely adapted to a lower nutrient availability (Manzoni, 2017), preventing the reduction of microbial abundance. Alternatively, based on the conceptual model of C allocation for low LCI litters (Soong et al., 2015), the comparably lower lignin contents of S imply an availability of more energy-rich free cellulose. Hence, providing more utilizable energy-rich substrate for decomposers. However, overall differences in cellulose and hemicellulose contents between species were insignificant (Table 7). Although microbial biomass of S litter was increasing, cumulative CO_2 production of phase 2 remained unaffected; this is presumably

clarified by C use efficiency: Even though C use efficiency is known to be lower for high C:N ratio litters (Sinsabaugh et al., 2013), recent concepts for a flexible C use efficiency suggest an increase with progressing decomposition for litters with poor N contents (Manzoni, 2017). Hence, more substrate can be assimilated into biomass than is lost as CO_2, reasoning the stable respiration rates.

Microbial biomass was also found to increase in L litter from April to July and remained rather stable until December. Similarly to S, microbial growth occurred adjusted to the low N availability. Interestingly, initial microbial biomass was significantly higher in L than in S, which implies a more efficient microbial metabolism in L. Given the poor availability of extractable C in L litter, and due to its high lignin contents presumably associated with low amounts of unprotected cellulose (Soong et al., 2015), it is assumed that throughfall derived DOC was efficiently utilized for microbial biomass assimilation. The substantially lower mass loss is associated with the poor degradability of L litter but did not show any signs of N-related retardation in later stages. The increase in CO_2 efflux for phase 2 (Table 2) is suggested to be caused by intensified lignin degradation (Soong et al., 2015, Moorhead et al., 2013). Alternatively, one particular incident prominently contributed to the cumulative CO_2 production of phase 2; a remarkably rapid increase in respiration of L litter was observed for the sampling on August 11th (Fig. 10). Since soil moisture content was declining due to dry climatic conditions at the time, this peak deems unusual; however, it must be considered that data visualized in Figure 10 represent a snapshot of the conditions at the time of sampling. The occurrence of a short precipitation event following a prolonged dry period one day prior to sampling (ZAMG, 2019) is not captured in the displayed data, but is suggested to be causative of this respiration peak. This rewetting of soil and litter after dry conditions, also known as *Birch*-effect (Unger et al., 2010), stimulates mineralization due to osmotic stress of the microbial community and rapid utilization of dead microbial biomass, resulting in a subsequent increase in CO_2 efflux. Due to dissimilarities in canopy cover and physical litter traits, changes in temperature and moisture regime may be more severe in the L stand, e.g., transmission of light and infiltration of throughfall into the mineral soil are enhanced, but simultaneously the desiccation of litter and top mineral soil occurs more rapidly, explaining a more pronounced effect for L than for S and DF.

4.3 Litter Leaching and throughfall DOC

The fraction of DOC leaching in this study ranged between 3.4 and 6.5 mg C per g of litter dry mass, which accounted for a C flux of 2-5 % from the total C fluxes by leaching and respiration. Partitioning into leaching was found to be highest for L litter (5.2 %) lowest for S (2.1 %), and for DF to be intermediate (3.2 %). Results indicate that leaching of DOC varies between species due to chemical and physical litter traits, however leaching dynamics were also strongly influenced by throughfall. Especially for L clear differences in quantity and continuity of leaching dynamics (Table 4, Fig. 11) were observed.

Depending on the method, the duration of the study, the litter species and the stage of decomposition, estimations of DOC fluxes are highly diverse. Losses by leaching of DOC have been shown to range from 1 to 40 % of the total C loss obtained from artificial leaching experiments in the laboratory (Don and Kalbitz, 2005, Hagedorn and Machwitz, 2007, Kiikkilä et al., 2012, Magill and Aber, 2000, Qualls and Haines, 1992, Soong et al., 2015). Estimates of DOC leaching from laboratory studies however rather display potential leaching rates than those expected *in situ* (Soong et al., 2015). Field studies from broadleaf litter decomposition reported C losses via DOC leaching to range between 2 and 5 % of the total C loss in oak and beech litter (Kammer et al., 2012, Tietema and Wessel, 1994), which are rather similar to those observed here.

Contrasting to findings from Don and Kalbitz (2005) and Klotzbücher et al. (2011), leaching rates in this study did, albeit weakly, relate to mass loss dynamics. For S and DF, mass loss as well as DOC production levelled off in phase 2, whereas L litter exhibited a slight increase in DOC and mass loss (Table 4, Fig. 11). Similarly, patterns in DOC leaching rates corresponded to that of microbial respiration rates in DF and L, with declining leaching and respiration rates for DF and increasing rates for L (Table 2 and Table 4).

As opposed to laboratory leaching studies, this *in situ* study design allowed to evaluate natural leaching dynamics in context with precipitation events. Leaching processes were found to be strongly driven by precipitation, and hence by the input of throughfall DOC (Fig. 11). In a synthesis, Michalzik et al. (2001) found throughfall fluxes to explain 46 % of the variation in forest floor leaching processes and hence assumed throughfall to promote organic matter leachates including C in the forest floor. Also Neff and Asner (2001) rendered that as soon as precipitation is strong enough to initiate a waterflow in the litter layer, it consequently also induces leaching. In accordance with these findings, highest DOC fluxes in this study were found in the L stand, where along with the highest throughfall

rates (Table 6) also the highest input of DOC via throughfall occurred (Table 4). During the first phase, differences in DOC leaching between species were insignificant which may also be ascribed to the significantly higher throughfall input in the L stand (Table 4). The remarkable rise in leaching for all litter types from November on (Fig. 11) is probably also associated with throughfall: precipitation rates were found to sustainably increase along with simultaneously lower soil temperatures. Therefore, it is assumed that the seasonally related change in moisture regime of soil and forest floor promoted further leaching. However, DOC fluxes have also been found to partly decouple from throughfall input, e.g., for L at sampling campaigns on July 24th and August 11th. A high amount of throughfall DOC was measured in the L stand but was not reflected in the leaching rates (Fig. 11). Due to the clearly warmer and drier conditions in the L stand for these sampling dates (Fig. 10) it is possible that part of the litter derived DOC evaporated prior to the next sampling and therefore leaching rates for L on these days are presumably underestimated.

Due to differing stand parameters such as basal area and density (Table 1), a variation in the amount of throughfall (Table 6) is consequential. Barbier et al. (2009) summarized substantial influence of basal area and stand density on the amount of throughfall across studies. Here, throughfall showed opposing patterns than basal area, e.g., lowest throughfall rates were found in DF which had the highest basal area (Table 1 and Table 6). Canopy cover was closed for DF and S, which was also reflected in higher needle biomass for these species (Table 1). Contrasting, L featured a rather open canopy as a consequence of more intense thinning necessary to cultivate L stands and its specific crown architecture (McComb, 1955); both parameters which are promoting higher throughfall rates.

The varying rates in throughfall DOC, however, were rather surprising (Fig. 11, Table 4). Throughfall DOC was not solely associated with the amount of rainwater passing through the canopies (e.g., increasing DOC fluxes with increasing throughfall), it was also strongly influenced by the respective tree species. Although S and L both had rather high throughfall rates (Table 6), the DOC input varied significantly. This is suggested to be related to canopy exchange processes such as leaching or washing off organic matter from needles and branches (Berger et al., 2008, Le Mellec et al., 2010). Amounts of needle biomass (Table 1) were ranked S > DF > L, and hence do not support this assumption. However, rather than biomass only, leaf area is assumed to influence the DOC input by throughfall. According to values obtained from Withington et al. (2006), larch needles have a specific leaf area almost twice as large (103 cm^2 g^{-1}) than that of spruce (54 cm^2 g^{-1}), which facilitates deposition of particles on the needle surface (Le Mellec et al., 2010). Douglas fir exhibited an

intermediate specific leaf area (74 cm^2 g^{-1}) explaining higher DOC input by throughfall relative to S, despite significantly lower throughfall rates.

The enhanced leaching processes within the canopy of the L stand could be assigned to high amounts of soluble phenolics in L litter, as determined by Kuiters and Sarink (1986): The content of soluble phenolics was reported to be eight times higher in L compared to S and DF, and in contrast to evergreen conifers, they are leached more rapidly from L needles. This may be associated to the physical differences suggested by Don and Kalbitz (2005): coniferous litter like S and DF have a thick epidermis and hypodermis which protects inner tissue from degradation and thus impedes leaching processes. Larch foliage however presumably offers a less advanced tissue protection causing alleviated leaching, which is indicated by its comparably lower needle life span (0.51 years, Withington et al., 2006). Findings by Zukswert and Prescott (2017) support this assumption, who found foliar traits from a North American larch species (*Larix occidentalis*) such as cuticle thickness to distinctly differ from other coniferous species like DF.

It is important to note that is not possible to directly assign DOC fluxes from this study to throughfall or actual litter leaching. Measured leaching rates may therefore compose of throughfall DOC, litter derived DOC and DOC derived from microbial processes; their origin requires extended research and therefore remains unclear; a potential target for future studies which may allow for more precise evaluation. Considering the comparatively higher DOC input by throughfall, it needs to be acknowledged that a large amount of the leaching flux of L may not be litter derived. Nonetheless, many studies have reported that L litter does have high contents of water extractable substances (e. g. Hobbie et al., 2006, Kuiters and Sarink, 1986, Voříšková et al., 2011, Zukswert and Prescott, 2017) indicating a correspondingly higher leaching potential. Accordingly, greatest decrease in total C contents was found in L litter (Table 7).

The relatively low respiration rates of L litter measured in this study (Fig. 10) further suggest, that instead of being emitted to the atmosphere, large amounts of C have entered the mineral soil via leaching. In favor of DOC from L litter entering the mineral soil instead of being respired is the lower biodegradability of L litter derived DOC, which was reported by Hagedorn and Machwitz (2007) and is accounted to the progressive microbial breakdown of lignin (Don and Kalbitz, 2005, Hagedorn and Machwitz, 2007, Soong et al., 2015).

Leaching rates of DF and S were found to be lower for phase 2, whereas leaching of L litter even increased. This might be linked to distinct origins of DOC occurring throughout the course of

decomposition: In the early stage of decomposition, DOC is mainly derived from leaching of soluble litter compounds (e.g., soluble carbohydrates, phenolics). Whereas at later stages the composition of DOC changes towards substances derived from the degradation of structural litter compounds such as cellulose or lignin, and microbial products (e. g. necromass, enzymes; Berg and McClaugherty, 2014, Don and Kalbitz, 2005, Hagedorn and Machwitz, 2007, Kalbitz et al., 2006, Magill and Aber, 2000, Soong et al., 2015). In accordance with these findings for early-stage decomposition, the analysis of litter revealed significantly higher TEC contents in DF and S (Table 7), indicating that a greater amount of labile litter C could have been potentially leached from DF and S than in L litter. The depletion of such labile litter components during the process of decomposition is a potential explanation for the lower leaching rates of DF and S in phase 2.

In contrast, the relatively continuous leaching behavior of L litter is possibly linked to an enhanced degradation of lignin which, in this magnitude, may have not occurred in the other litter types. Kalbitz et al. (2006) reported that more intense degradation leads to enhanced production of dissolved organic matter, whereas if lignin is only lightly degraded, the dissolved organic matter production declines. The intensity in which lignin is attacked by microorganisms may vary depending on a multitude of factors, e.g., the availability of immediately utilizable C for microbial catabolism (Klotzbücher et al., 2011), abundancy and composition of decomposers (Moorhead and Sinsabaugh, 2006) or the interference in enzyme production by N (Berg and McClaugherty, 2014, Manzoni, 2017, Moorhead and Sinsabaugh, 2006). Here, chemical characteristics suggest the latter to apply: Douglas fir and L litter both are rich in lignin but their N contents differ significantly (Table 7), indicating that less lignin might be degraded in DF due to the presumably insufficient production of lignolytic enzymes.

Alternatively, the higher TEC (Table 7) contents of DF and S may have just as well been catabolized instead of leached, as indicated by their enhanced microbial activity (Table 7) and respiration rates (Table 2 and Fig. 10). However, high initial leaching and respiration rates do not have to be exclusive: In a laboratory study, Klotzbücher et al. (2011) proposed additional labile compounds in litter to be readily available by initial degradation processes such as periodic drying and rewetting cycles. This *excess C* is not respired or incorporated into biomass by microorganisms, and hence allows for large initial leaching rates as well as high microbial respiration rates in needle litter.

The LCI is proposed by Soong et al. (2015) to explain leaching versus respiration patterns in later phases of decomposition, after labile C has become depleted. Accordingly, litter types with a low LCI were found to produce more DOC in relation to CO_2 during the later stages, caused by the abundance

of free cellulose. Results here, however, do not support this finding as the LCI was lowest in S litter, followed by L and DF (Table 7), and leaching dynamics (Fig. 11, Table 4) did not match this hypothesis. However, findings from Soong et al. (2015) are based on a laboratory study, where C and nutrient supply like N were limited. Throughfall DOC and N availability through external sources affected leaching rates and may have masked possible relations of LCI and leaching rates in this study. Consistent with Hagedorn and Machwitz (2007), no pattern between C:N ratio and leaching rates was found.

The high leaching activity observed in this study for L is further in line with findings regarding physical litter traits: According to Zukswert and Prescott (2017), many of these physical litter traits co-vary and can be ascribed to either coniferous or broadleaved species. Larch litter, however, is an exception to this; their study investigated *Larix occidentalis* and found this deciduous conifer species to significantly differ from other conifers concerning physical litter traits. Dominant traits found in *L. occidentalis* were associated with higher leaching rates, such as a high specific leaf area, great amounts of water-soluble compounds, and lower leaf toughness. These findings are of relevance for litter leaching as well as for above mentioned canopy exchange processes. Furthermore, they indicate that many soluble compounds in L litter could have already been leached prior to the beginning of this study: Contrasting to results presented here, they found a rapid initial mass loss for L litter due to leaching of solubles, and a considerable retardation of decomposition for later phases. If litter solubles really have been leached beforehand, it must be considered that observed mass loss of this study would be underestimated.

It is proposed that lignin degradation does occur in different magnitudes between litter species, with most intense degradation taking place in L litter. Along with the higher throughfall derived DOC input, this could explain the increasing leaching rates with progressing decomposition and further, account for the declining leaching rates of DF and S litter. Moreover, this study demonstrates the considerable impact by throughfall on litter leaching dynamics.

4.4 Soil organic C stocks and forest floor C dynamics

Forest floor and SOC stocks investigated by Hechenblaikner (2019) are shown in Table 1. Highest forest floor OC stocks and highest mineral OC stocks were found beneath the S stand (S > DF > L).

Forest floor as well as mineral SOC stocks significantly differed between species and were ascribed to variability in litterfall and stand density; however, differences in total C stocks between species were insignificant. Normalizing measured SOC stocks to stand parameters revealed quite contrasting results: Highest values were now found for the L stand (Fig. 12-14), with significant differences when compared to the other species. Notably, differences also persist for total C stocks (21.1, 11.1, 9.8 kg C kg^{-1} litterfall for L, S and DF respectively; Table 1). These findings are in line with the second hypothesis (H2) stating that higher DOC leaching is reflected in the SOC pool. Although it has been aimed to explain tree species effects on SOC stocks by accounting litterfall input and co-varying stand characteristics (e. g. Blaško et al., 2020, Hansson et al., 2011), to the best of one's knowledge this is the first study normalizing SOC pools by an actual input variable.

Differences were most evident when normalizing SOC stocks to the C input by litterfall, where L shows two-fold higher stocks than S or DF (Fig. 12), owed to its substantially lower litterfall rates. In connection with litterfall input it needs to be mentioned that abundance of ground vegetation differed between stands: Prominent ground vegetation comprising of *Rubus fructicosus* and beech regeneration, occurred only in the L stand which is due to its light transmissive canopy. Hence, an additional input in litterfall by ground vegetation is plausible. However, measured litterfall was sorted and analysed in different fractions, e.g., with and without external litter input by ground vegetation etc; but even when external litter was included, the contribution of ground vegetation did not alter the observed relations in litterfall input, suggesting its impact to be neglectable. Belowground litter input was not investigated in this study, but potentially accounts for an equal or even higher input than aboveground litterfall (Cotrufo et al., 2013, Mambelli et al., 2011, Vesterdal et al., 2013) and therefore remains a field for prospective studies.

Soil OC stocks normalized to basal area (Fig. 13) displayed a tendency for lower SOC pools in highly productive species, as seen in the significantly lower stocks in the DF compared to the L stand. This matches with findings that a higher tree productivity potentially indicates a more rapid turnover of SOM and the C therein (Gärdenäs, 1998), by sequestering more C in aboveground biomass (Blaško et al., 2020).

When normalizing SOC to stand density, C storage is slightly higher for DF than S (Fig. 14) and species-specific differences are less pronounced. This seems unusual since density was found to differ considerably between stands (Table 1). These rather vague results are presumably accounted to the high variance in density observed at plot-level. Stand density however is also reflected in litterfall

rates (S > DF > L), therefore it is concluded that litterfall and basal area mark more suitable indicators for this study to determine species specific differences in organic matter input.

In a comprehensive review, Vesterdal et al. (2013) summarizes evidence suggesting that SOC pools are altered by tree species effects; however, it remains difficult to draw species specific conclusions, especially concerning mineral soil C pools. Previous studies investigating SOC stocks of DF, L and S revealed inconsistent results: Among multiple species, Schulp et al. (2008) found highest forest floor- as well as highest mineral SOC stocks beneath a 60-year old *Larix kaempferi* stand; Mueller et al. (2015) reported combined organic C pools of forest floor and top mineral soil to be S > DF > L. In a meta-analysis, Gärdenäs (1998) rendered amounts of SOM in the forest floor to be in the order S > L > DF. Findings from Hechenblaikner (2019) for this study site only partly match with above results but generally approve with conclusions from other studies (e. g. Mueller et al., 2015, Vesterdal et al., 2008, Vesterdal et al., 2013), where it has been suggested that the C distribution between forest floor and top mineral soil, rather than the total C stocks varies between species. Tree species effects on C sequestration are said to be less pronounced in the organic horizon than they are in the mineral soil; probably due to a more rapid turnover in the organic horizon and the heterogeneous spatial distribution of C with soil depth in mineral soils (Mueller et al., 2015, Vesterdal et al., 2013).

When comparing measured total C stocks (forest floor C + SOC in 0-10 cm, Table 1), S and DF showed a rather similar distribution with 18.0 and 16.3 % of total C stored in the forest floor, respectively, whereas for L the fraction is markedly lower (11.4 %). This seems somewhat contradicting to mean residence time and corresponding turnover rate of forest floor C found in L (Table 8), which would indicate a higher accumulation of C. Also, the slower decomposition of L litter according to the mass loss study does counteract this finding. However, litterfall input for L was substantially lower than for S and DF, and in addition, its comparably lightweight needles are more likely to be carried away by wind. Therefore, drawing conclusions for SOC storage solely based on these parameters seems unreliable and is in accordance with Vesterdal et al. (2013), who also renders that C storage cannot be directly linked to turnover rates or litterfall input only; instead a comprehensive investigation of input and output processes during decomposition is needed (Vesterdal et al., 2013). Therefore, in accordance to (Cotrufo et al., 2010a), not the quantity in input (e.g., by litterfall), but rather the proportion effectively contributing to SOM formation is decisive. Here, findings suggest that the high SOC storage in L results from less C being lost by microbial respiration, paired with higher leaching rates and a greater input of throughfall DOC.

Dissolved organic C fluxes from throughfall were significantly higher in the L stand and in addition, presumably affected SOC pools. The input of throughfall derived DOC has been found to intensify leaching processes from the forest floor (Michalzik et al., 2001) and further, may indirectly promote SOM formation: Previous studies (Guggenberger and Zech, 1994, Michalzik et al., 2001) stated that roughly half of the DOC fluxes in throughfall are composed of microbial products which are washed from the canopy, whereof the major part of these microbial products is readily degradable. Since throughfall DOC and respiration rates did not seem closely related in L, it is proposed that throughfall derived C may have rather been used for assimilation of microbial biomass or as a readily utilizable source to degrade structural compounds like lignin (Klotzbücher et al., 2011, Michalzik et al., 2001). In comparison, the throughfall DOC inputs for S and DF were generally lower and it is suggested that larger amounts were utilized as a microbial substrate and hence were lost due to respiration.

It is further suspected, that higher SOC stocks of the L stand are also ascribed to its litter and leachate quality: Lignin degradation was found to presumably occur to a higher extent in L litter compared to the other litter types; this implies an increase in aromaticity and complexity of litter leachates, especially later in decomposition (Don and Kalbitz, 2005). Along with increasing aromaticity and complexity of leachates, its biodegradability declines, resulting in less of the DOC to be respired and therefore lost to the atmosphere; instead, greater amounts can be translocated into the soil. Supporting these assumptions, Hagedorn and Machwitz (2007) investigated DOC of L litter and found it to be among the least degradable due to its high molecular weight. Enhanced C pools due to low degradability of litter derived leachates is somewhat contradicting though to theories according to Cotrufo et al. (2013), who suggested that rather easily degradable constituents derived from litter are primarily responsible for the formation of SOM and the C therein; due to a more efficient usage of labile C by microbial decomposers. However, additional evidence concerning the relevance of more complex compounds for SOM formation supports the assumptions of this study here: For example, Kalbitz et al. (2005) demonstrated in a laboratory study that aromatic and complex compounds in dissolved organic matter are preferentially sorbed to mineral soil horizons (mineral associated organic matter) and therefore contribute substantially to a stable SOM formation. Also, recent findings by Córdova et al. (2018) demonstrate that low quality litter more efficiently accumulates mineral associated organic matter for SOM formation due to lower losses into respiration.

In clear contrast to Rubino et al. (2007), who did not find any relations between C partitioning and litter quality, results here allow to conclude that species specific differences in C partitioning largely depend on litter and leachate quality and are further influenced by throughfall dynamics. Suggestions

by Rubino et al. (2007), whereas differences in the amounts of litter derived C between species solely depends on microbial C use efficiency requires critical assessment which is not targeted in this study but remains a matter for future research.

Mass loss, leaching and respiration were evaluated by independent experiments, which implies that values do not directly correspond: Mass balance of the weighed litter mass loss from the litter bag experiment and the total C loss of litter by respiration and leaching did not match, as the total C loss in respiration and leaching exceeded the calculated C loss from the litter bag study. Depending on the species, differences between the independent estimates on C loss via fluxes and mass loss ranged between 32 and 67 % (see 3.1., Tables 2 and 4). This considerable discrepancy is partly owed to the study design, as processes were investigated simultaneously but also individually, using independent methods with differing uncertainties, e.g., it was already mentioned that fragmentation is largely limited due to the litter bags. The discrepancy is also related to natural circumstances encountered in a field study: Carbon input due to ingrowth of microorganisms and exchange of nutrients cause additional mass to be transferred into the decomposing litter. Berg and McClaugherty (2014) hence refer to litter mass loss as *net mass loss* because the evaluated mass loss does not exclusively relate to the originally present mass. However, although the mass balance from respiration and leaching does not match the balance from the mass loss experiment, the conducted quantification of C loss partitioning during decomposition into microbial respiration and leaching remains unaffected.

5 Conclusions & Implications

By means of this study, (1) pathways of litter derived C during decomposition were quantified, where a minor part with 2 -5 % of the measured C fluxes was partitioned into leaching, and 95 – 98 % into microbial respiration. It was shown that litter mass loss and (2) C partitioning pathways during litter decomposition vary by tree species: Conditioned by high lignin and low N contents, L litter mass loss was found to be substantially lower in relation to mass loss of S and DF. Significant differences between species for litter mineralization to CO_2 by microbial respiration and leaching of DOC were found, whereas respiration rates were significantly lower for L litter compared to S litter and leaching rate as well as leaching pattern of L litter differed significantly compared to that of S and DF. In line with the first hypothesis (H1), litter properties are suggested to determine partitioning processes rather than environmental factors: Lignin, C and N contents paired with microbial dynamics during decomposition were primarily responsible for low respiration of L litter and correspondingly higher rates for S and DF litter. High contents of lignin and the magnitude in which it is degraded are decisive for patterns in litter leaching; furthermore, species specific physical litter traits are suggested to be of relevance. Throughfall strongly influences litter leaching into the soil, whereas more transmissive canopies promote leaching fluxes. Increased input of throughfall derived C due to canopy exchange processes was identified to take place within the L stand. It is assumed that the chemical composition of litter leachates is a determining factor for its translocation into the soil. For this study, the stand parameters (3) litterfall and basal area characterized suitable proxies for stand specific C input; accordingly, they were used to normalize SOC pools for different C input to allow for a better comparison between tree species. It was demonstrated that significant differences in C partitioning during decomposition, namely higher leaching of DOC paired with lower rates of microbial respiration are linked to significantly larger (normalized) SOC pools in the top layer of mineral soils of L stands. These findings support the second hypothesis (H2) of higher DOC leaching rates leading to higher SOC stocks.

Many predictions and models from laboratory studies were found to not apply under field conditions here, indicating further demand for *in situ* studies of this kind. Although the simplicity of the used approach is of advantage for replicate studies, it is advisable for future studies to make use of more advanced techniques to investigate decomposition, e.g., isotopic labelling to securely identify C pathways. Isotopic labelling does also allow to study the fraction of litter that is lost due to fragmentation; a process which cannot entirely be accounted for in litter bag studies. Assigning leaching fluxes to their respective origin was not possible by means of this study, as it requires

detailed investigation of the chemical composition of organic matter leachates. It remains of importance for future research though, as it would improve estimations of leaching processes and may further clarify whether organic matter leachates are utilized as a substrate for microbial metabolism rather than being translocated into the soil. Examining litter decomposition in monocultural stands as it was done here improves knowledge on species specific effects. However, in hindsight of climate change, mixed stands are expected to increase their share. Therefore, studies ought to emphasize on investigating the effects of litter admixtures on decomposition. Belowground litter was not included in this study, but due to its vital role in C input of forest ecosystems is advised to be targeted in future research.

6 Supplements

6.1 Analysis of lignin, cellulose and hemicellulose

To characterize the chemical composition of the litter, NDF, ADF and ADL analysis was performed based on the van Soest procedure (Van Soest et al., 1991, Van Soest, 1963) and according to the ANKOM Technology Methods (Gesellschaft für Analysentechnik HLS, 2014b, Gesellschaft für Analysentechnik HLS, 2014a, ANKOM Technology, 2016). A neutral detergent fiber analysis (NDF) was used to determine the amount of cellulose, hemicellulose and lignin via digestion with a detergent solution (see 7.1.3.). Regarding the ADF (acid detergent fiber) procedure, the residues after digestion with Cetyltrimethylammoniumbromid (CTAB) and H_2SO_4 are predominantly cellulose and lignin, whereas the residues of the ADL (acid detergent lignin) procedure consist mainly of lignin. The fraction of hemicellulose was determined via subtraction of ADF from NDF, and calculated cellulose as ADF minus ADL. All analyses were performed using the ANKOM 200 Fiber Analyzer at the Institute of Animal Nutrition, Livestock Products and Nutrition Physiology (TTE) at the University of Natural Resources and Life Sciences, Vienna.

Analysis was conducted for initial litter sampling in April 2018. The litter used for the litter bags was collected in March 2018, and the litter bags were then incubated in the field in April 2018 for 10 and 11 days respectively.

Samples of 5.5 g from each of the six replicates (plots) per tree species were ground with a cyclone mill to pass through a 1 mm screen. Subsequently, samples were dried at 40 °C for 48 hours. For NDF, ADF and ADL analysis, 0.5 g of each sample were weighed into ANKOM F57 Filter Bags and heat sealed. After grinding, there was not enough material left from one of the Douglas fir replicates (D4), so for this sample only the determination of ADL was conducted. In total, 2 x 18 samples (ADF and NDF analyses for 3 x 6 samples) and 1 x 17 samples (ADL analysis for 2 x 6 and 1 x 5 samples) were analysed. Two blank bags were run along with every procedure as a control. Dry mass of the ground samples was determined after drying samples in the oven at 103 °C for 4 hours.

6.1.1 Determination of ADF

Reagents used for the acid detergent solution were 20 g of CTAB mixed with 27,2 ml of H_2SO_4. Before loading samples into the ANKOM 200 Fiber Analyzer vessel, it was ensured that the sample

was distributed homogenously inside each filter bag. Samples were then put into the vessel and 2000 ml of the acid detergent solution was added. The ADF extraction process was performed at a temperature of 100 °C (+/- 0,5 °C) and 10…25 psi operating pressure for 60 minutes. Following the extraction process, the fiber analyzer vessel including samples was then rinsed three times for five minutes with distilled H_2O at a temperature of 70 °C – 90 °C. Using pH paper after the third rinse assured the samples being acid free. The samples were removed from the vessel and excess water gently pressed out of the filter bags. Filter bags were then soaked in acetone for 3 to 5 minutes and afterwards air dried until acetone was completely evaporated. The filter bags were dried in the oven overnight at 103 °C. After drying, the filter bags were put into a MoistureStop Desiccant Pouch until cooled to ambient temperature and then weighed. To determine the amount of organic matter the samples were ashed in pre-weighed crucibles at 550 °C for at least 3 hours. The percentage of organic matter ADF based on dry mass of litter was defined according to the following equation:

$$\%\ ADF_{OM}\ (DM\ basis) = \frac{\left(W_4 - (W_1\ \times\ C_2)\right) \times\ 100}{W_2\ \times DM} \tag{7.01}$$

Whereas W_4 represents the weight after the extraction process corrected for organic matter, W_1 represents the bag tare weight, W_2 the sample weight and C_2 the correction for the blank bag (oven dried weight corrected for organic matter divided by original blank bag weight). *DM* represents the correction for dry matter.

6.1.2 Determination of ADL

The determination of ADL is in accordance to the procedure of ADF determination; after the extraction process, the samples were dried and then submerged in 72 % of H_2SO_4 in a beaker for 3 hours. Samples were agitated in an hourly interval and afterwards thoroughly rinsed with distilled water until all acid was removed and pH paper showed neutral colour. The samples were subsequently rinsed with acetone for three minutes and upon complete evaporation of all acetone dried in the oven for 103°C overnight. Weighing and ashing was according to the procedure for ADF. The percentage of organic matter ADL based on dry mass of litter was defined as:

$$\%\ ADL_{OM}\ (DM\ basis) = \frac{\left(W_4 - (W_1\ \times\ C_2)\right) \times\ 100}{W_2\ \times DM} \tag{7.02}$$

Variables are synonymous with the ADF formula.

6.1.3 Determination of NDF

The neutral detergent solution is made of 93 g Ethylenediamine Tetraacetic Acid (EDTA) and 34 g of Di-Sodium Tetraborate Decahydrate filled up with 1 liter of distilled H_2O and heated to solubilize. After cooling down to ambient temperature, 150 g of Sodium Dodecyl Sulfate (SDS) pellets and 50 ml of Triethylene Glycol were added and again heated. 22,8 g of Disodium Hydrogen Phosphate were solubilized in another beaker with 2 l of distilled H_2O. Both solutions were mixed, filled up with distilled H_2O to 5 l and ensured to have a pH value of 6,95 to 7,05.

For the extraction in the ANKOM 200 fiber analyzer, 1600 ml of the neutral detergent solution and 34 ml of heat-stable bacterial alpha amylase was used to determine the fiber residues (lignin, cellulose, hemicellulose) for the 17 samples.

Following the extraction, samples were rinsed with acetone, dried, weighed and ashed according to the ADF procedure. The percentage of organic matter NDF based on dry mass of litter was defined as:

$$\%\ NDF_{OM}\ (DM\ basis) = \frac{\left(W_4 - (W_1\ \times\ C_2)\right) \times\ 100}{W_2\ \times DM} \tag{7.03}$$

Variables are synonymous with the ADF formula.

6.2 Supplementary data

Table 9. P values for pairwise comparisons between stands for soil temperatures, soil moisture content and litter moisture content with repeated measures ANOVA by mixed linear models. For throughfall data p values, one-way ANOVA and Tukey's HSD post-hoc test were used. Significant differences are highlighted in bold.

	S - D	L - D	L - S
Phase 1			
Temperature	1	**< 0.001**	**< 0.001**
Soil moisture	0.475	0.439	1
Litter moisture	1	0.072	0.089
Throughfall	0.081	**0.015**	0.392
Phase 2			
Temperature	0.638	**0.019**	**< 0.001**
Soil moisture	0.221	0.942	**0.012**
Litter moisture	1	**0.001**	**0.001**
Throughfall	0.120	**0.016**	0.291
Total			
Temperature	1	**< 0.001**	**< 0.001**
Soil moisture	0.099	1	0.234
Litter moisture	1	**< 0.001**	**< 0.001**
Throughfall	0.086	**0.013**	0.322

S = Norway spruce, *D* = Douglas fir, *L* = European larch.

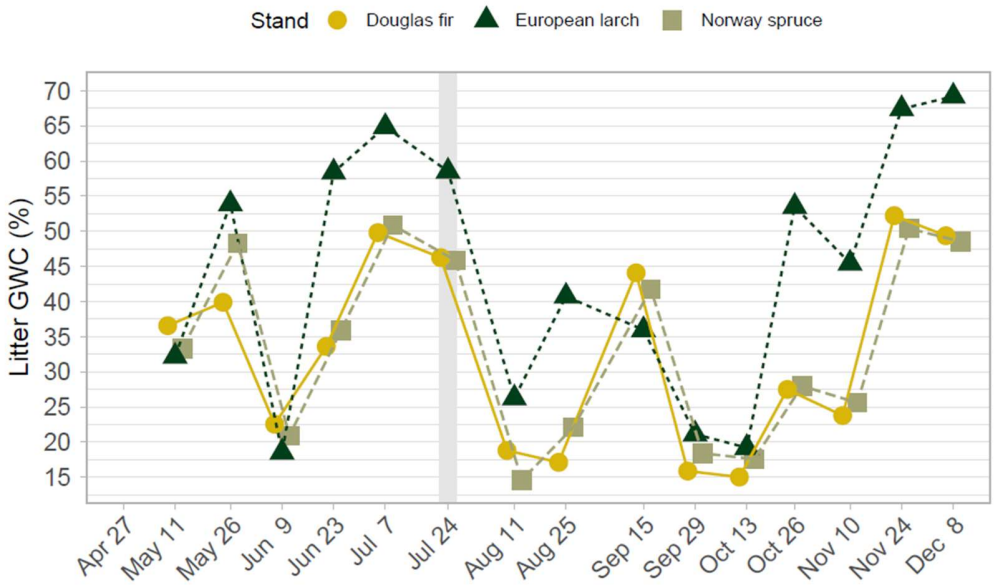

Figure 15. Litter moisture content from biweekly samplings in European larch, Douglas fir and Norway spruce stands. No data available for sampling in April. Given are mean values. Beginning of phase 2 is marked by grey vertical line.

7 Literature

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