

**Dynamics of multiple elements in litter decomposition
under various disturbances**

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von

Liyan Zhuang

Aus

Zhejiang, China

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Vorsitzende:	Prof. Dr. Claudia Knief
1. Gutachterin:	Prof. Dr. Andrea Schnepf
2. Gutachter:	Prof. Dr. Roland Bol
Fachnaches Mitglied:	Dr. Thomas Gaiser

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SUMMARY

Summary

Both artificial disturbance and climate change regimes can strongly affect soil carbon (C) sequestration and nutrient dynamics through decomposition processes of above- and belowground residues in terrestrial ecosystems. This requires new directions in managing future forests. I conducted decomposition experiments on foliage and root litter in different ecosystems and different types of disturbance, including nitrogen deposition, elevation gradients, and clearcutting. My thesis aims to: i) investigate the decomposition and nutrient release pattern of contrasting litter species in response to N deposition in already nitrogen-rich subtropical forests; ii) compare the carbon decomposition of belowground root litter (humification and mineralization) in response to an elevation gradient in an alpine forest; and iii) explore the role of litter affinity, in particular home-field advantage, on litter decomposition and nutrient mineralization after clearcutting in a temperate forest that is managed to achieve a conversion from monospecific plantations to more natural deciduous forests in a temperate climate.

I collected leaf and root samples from local ecosystems and conducted litterbag experiments in individual forest ecosystems, respectively. Three main experiments were performed. In the first experiment, one-year *in situ* decomposition of low-quality *Michelia wilsonii* and high-quality *Camptotheca acuminata* with N additions (0 kg N ha⁻¹ yr⁻¹, 20 kg N ha⁻¹ yr⁻¹ and 40 kg N ha⁻¹ yr⁻¹) at the western edge of the Sichuan Basin of China was studied. In particular, mass loss rate, carbon, nitrogen and phosphorus dynamic were studied. The second experiment was a two-year litterbag experiment with root litter of three diameter classes (0-2, 2-5 and 5-10 mm) of two common subalpine tree species (*Picea asperata* and *Abies faxoniana*) at two elevations (3037 m and 3580 m, varied in soil temperature, moisture and snowpack) on the eastern Tibetan Plateau, China. This experiment focused in particular on humification, humified substance was extracted with modified alkaline extraction. Thirdly, a transplant reciprocal litter decomposition experiment of Norway spruce (*Picea abies*) and European Beech (*Fagus sylvatica*) within the forest and clear-cut area and for two soil types (Cambisols and Gleysols) in Eifel National Park (Wüstebach Germany) was performed; decomposition home-field advantage, carbon, nitrogen, phosphorus, calcium, and of the stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined.

My results indicated that nitrogen addition negatively affected low-quality *M. wilsonii* litter decomposition, but not high-quality *C. acuminata* litter. Nitrogen addition caused immobilization of nitrogen and phosphorus in *M. wilsonii* which decreased the carbon-to-phosphorus ratios in the later decomposition stages. Nitrogen addition had no effect on carbon mineralization for both species. When considering the climatic condition, elevation gradients did not affect formation of humic substances from roots. Snowpack and freeze-thaw cycles change with elevation. This offsets the expected temperature effect on the belowground root humification process in an alpine forest. However, root diameter increases with cellulose and carbon-to-phosphorus ratio, leading to decreased mass loss rate and concentrations of humic substance, humic acid and fulvic acid. Clearcutting management significantly elevated soil moisture and temperature status, changed the field-litter affinity of spruce forest (masked decomposition home-field advantage in a spruce forest). Increased beech decomposition rate and litter nitrogen release further promoted soil carbon and nitrogen cycling in the clearcut site. This phenomenon was more evident in the comparable acidic and moisture-deficient Cambisols than in Gleysols present in the catchment.

In summary, my study clearly demonstrated that the decomposition rate, as well as carbon, nitrogen and phosphorus release from leaf and root litter are highly related to litter substrate quality in forest ecosystems. I especially saw a diversity of responses in term of litter quality and extreme disturbance condition. Therein, nitrogen deposition and elevation had less influence on carbon loss of native litter, whereas clearcutting management promoted the decomposition of non-dominant species. Suppression of nutrient release from high-lignin litter under disturbance and warming condition underlined the necessity to reconsider the current forest structure and management. This study illustrates how disturbance and climate change impact, together with plant species and edaphic conditions at local levels, can help explain external-induced changes in ecosystem functions such as soil organic matter formation and nutrient cycling and provide a basis for further development of sustainable forest management.

ZUSAMMENFASSUNG

Zusammenfassung

Sowohl künstliche Störungen als auch der Klimawandel können die Kohlenstoffsequestrierung im Boden und die Nährstoffdynamik aufgrund von Zersetzungsprozesse von Wurzel- und Blattstreu in terrestrischen Ökosystemen stark beeinflussen. Dies erfordert neue Wege bei der Bewirtschaftung künftiger Wälder. Ich habe Zersetzungsexperimente mit Laub- und Wurzelstreu in verschiedenen Ökosystemen und unter verschiedenen Störungsarten durchgeführt, darunter Stickstoffdeposition, Höhengradienten und Kahlschlag. Meine Dissertation zielt darauf ab: i) die Zersetzungs- und Nährstofffreisetzungsmuster verschiedener Streuarten als Reaktion auf Stickstoffeinträge in bereits stickstoffreichen subtropischen Wäldern zu untersuchen; ii) den Kohlenstoffabbau von unterirdischer Wurzelstreu (Humifizierung und Mineralisierung) als Reaktion auf einen Höhengradienten in einem alpinen Wald zu vergleichen; und iii) die Rolle der Streuaffinität, insbesondere des Heimvorteils, auf den Streuabbau und die Nährstoffmineralisierung nach einem Kahlschlag in einem Wald der gemäßigten Zonen zu untersuchen, der bewirtschaftet wird, um eine Umstellung von monospezifischen Plantagen auf natürlichere Laubwälder in einem gemäßigten Klima zu erreichen.

Ich sammelte Blatt- und Wurzelproben aus lokalen Ökosystemen und führte in den einzelnen Waldökosystemen jeweils Streuabbauversuche durch. Es wurden drei Hauptexperimente durchgeführt. Im ersten Experiment wurde die einjährige In-situ-Zersetzung von weniger hochwertigem *Michelia wilsonii* und hochwertigem *Camptotheca acuminata* mit N-Zusätzen (0 kg N ha⁻¹ yr⁻¹, 20 kg N ha⁻¹ yr⁻¹ und 40 kg N ha⁻¹ yr⁻¹) am westlichen Rand des Sichuan-Beckens in China untersucht. Untersucht wurden insbesondere die Massenverluste sowie die Dynamik von Kohlenstoff, Stickstoff und Phosphor. Der zweite Versuch war ein zweijähriges Streuabbau-Experiment mit Wurzelstreu dreier Durchmesserklassen (0-2, 2-5 und 5-10 mm) von zwei verbreiteten subalpinen Baumarten (*Picea asperata* und *Abies faxoniana*) in zwei Höhenlagen (3037 m und 3580 m, mit unterschiedlichen Bodentemperaturen, Feuchtigkeit und Schneedecken) auf dem östlichen tibetischen Plateau, China. Dieser Versuch konzentrierte sich insbesondere auf die Humifizierung; die humifizierte Substanz wurde mit einer modifizierten alkalischen Extraktion extrahiert. Drittens wurde ein Experiment zur wechselseitigen Streuzersetzung von Fichte (*Picea abies*) und Rotbuche (*Fagus sylvatica*) im Wald und im Kahlschlaggebiet und für zwei Bodentypen (Cambisole und Gleysole) im Nationalpark Eifel (Wüstebach Deutschland) durchgeführt; Heimvorteil bei der Zersetzung, Kohlenstoff, Stickstoff, Phosphor, Kalzium und die stabilen Isotope $\delta^{13}\text{C}$ und $\delta^{15}\text{N}$ wurden bestimmt.

Meine Ergebnisse deuten darauf hin, dass die Zugabe von Stickstoff die Zersetzung der Streu von *M. wilsonii* negativ beeinflusst, nicht aber die der hochwertigen Streu von *C. acuminata*. Der Stickstoffzusatz bewirkte eine Immobilisierung von Stickstoff und Phosphor in *M. wilsonii*, wodurch sich das Verhältnis von Kohlenstoff zu Phosphor in den späteren Zersetzungsstadien verringerte. Die Stickstoffzugabe hatte bei beiden Arten keine Auswirkungen auf die Kohlenstoffmineralisierung. Unter Berücksichtigung der klimatischen Bedingungen wirkten sich die Höhenunterschiede nicht auf die Bildung von Huminstoffen aus den Wurzeln aus. Die Schneedecke und die Frost-Tau-Zyklen ändern sich mit der Höhenlage. Dadurch wird die erwartete Auswirkung der Temperatur auf den unterirdischen Humifizierungsprozess der Wurzeln in einem alpinen Wald kompensiert. Der Wurzeldurchmesser nimmt jedoch mit dem Zellulose- und P-Kohlenstoff-Phosphor-Verhältnis zu, was zu einer Verringerung der Massenverluste und der Konzentrationen von Huminstoffen, Huminsäure und Fulvosäure führt. Durch die Kahlschlagbewirtschaftung wurden die Bodenfeuchtigkeit und die Bodentemperatur signifikant erhöht und die Streuaffinität von Fichtenwäldern verändert (maskierter Heimvorteil bei der Zersetzung im Fichtenwald). Die erhöhte Zersetzungsrate der Buche und die Freisetzung von Stickstoff aus der Streu förderten den Kohlenstoff- und Stickstoffkreislauf des Bodens im Kahlschlaggebiet weiter. Dieses Phänomen war in den feuchtigkeits- und nährstoffarmen Braunerden deutlicher zu beobachten als in den im Einzugsgebiet ebenfalls vorhandenen Gleyböden.

Zusammenfassend lässt sich sagen, dass meine Studie deutlich gezeigt hat, dass die Zersetzungsrate sowie die Freisetzung von Kohlenstoff, Stickstoff und Phosphor aus der Blatt- und Wurzelstreu in hohem Maße von der Qualität des Streusubstrats in Waldökosystemen abhängt. Vor allem bei der Streuqualität und extremen Störungsbedingungen konnte ich eine Vielfalt von Reaktionen feststellen. Dabei hatten Stickstoffdeposition und Höhenlage weniger Einfluss auf den C-Verlust der einheimischen Streu, während die Kahlschlagbewirtschaftung die Zersetzung der nicht dominanten Arten förderte. Die Unterdrückung der Nährstofffreisetzung aus Streu mit hohem Ligningehalt unter Störungs- und Erwärmungsbedingungen unterstreicht die Notwendigkeit, die derzeitige Waldstruktur und -bewirtschaftung zu überdenken. Diese Studie veranschaulicht, wie Störungen und die Auswirkungen des Klimawandels zusammen mit Pflanzenarten und edaphischen Bedingungen auf lokaler Ebene dazu beitragen können, von außen verursachte Veränderungen der Ökosystemfunktionen wie die Bildung organischer Substanz im Boden und den Nährstoffkreislauf zu erklären und eine Grundlage für die weitere Entwicklung einer nachhaltigen Waldbewirtschaftung zu schaffen.

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List of abbreviations

ANOVA	Analysis of Variance
AIF	Acid insoluble fraction
C	Carbon
<i>C acuminata</i>	<i>Camptotheca acuminata</i>
Ca	Calcium
CDI	Climate decomposition index
FA	Fulvic acid
FAO	Food and Agriculture Organization of the United Nations
GS1	the first growing season
GS2	the second growing season
H ₂ O ₂	Hydrogen peroxide
H ₂ SO ₄	Sulfuric Acid
HA	Humic acid
HD	Humification degree
HFA	Home-field advantage
HFAi	Home-field advantage index
HN	High-N addition
HNO ₃	Nitric acid
HS	Humic substances
ICP-MS	Inductively coupled plasma mass spectrometry
IUSS	International Union of Soil Sciences
K ₂ Cr ₂ O ₇	Potassium dichromate
KDN	Kjeldahl determination
LIDET	Long-term intersite decomposition experiment

LIST OF ABBREVIATIONS

LN	Low-N addition
<i>M. wilsonii</i>	<i>Michelia wilsonii</i>
MT	Daily mean soil temperature
N	Nitrogen
NaOH	Sodium Hydroxide
Na ₄ P ₂ O ₇	Tetrasodium pyrophosphate
NAT	Negative accumulated temperature
NH ₄ NO ₃	Ammonium nitrate
P	Phosphorus
PAT	Positive accumulated temperature
pH	Potential of Hydrogen
SMI	Substrate quality-matrix quality interaction
SOM	Soil organic matter
SWC	Soil water content
TBI	Tea Bag Index
TOC	Total organic carbon
VPDB	Vienna Pee Dee Belemnite
W1	the first winter
W2	the second winter

1. GENERAL INTRODUCTION

1. General introduction

1. GENERAL INTRODUCTION

1.1 Rationale

Natural and man-made disturbances have consequences on ecosystems functioning and thus human well-being. Plant litter decomposition is an important ecological process in functioning of both natural and managed ecosystems. It is affected by changes in litter chemical properties and climatic conditions (Pandey et al., 2007; Petraglia et al., 2019; Vivanco and Austin, 2019). It is a primary mechanism for nutrient cycling and links above- and belowground carbon (C) transmission (Berg and McClaugherty, 2014; Prescott, 2010; Sun et al., 2018). Forest disturbance changes physical and chemical conditions or species functional composition of habitat and consequently leads to long-term variation in soil organic matter (SOM) and ecosystem services (Bengtsson et al., 2000; Bobbink et al., 2010; Bonan et al., 2013; Dib et al., 2014).

Litter chemical components and climate conditions are the primary regulators of decomposition processes (Parton et al., 2007). At the global scale, mean annual temperature and precipitation substantially correlate with plant breakdown (Kwon et al., 2021). The relationship between litter chemistry and decomposition rates has also been widely investigated (Aerts, 1997; Cornwell et al., 2008). Litter chemistry with low C: N ratios and low polyphenols concentrations contributes to faster degradation (Becker and Kuzyakov, 2018; Djukic et al., 2018; Kriiska et al., 2021).

Furthermore, Field and laboratory studies continue to provide evidence that litter quality and climate regime shape soil decomposer functional abilities and hence the rate of litter decomposition within biomes (Keiser and Bradford, 2017). Such specific litter-field affinity (home-field advantage, HFA) can contribute to faster decomposition rate of plant species which the litter originated (home field) than in areas dominated by other species (Ayres et al., 2009; Gholz et al., 2000). Specialization of soil biota groups adapted to their particular substrate types is projected to have a faster decomposition rate at home habitats (Perez et al., 2013; Strickland et al., 2009). Of course, the local climate also makes an effort in this interaction (Veen et al., 2015; Vivanco and Austin, 2008). "Low-quality litter decomposes faster in a matrix of poor quality, and the interaction between the two becomes more negative as the litter and matrix become increasingly dissimilar in

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quality (Substrate quality-matrix quality interaction, or SMI, as described by Freschet et al. in 2012). This is an extension of the concept of home-field advantage (HFA)."

The concept of HFA suggests that plant litter decomposes faster in its native habitat than in an unfamiliar environment, and this has significant implications for nutrient release. However, the influence of HFA on nutrient release may be disrupted by plant or soil biota migration due to climate change or forest management (Ayres et al., 2009). However, there are still limits in terms of the incidence of HFA post-disturbance and how they influence HFA on both short-term (physiological adaptation) and long-term (forest conversation) scales.

Changes in the climate and increases in extreme weather event are among the reasons behind species distribution and some changes in growth. soil water regimes (waterlogging, surface drying and snow cover) are also predicted to change (Freppaz et al., 2018; IPCC, 2014). In the long term, this results in climate-driven shifts in plant composition and associated litter quality (Augusto et al., 2015; González and Seastedt, 2001), which may have significant consequences for litter decomposition and SOM accumulation in alpine forests (Baptist et al., 2010; Duboc et al., 2012; Elumeeva et al., 2018). In general, Climate warming has been reported to increase (Allison et al., 2010; Austin, 2002), decrease (Conant et al., 2008; Liu et al., 2021), or have no influence (Zhang and Wang, 2015) on litter degradation. High-altitude ecosystems are sensitive and vulnerable to climate change, since they experience stronger temperature fluctuations (Aerts, 2006; Schröter et al., 2005). Adverse climatic conditions in cold biomes leads to a higher retention time of organic matter in soils (Aerts, 2006; Chapin III et al., 2011). As a result, soil organic C stock in these regions is among the highest in terrestrial biomes (Djukic et al., 2010b).

In the Tibetan Plateau, climate has warmed by approximately 0.86 °C over the past half century (Figure 1-1). Climate scenarios predict further warming for the 21st century, with a greater increase in winter (Figure 1-2a), with an estimated increase between 2.7 and 3.1 °C. Precipitation is expected to slightly increase in the growing season (Figure 1-2b). Thus, these changes in factors that control litter decomposition process have important repercussions for the SOM sequestration

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and nutrient cycling in this cold region within elevation, especially relating to low-quality belowground roots.

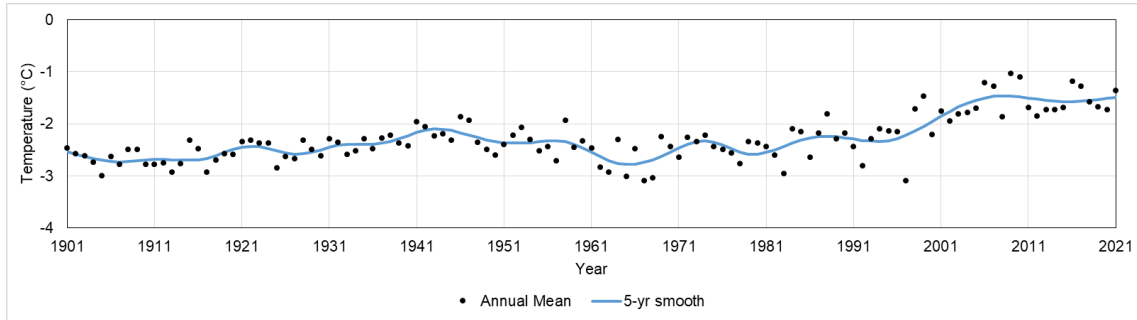


Figure 1-1 Observed average mean-temperature of Tibetan Plateau, China for 1901-2021. Data downloaded from Climate Change Knowledge Portal (<https://climateknowledgeportal.worldbank.org/country/china/climate-data-historical>) on Dec. 20th, 2022.

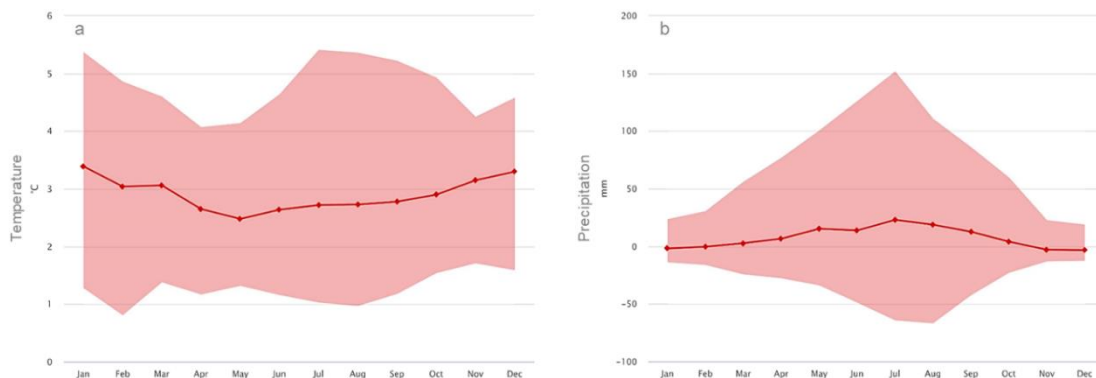


Figure 1-2. Estimated mean-temperature (a) and precipitation (b) anomaly of Tibetan Plateau, China for next 50 years (2060-2079). Reference period:1995-2014. Future climate scenarios are presented through SSP3-7.0 in CMIP6. SSP3-7.0 presents a pathway in which countries are increasingly competitive and emissions continue to climb, roughly doubling from current levels by 2100. Data downloaded from Climate Change Knowledge Portal (<https://climateknowledgeportal.worldbank.org/country/china/climate-data-historical>) on Dec. 20th, 2022.

Rockström et al. (2009) identified nine planetary boundaries to explore the safe operating space for humanity, in which N deposition is proposed as one of the most severe threats. They proposed a limitation of N deposition to 35 Tg N yr⁻¹ for

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the safe operating space of humanity and the Earth system (Rockström et al., 2009). Human activities today transform more nitrogen from the atmosphere into reactive forms than all terrestrial processes combined. Depending on atmospheric N deposition, plant litter responds from positive for the decomposition of high-quality litter to negative for the decomposition of low-quality litter through affecting soil N availability and the composition of decomposer community (Guo et al., 2017; Jiang et al., 2014; Knorr et al., 2005; Liu et al., 2015). Moreover, N addition is likely to promote early-stage decomposition in N-limited ecosystems (Knorr et al., 2005), but to inhibit decomposition in N-sufficient ecosystems through microbial “N-mining” and the synthesis of ligninolytic enzymes during the late stage of decomposition and soil acidification (Gong et al., 2020; Zhang et al., 2018b). Although much is known about the effects of increasing N deposition on decomposition, the regulators could strongly differ among ecosystem and plant types (Manning et al., 2008). Due to rising active N deposition, litter decomposition experiments on local or regional scale within high N deposition background can help to predict and initiate further development of sustainable forest management and biological diversity.

Clearcutting can cause changes in the dominant vegetation and the properties of plant species. Soil exposed to the new local climate in a clear-cut also differs greatly from the climate prevailing in the forest's interior (Keenan and Kimmins, 1993; Okland et al., 2003). In Germany, two third of forested areas are stocked with mono or mixed conifer forests (Hausler and Scherer-Lorenzen, 2001). Mixed forests can be expected to have higher stability and greater resilience than monospecific forests against disturbances such windstorms and insect calamities (Coll et al., 2018). Thus, forest management, including clearcutting, in Germany's forests is expected to modify conifer forests to more natural types of mixed beech forests. Shifts in species composition and abundance linking environmental factors by clearcutting can significantly impact decomposition, as well as carbon and nutrient cycles, according to respective local conditions (Kohout et al., 2018; Prescott, 1997).

In general, man-made disturbances or climate change can affect litter decomposition at different levels (Eastman et al., 2022; Kohout et al., 2018; Naudts

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et al., 2016; Xu et al., 2015; Zhang et al., 2018b). Owing to the high sensitivity of biological processes to disturbances (e.g., soil nutrient availability, temperature and soil water conditions), these disruptions might indirectly impact plant species composition and raise the risk of irreversible alterations in the functioning of forest ecosystems (Bowd et al., 2019; Pykälä, 2004; Reddy et al., 2016). Thus, understanding the impact of post-disturbance and global climate-impacted litter decomposition is critical for illustrating and modeling ecosystem SOM mineralization and forest conversation under global change.

1.2 State of the art

1.2.1 The general pattern of decomposition

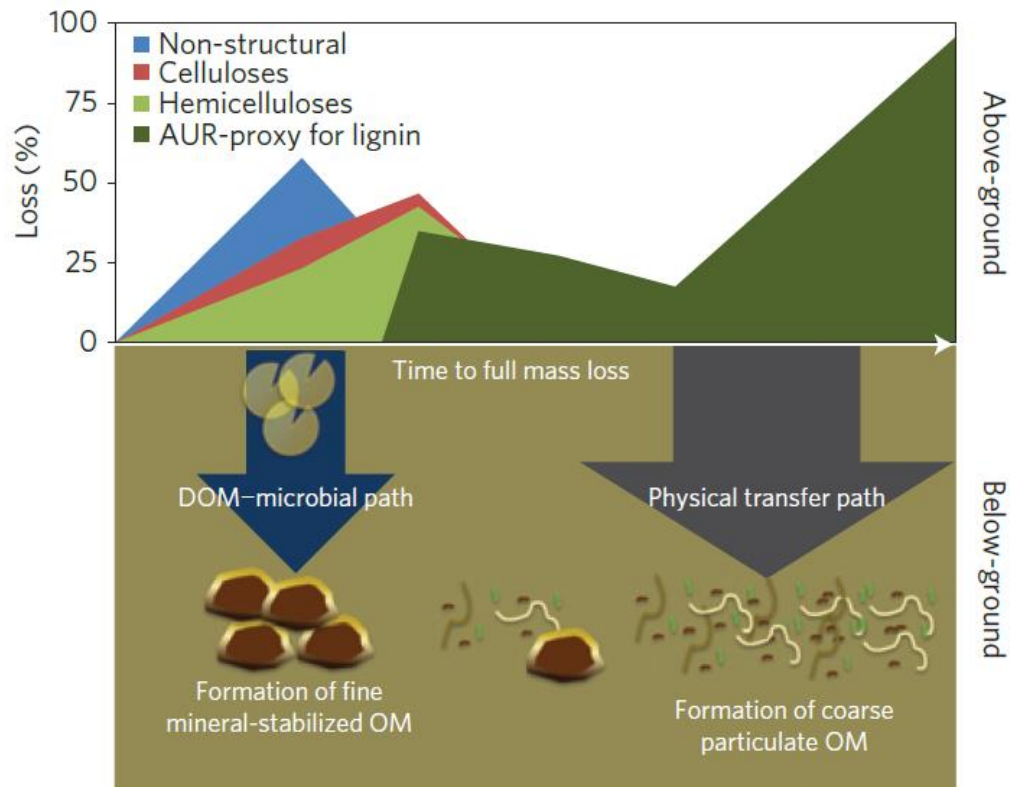


Figure 1-3. Schematic representation of SOM formation through biochemical and physical pathways from progressive loss of litter chemical components (from Cotrufo et al., 2015. *Nature Geoscience*.)

Litter decomposition is a physiochemical breakdown of dead organic material into CO₂ and inorganic nutrients by leaching, fragmentation and chemical

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reduction (Chapin III et al., 2011). It provides energy and nutrients for microbial and plant growth while also influencing C storage and ecosystem phylogeny on climate (Chapin III et al., 2011). Litter decomposition involves two simultaneous and fundamental sets of processes (Figure 1-3): 1) the leaching of soluble compounds to soil where most C and nutrients are progressively mineralized or immobilized (Soong et al., 2015); 2) the concomitant mineralization and humification of recalcitrant organic matter, such as cellulose, lignin, tannin, and other C compounds by a succession of decomposer community (Cotrufo et al., 2015). The main factors driving decomposition in various ecosystems are substrate quality, climate condition and decomposer communities (Aerts, 1997; Berg, 2014; Zhang et al., 2008). Litter is primarily composed of the labile nutrient fraction and recalcitrant organic matter. Its breakdown is regulated by interactions of temperature and moisture availability and chemical conditions (or quality), as well as the threshold of litter C: N: P stoichiometry to reach the decomposer and enzymatic nutrient demand (Cleveland and Liptzin, 2007; Sinsabaugh et al., 2008; Zhang et al., 2018c).

Plant litter inputs are essential resources for the stable fraction of SOM in terrestrial ecosystems. Litter decomposition and recycling is controlled by climate at global and regional scale (Aerts 1997). Litter quality is then viewed as a dominant regulator where climate become less restraining to microbial activity at local scale (Cornwell et al., 2008; Parton et al., 2007; Trofymow et al., 2002). The chemical properties of litter together with climate contribute to approximately 70% of the variation in global decomposition rates (Aerts, 1997; Zhang et al., 2008). However, the importance of these factors also changes through decomposition process and ecosystem management and even global environmental policy (Bradford et al., 2016).

1.2.2 Litter quality and N deposition

1.2.2.1 Litter quality regulates decomposition rates

Litter chemistry, particularly C fraction and nutrient content, is crucial to plant litter degradation. It affects decomposer communities composition and abundance at the different decomposition stages (Averill and Waring, 2018; Berg et al., 2003). Plant litter comprises various chemical compounds with a wide range

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of mineralization and sequestration characteristics (Rovira et al., 2008). In this respect, high-quality litter with low substrate C: nutrients ratios and low phenol content is associated with faster mineralization and more efficient accumulation of SOM (humification), rather than low-quality litter with high C: N ratios has a strong negative effect on litter degradation (Cotrufo et al., 2013). A reciprocal transplant experiment of litter across 28 sites in North and Central America at a wide range of natural and managed ecosystems showed that high-quality *Drypetes* litter decomposed significantly faster than low-quality pine litter (Harmon et al., 2009). Zhang et al. (2008) constructed a comprehensive global database of litter decomposition rate constants (k values) and concluded that decomposition was faster in the order of grass > broadleaf > root > conifer needles > woody litter. Similarly, Palviainen et al. (2004b) showed that the decomposition rate and release of C, N, and P from Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* Karsten) were slower than silver birch (*Betula pendula* Roth.). Foliage was observed to have higher mass loss rates than roots in above species, supporting the concept that substrate chemical properties are an important predictor of the degradation process at both regional and global scales (Gholz et al., 2000).

The distribution and concentration of metals like K, Ca, Mg and Al can also influence mass loss rate. They appear as a cation in exchange reactions between soil and solution. The release or immobilization of metal ions from decomposing litter varies according to the plant initial metal concentration (Lucas-Borja et al., 2019; Van Nevel et al., 2014). The net accumulation indicates the metal ions are fixed by the primary OM or humic substances in litter residuals. Polyvalent metal ions intend to form highly stable complexes with humic substances, produced as secondary products during the decay of OM (Laskowski and Berg, 1993, 2006). Moreover, there is evidence that conifers are more adapted to acidic soils than angiosperm species, and this may be related to differences in the litter produced by these two groups of plants and the resulting effects on soil pH and carbon storage (Dauer et al., 2007, Ross et al., 2008). Thus, litter and soil Ca as well as soil acidification, possibly lead to greater soil C storage, especially in a substantial proportion of conifers (Reich et al., 2005).

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1.2.2.2 Decomposition stages and related substrate quality

Furthermore, changing residual quality during the course of decomposition is a consequence of the different degradation rates of the various chemical constituents (Purahong et al., 2016). Soluble compounds (e.g., non-lignified cellulose and hemicellulose) in plant litter rapidly leach out, resulting in a relative accumulation of more recalcitrant compounds (Berg et al., 2001; Rovira et al., 2008). This triggers and mediates the colonization succession (microbial composition and abundance) as decomposition progresses (Purahong et al., 2016).

The early stage of litter decomposition (*ca.* 0-30% of mass loss) is sensitive to environmental changes and N contents in initial litter, which can be detected by bacteria indicator species such as basidiomycete yeasts (Berg and McLaugherty, 2014; Gómez-Brandón et al., 2020). In comparison, lignified tissue stimulates the later-arriving fungal species like white-rot fungi and the secretion of manganese peroxidase (MnP). High substrate Mn concentration is important to degrade the phenolic structure of lignin or humic acids on far-going decomposition (Berg and McLaugherty, 2014; Hatakka, 2001). A Mn-fertilized experiment in both forest and cropland confirmed that the added Mn stimulated MnP enzyme activity and increased late-stage decomposition where lignin dominated in a 2-year observation (Sun et al., 2019). Keiluweit et al. (2015) illustrated that the formation of short-lived reactive Mn^{3+} was tightly coupled to aromatic oxidation products in litter breakdown, directly providing evidence for Mn^{3+} -based oxidizers. Litter Mn concentration was shown to also regulate the litter degradation rate and limit value. Berg and McLaugherty (2014) calculated a complete decomposition (i.e., a limit value of 100%) from lodgepole pine with a high Mn concentration, whereas grey alder had a low limit value (51%) due to a low Mn concentration. Similar phenomena are shown in other species and locations (Herndon et al., 2015; Trum et al., 2015; Whalen et al., 2018).

1.2.2.3 Decomposition under N addition

Reactive N deposition of anthropogenic origin has increased globally since the 19th century and now dramatically exceeds the magnitude of natural fluxes (N cycles: past, present, and future, Galloway et al., 2004). Elevated soil N content from N emission potentially affects the vitality of forest ecosystems (Britton et al.,

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2018; Gong et al., 2020; Jia et al., 2019; Pei et al., 2019) by affecting various processes, associated with SOM decomposition (Knorr et al., 2005; Růžek et al., 2021; Zhang et al., 2018a). Most terrestrial ecosystems are naturally N-limited (LeBauer and Treseder, 2008; Vitousek et al., 2022). Deposition of reactive N in these systems can mitigate N limitation, altering soil stoichiometry and nutrients cycling, thus stimulating aboveground ecosystem productivity (Liu and Greaver, 2010) and ultimately enhancing ecosystem C and N stocks (Feng et al., 2017; Feng et al., 2022). However, long-term or excessive N input can saturate and exceed the demand for N, leading to toxicity or inhibition of biota or enzyme activities (Hagedorn et al., 2012). Moreover, N-saturated ecosystems normally have a high nitrification rate in soil, reduced basic cation (Eastman et al., 2022), and lower soil pH (Xiao et al., 2020). These implications may negatively affect or neutralize biological P uptake and litter breakdown (Zhou et al., 2018b). Hence, the effects of increased N deposition on litter decomposition are inconsistent and are likely to differ strongly among plant types and ecosystems (Bradford et al., 2016).

The relative importance of various indicators changes during the course of the decomposition process with nutrient availability and residual quality. In the later stage of decomposition (> 30% of mass loss), N may exert an adverse effect on decomposition through the inhibition of oxidative enzymatic activities. Additional N in this period showed an inhibition on both C and N release from the N-rich foliar at the later stage, but not from the N-poor litter. This indicated that initial litter N interacted with input N, affecting litter N release. The decrease in gross N release caused a decline in net N release from N-rich litter, while a decline in net N release from N-poor litter was due to the increase in gross N immobilization (Pei et al., 2020).

China is expected to experience a rapid increase in N deposition, estimated as $\approx 20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in 2011-2015 (Yu et al., 2019). This is regionally different due to precipitation and cloud cover, e.g., the western edge of the Sichuan Basin, a region with heavy rainfall and frequent cloud cover, suffers much higher N deposition than the mean value across China. Exploring the litter decomposition and nutrient dynamic under extreme N conditions is required to understand soil C storage and N dynamics in future forests and their respective litter-soil systems

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1.2.3 Climate change and belowground warming

1.2.3.1 Climatic conditions effects on the decomposition process

Climate is the most dominant factor controlling litter decomposition. In a long-term inter-site decomposition experiments dataset, Harmon et al., (2009), generally saw a suppression of decomposition in the cold, dry regions, such as boreal forest or tundra, but a promotion in warm, moist subtropical or tropical forests. This was expressed by means of the climate decomposition index (CDI), describing the impact of variation of temperature and water on decomposition. Climate gradients, including both moisture availability and temperature, is sensitive to plant decomposition and thus affect soil nutrient turnover (Kwon et al., 2021).

Climate can mediate litter decomposition directly by regulating decomposer activity (Aerts, 2006; Fry et al., 2019). For instance, Garcia-Palacios et al. (2013) synthesized and evaluated at the global and biome scales that soil fauna had a more significant positive effect on litter decomposition rates than precipitation and minimum temperature increase. Soil exclusion negatively affected the decay rate in tropical wet forests and cold or dry biomes. However, litter decomposition may be limited by some particular seasonal pattern, such as extreme seasonal precipitation, dry summer, or the temporal separation of high temperature and precipitation (Adair et al., 2008; Hart et al., 1992). In Mediterranean ecosystems, specific dynamics of climatic conditions regulate litter decomposition and SOM sequestration. In summer, high temperatures but low soil moisture can strongly inhibit microbial growth and activity (Fioretto et al., 2005; Santonja et al., 2017), whereas the milder and wetter spring and autumn seasons induce higher metabolic rates of microbes temporarily enhancing the litter degradation (Bonanomi et al., 2021).

In addition, water availability could become the dominant factor to direct litter decomposition at local scales, particularly in desert or semi-arid regions where water is the primary limiting factor (Lopez-Sangil et al., 2018; Wang et al., 2017). Even in a region where mean annual precipitation (MAP) was high, seasonal drought could dominate the course of decomposition. Such as in Canada,

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actual evapotranspiration (AET) is significantly correlated to litter decomposition rates at the forest sites due to water deficit in summer (Moore et al., 1999).

1.2.3.2 Root decomposition

Much research has been done on the dynamic and functioning of aboveground plant decomposition, while belowground ecosystems related to those aboveground traits need far more attention. A meta-analysis of litter input along temperature gradients (i.e., tropical, temperate, boreal and alpine forests) summarized that root litter account for 48% of annual litter inputs, higher than both leaf litter (41%) and other woody litter (11%) (Freschet et al., 2013). In comparison between above- and belowground decomposition, fine root decomposition does not mirror those of leaf litter. Hobbie et al. (2010) suggested that C and N mineralization patterns in decomposing roots and leaf litter did not potentially reinforce each other. Furthermore, microbial communities are not homogeneous, varying across time and space in compositing due to environmental factors and/or litter composition (Luo et al., 2017). Recent work has highlighted that life belowground, including animals and microorganisms, contributes significantly to shaping aboveground biodiversity and the functioning of terrestrial ecosystems (Bardgett and van der Putten, 2014). A C isotopic tracer study found that fine root brought about one-third more soil C retention than leaf litter in temperate ecosystems (Bird et al., 2008). Root litter moreover preferentially stabilized microbially derived C and N in stable SOM fraction as humin as long turnover rates (Mambelli et al., 2011).

1.2.3.3 Decomposition and warming

The Earth's climate will have warmed by 1.0-3.7 °C at the end of this century (IPCC, 2014). Given the temperature sensitivity of litter decomposition, warming will significantly affect ecosystem nutrient cycling and soil C sequestration and loss through: (1) direct climate effects, mainly including elevated temperature and following dramatically changed precipitation regimes in terrestrial ecosystems, (2) climate-induced changes to plant species composition in a given ecosystem, (3) and thus changes to litter quality of these given species. It is considered that climate warming will promote litter decomposition humification with corresponding repercussions for soil C sequestration, especially in cold biomes

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(high-latitude and high-altitude regions), which are strongly temperature limited. Warming may extend the growing season and shorten the wintertime; both would contribute to a stimulation of metabolic activities and litter nutrients mineralization and the C humification process.

Climate and substrate chemistry have long been recognized as the leading controls of decomposition. Climate usually stimulates decomposition through elevated temperature and moisture (Zhang et al., 2008). However, the inhibition occurs when temperature is lower than 10°C or in dryland or wetland systems (moisture <30% or >80%) (Prescott, 2010). Our current understanding of plant residual mineralization and humification focuses mostly on the litter from aboveground plant parts. Much less known about the decomposition of belowground litter (roots) within changing climate.

Roots, linking above- and belowground carbon processes and nutrient cycling, fundamentally affect soil C balance (Bardgett et al., 1998; Gill and Finzi, 2016). Recent experimental evidence suggests that the decomposition processes above- and belowground are decoupled due to the difference in physiobiological competition between above- and belowground (e.g., photodegradation and soil decomposer community) (Keiser and Bradford, 2017; Keiser et al., 2021), with generally more stable environmental conditions belowground (Guo et al., 2021; Zuo and Knops, 2018). Root decomposition is expected to be highly responsive to temperature and precipitation changes (Allison et al., 2007; Silver and Miya, 2001), given that these two factors are important in soil enzyme activity (Jones et al., 2011). Increased precipitation can strongly promote root C mineralization and humification or have no effect, depending on the intensity and duration of the precipitation as well as the soil type and the specific plant species involved (Knoepp et al., 2018; Liu et al., 2021). Decreased soil moisture inhibits nutrient turnover due to changes in root C: nutrient stoichiometry (dryland). Thus, warming and changed precipitation can affect root decomposition, for instance, across the decomposition stage or with the changes in substrate quality (Liu et al., 2021; Norby and Jackson, 2000).

The Tibetan Plateau is predicted to experience "much greater than average" increases in surface temperature in the future (Stocker, 2014), and is one of the

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most sensitive regions to global warming. Previous studies have investigated the effect of climate change on litter decomposition along an increasing elevation, comprising vegetation types, soil microbiology, and snow cover (Berger et al., 2015; Djukic et al., 2010a). Litter decomposition and associated C release are usually decreased with elevation in alpine forests (Margesin et al., 2016). However, some plants mass loss rate and C compounds are demonstrated to increase along an elevational gradient (Berger et al., 2015). Belowground roots account for about 50% of terrestrial net primary production and highly impact C sequestration and nutrient cycling (Iversen et al., 2015). However, it is less clear how climate warming and altered soil hydrothermal conditions would affect root decomposition and C sequestration in cold alpine regions.

1.2.4 Home-field advantage and clearcutting management

1.2.4.1 Interaction between climate and litter quality

Recently, Keuskamp et al. (2013) initiated the Tea Bag Index (TBI, Green tea, more labile material; Rooibos tea, more recalcitrant material) as a standardized and straightforward method for a better understanding of decomposition processes – especially in the early-stage of decomposition – through an assessment of the different drivers and by pinpointing the role of the interactions among environmental factors. Harmonized data from local and standard litter (*Fagus sylvatica* and green tea, and *Pinus nigra* and rooibos tea) responding to changes in temperature and precipitation suggests the suitability of standard litters (TBI) for further examining the environmental drivers of decomposition (Didion et al., 2016). Djukic et al. (2018) tested the TBI at 336 sites (ranging from -9 to +26 °C MAT and from 60 to 3113 mm MAP) across different ecosystems and concluded that climate played a significant role in the decomposition of both litter types (explaining 64% of the variation for Green tea and 72% for Rooibos tea). On the other hand, climate also plays an indirect role in decomposition through changes in tree species distributions in long-term scenarios and consequently in variation in litter quality and quantity (Dyderski et al., 2018a). Therefore, climatic condition incorporating litter traits influences litter decomposition rates.

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1.2.4.2 The decomposition home-field advantage (HFA)

It has been found that local factors, such as those related to the litter quality and soil, are often equal to or more important than other factors in determining litter mass loss rates. In particular, local adaptation of decomposer communities explains the more rapid decomposition of plant litter in their original habitat ('home') than in other habitats ('away') (HFA, Gholz et al., 2000). Simultaneously, biogeochemical models leave about 30% of the variation in litter decomposition unexplained. The HFA effects can be recognized as a term that illustrates part of this remaining variability. Veen et al. (2015) confirmed the occurrence of decomposition HFA effects on average 7.5% faster at home, worldwide.

Decomposition of HFA was firstly introduced into ecosystem ecology in the early 2000s by Gholz et al. (2000). Wang et al. (2013) confirmed by means of a meta-analysis of 33 publications in global forest ecosystems that broadleaf litter (4.4%) had a higher decomposition HFA than conifers (1.0%). Veen et al. (2015) demonstrated recently that the home-field effect was not restricted to litter types or regional climate, but the discrepancy in plant communities between the 'home' and 'away' environment. Gymnosperm species, like conifers, generally have lower levels of cellulose and higher levels of lignin and extractives in their cell walls compared to angiosperms. These differences in the plant cell wall matrix can influence the adaptation and survival of fungi in their habitat by providing different nutritional and physical challenges (Skrede, 2021). Furthermore, the presence of certain phyllosphere community explains the increase of decomposition rates at home relative to away (i.e., greater HFA).

Soil microbial community subsequently takes over the effect of phyllosphere communities on home-field effect as the decomposition process continues (Fanin et al., 2021). This indication probably holds not just for foliage but also decaying roots, and perhaps even more so for roots owing to the *in situ* decomposition in their growing medium (i.e. the rhizospheric soil) and does not move after senescence. Transplants of Chinese cork oak and Chinese red pine within the ingrowth core showed that the presence of moderate local roots was essential for foliage HFA by enzymatic function, while the entire exclusion of roots led to the suppression of HFA (Tian et al., 2018).

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However, Keiser and Bradford (2017) pointed out that climate ‘masks’ the independent influence of the soil decomposer community over long-term litter degradation, because the direct positive effects of a more favorable climate on decomposition rates appears to be correlated with greater functional potential of the decomposer communities. This masked phenomenon was also confirmed in our own review of HFA cases, i.e., no relationship was found between home effect and climatic condition (MAT and MAP) (Figure 1-4).

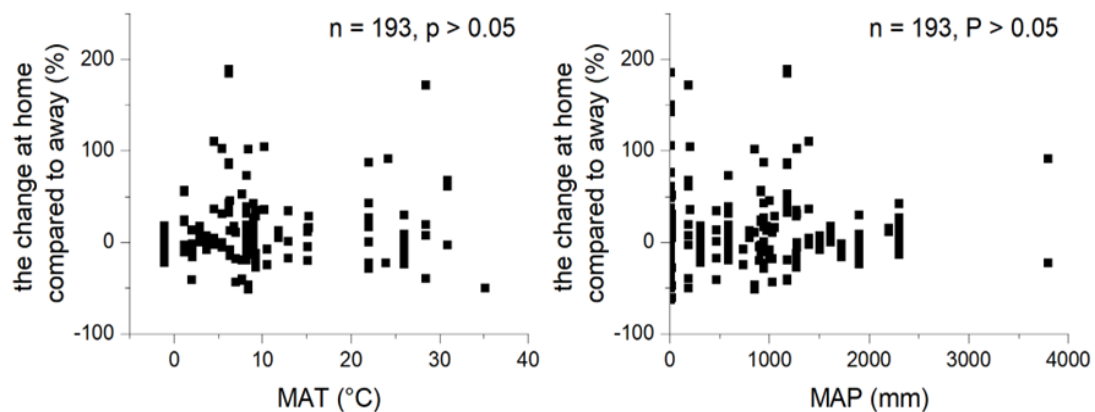


Figure 1-4 In 193 data points from different literature sources, no relationships between environmental condition (MAT and MAP) and HFA effect was found (at significance level 0.05). references data see Table C-1.

1.2.4.3 Litter decomposition in clearcuttings

Forest management not only changes forest structure and associated soil C sink strength (Jandl et al., 2007; Johnson and Curtis, 2001), but it also influences water vapor content within the overlying atmosphere and local micro-climate (Keenan, 2015). Climate change also increases frequencies of extreme weather and natural disasters, such as catastrophic wind, insect outbreaks and forest fires (Dyderski et al., 2018b; Seidl et al., 2016; Seidl et al., 2014). These Disturbance lead to migration and evolution (local adaption) due to the death of the original dominant tree (Bussotti et al., 2015; Dyderski et al., 2018b). In Central Europe, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) for conifer, and beech (*Fagus sylvatica*) and oak (*Quercus spp.*) for broadleaf are the most common stand-forming species in temperate forests (Europe and Unece, 2015). Moreover, more than 95% of the area is under various intensities management (Bengtsson et al.,

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2000; Europe and Uenece, 2015). Clear-cut logging is a common practice that transforms the forests and communities in many European temperate forests (Dymov, 2017). The prevailing biogeochemical processes after clearcutting are essential but uncertain regarding the resilience of original species and the new plant adaption to environmental changes in the successional processes (Heilmeier, 2019; Pridacha et al., 2021). It is currently not well understood how the abiotic and biotic changes in a clear cutting succession affect an individual plant species or the whole forest.

Clear-cut harvesting removes most aboveground biomass. Simultaneously, these sites are subjected to a substantial amount of one-time input of dead roots. The decomposition of root litter mineralized 35% to 50% of initial root mass 1 or 2 years after clearcutting of coniferous stands (Li and Lange, 2015; Lytle and Cronan, 1998). The remaining recalcitrant compounds from stand-forming species may take years or decades to incorporate as stable SOM into the humus layer. Nonetheless, Tian et al. (2018) found that the appearance of a moderate amount of local roots is essential for HFA decomposition in leaf litter and related to the affinity effect by stand-specific root-enzyme interaction. However, very few studies have assessed the appearance of the HFA effect on post-clearcutting decomposition, which could benefit from building up a detailed and predictable forest management strategy according to the forest status.

Clearcutting sites normally quickly occupied by fast-growing, early successional vegetation (grass, ferns, forbs, and low woody shrubs), which is a strong competitor for water and nutrients than the slowly developing hardwood species (Balandier et al., 2005). More slowly developing woody species achieve site dominance and become more competitive over time through light competition (Elliott and White, 1993; Parker et al., 2009). Subsequent observations in post-clearcutting stands usually shift from single-domination towards a mix of hardwoods species, and site conditions can determine the distribution of species in clear-cuts (Oliver, 1996; Swaim et al., 2018). Finally, the progressively stable edaphic environments and reduced competition between vegetation in post-harvest are associated with the appearance of HFA for new species in closed canopies. At the same time, there is a need for gathering reliable scientific

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knowledge on the influence of clearcutting on different successional stages of forest ecosystems.

1.3 Objective

Ecosystem functioning and resilience are dependent on a dynamic relationship between plant species and their abiotic environment, as well as the physical and chemical interactions within the environment. Restoration of these interactions and processes following disturbances and climate change is of great significance to maintaining ecosystem services. Litter decomposition plays a vital role in maintaining the health and balance of ecosystems, and it is of key importance to understand its functioning after disturbances and during climate change. Hence, we conducted litter decomposition experiments in different forest ecosystems following various extreme disturbances and climate conditions (N deposition, elevation, clearcutting), aiming to: i) assess the pattern of litter mass loss rate, including carbon sequestration and nutrients mineralization beyond disturbance on a local level; ii) explore how litter quality, edaphic condition and litter-soil interaction regulate litter mineralization and immobilization in different disturbance and environmental conditions. The results are expected to indicate litter C and nutrient release patterns in changing environments at local scales and further develop sustainable forest management in the future.

To achieve these aims, *in situ* litter decomposition experiments were carried out in a subtropical forest with high N deposition background and in an alpine forest that is temperature sensitive, as well as a reciprocal transplant litter experiment in a German temperate forest following clearcutting management.

Specifically, following questions were addressed.

i) How do the decomposition and nutrient release pattern of contrasting litter species respond to N addition in forests with already high N background deposition in Sichuan, China?

ii) How does C humification (sequestration) of belowground root litter respond to different elevations in an alpine forest in Tibetan Plateau, China?

1. GENERAL INTRODUCTION

iii) How does clearcutting management in a German temperate forest and corresponding changed edaphic conditions affect litter decomposition, nutrient mineralization and field-litter affinity? How is this field-litter affinity (HFA)

The three hypotheses were answered in the next three Chapters and finally answered in the synthesis (Chapter 5) of this thesis.

2. Nitrogen additions retard nutrient release from two contrasting foliar litters in a subtropical forest, southwest China

Modified on the basis of the manuscript

Liyan Zhuang, Qun Liu, Ziyi Liang, Chengming You, Bo Tan, Li Zhang, Rui Yin, Kaijun Yang, Roland Bol and Zhenfeng Xu

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2.1 Introduction

The decomposition of plant litter is a key determinant of carbon (C) and nutrient cycling in terrestrial ecosystems. It is a primary source of energy and nutrients for complex detritus-based food webs and constitutes an important ecosystem service by recycling nutrients, renewing soil fertility, and carbon sequestration (Abelho, 2016). Studies have demonstrated that litter decomposition is controlled by both internal chemical components and external environmental conditions (e.g., climate and soil decomposers) (Zhang et al., 2008). Reactive nitrogen (N) deposition has increased dramatically over the last several decades in tropical areas (Knorr et al., 2005; Liu et al., 2011b; Matson et al., 2002). Elevated N deposition consequently increases soil N availability (Manning et al., 2008), which could further have complex and profound influences on litter decomposition in subtropical forests.

Nitrogen deposition, as a global change driver, has great potential to affect plant litter decomposition in terrestrial ecosystems (Berg and Matzner, 1997). It has been reported that N additions cause positive, negative, or neutral effects on litter decomposition (Berg, 2014; Liu et al., 2007; Zhang et al., 2018b). The effect of N input on decomposition is regulated by substrate quality, N addition rates, and ambient N deposition (Knorr et al., 2005; Manning et al., 2008). In N-deficient ecosystems, N addition generally stimulates the decomposition by increasing soil N availability or reducing the C: N litter ratios (Norris et al., 2013). However, in N-sufficient sites, the added N often shows an inhibitory or neutral effect on litter decomposition and nutrients mineralization due to the saturation of soil N availability and the suppression of enzymic synthesis (Carreiro et al., 2000; Downs et al., 1996; Hobbie, 2008; Mo et al., 2006; Zhou et al., 2017). The response of litter decomposition to environmental changes may largely depend on the litter's initial nutrient conditions (Reich et al., 2005; Zhang et al., 2016). As far as we know, nutrient-rich litter generally decays faster relative to nutrient-poor litter (Micks et al., 2004; Zhu et al., 2016). Regarding N additions, the effect of added N on litter decomposition and nutrient release generally varies among litter types and decomposition stages. A previous meta-analysis also indicated that N additions stimulated the decomposition rate of high-nutrient litter, but inhibited the

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decomposition of low-nutrient litter (Knorr et al., 2005). Additionally, the impact of N additions is positive in the initial phase, but negative in the late stage (Berg and Matzner, 1997; Parton et al., 2007). As a result, it is important to investigate N deposition responses of different-quality litters coexisting in an ecosystem using a N manipulation experiment, particularly in high-N-deposition subtropical forest ecosystems.

N deposition has risen significantly in China in the last several decades (Yu et al., 2019). Increasing N deposition may be favorable to C sequestration in subtropical forests (Yu et al., 2014). Atmospheric wet N deposition on the western edge of the Sichuan Basin (known as the “rainy zone of west China”) is much higher than the mean value across China, as a result of rich rainfall and reactive N (Xu et al., 2018). Previous studies have indicated that extremely high N additions (100 and 150 kg N ha⁻¹ yr⁻¹) constrained the litter decomposition rate in subtropical forests (Chen et al., 2017; Tu et al., 2014a; Tu et al., 2013). However, the effect of N deposition on foliage decomposition and nutrients mineralization may vary between litter types (nutrient-rich vs. nutrient-poor) or decomposition stages (early vs. late). To examine the aforementioned scientific hypothesis, a field experiment was conducted to examine the effect of simulated N deposition on mass loss and C, N, and phosphorus (P) release, as well as the stoichiometric dynamics of two contrasting broad-leaved litter types. *Michelia wilsonii* is an evergreen tree species, but *Camptotheca acuminata* is a deciduous tree species. There were significant differences in litter matrix between the two tree species. Initial N and P concentrations were lower in the *M. wilsonii* litter relative to those of the *C. acuminata* litter. Conversely, lignin, cellulose, C: N, C: P, and lignin:N were significantly higher in the *M. wilsonii* litter versus the *C. acuminata* litter (Liu et al., 2018b). The main objectives of this study were to: (i) examine the effect of N additions on the decay rate as well as the C, N, and P release of two litters; and (ii) determine if the N-induced effect varied between two contrasting litter types.

2.2 Materials and methods

2.2.1 Site description and experimental design

The study was conducted in the Dujiangyan Experimental Forest of the Sichuan Agricultural University, Southwestern China (31°01'–31°04' N, 103°37'–

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103°43' E, 896–1320 m a.s.l.). This forest is characterized by a canopy composed of *M. wilsonii* and *C. acuminata*. Mean annual precipitation is 1243 mm. Mean annual temperature is 15.2 °C, with a minimum in January (−1.4 °C) and maximum in July (31.6 °C). The soil type is classified as Ferralsol with old alluvial yellow loam, according to the FAO (Food and Agriculture Organization of the United Nations) classification system. The basic topsoil properties (0–20 cm) are as follows: organic C 15.76 g kg⁻¹, total N 1.92 g kg⁻¹, total P 0.32 g kg⁻¹, and pH 5.73.

Experimental plots were established in November 2015, according to the ambient atmospheric wet N deposition (36.2 kg N·ha⁻¹·yr⁻¹) in the study site (Yang et al., 2018). Three N addition levels of 10 × 10 m in triplicates were established for this experiment: control (Control: 0 kg N ha⁻¹ yr⁻¹), low-N addition (LN: 20 kg N ha⁻¹ yr⁻¹) and high-N addition (HN: 40 kg N ha⁻¹ yr⁻¹). Both LN and HN treatments roughly simulate the scenarios that wet N deposition would be increased by about 50% and 100%, respectively. Ammonium nitrate (NH₄NO₃) solution was applied monthly in 12 equal applications from December 2015 to December 2016. There were no significant differences in soil temperature or moisture under different N addition treatments (Liu et al., 2018b).

2.2.2 Litterbag experiment

Both *M. wilsonii* and *C. acuminata* were chosen in this study because they are the two dominant tree species in this site. In addition, they represent two contrasting litter types (evergreen and rich-nutrient vs. deciduous and low-nutrient) in subtropical areas. We collected fresh litter from the forest stand adjacent to the N manipulation site in late October 2015. Air-dried material of approximately 15.00 ± 0.01 g of two species was placed into 20 × 25 cm nylon mesh bags with a 1.0 mm mesh on the surface and 0.055 mm mesh on the bottom. Duplicate litter bags were placed on the surface in the respective treatment section in early January 2016. Meanwhile, two litterbags of each species were retrieved from each plot for determination of initial chemical properties, and were harvested after 46, 105, 164, 284 and 351 days from each plot. Soil particles and other extraneous materials were removed from the harvested litters, and the cleaned samples were then oven-dried (85 °C for 48 h) to constant mass and the mass remaining was weighed.

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2.2.3 Chemical analysis

The oven-dried litter samples were ground and sieved. The sieved samples were used for chemical analysis. The organic carbon (C), total nitrogen (N), and total phosphorus (P) concentrations were determined with the methods of dichromate oxidation, Kjeldahl determination (KDN), Top Ltd., Zhejiang, China) and phosphomolybdenum yellow spectrophotometry (TU-1901, Puxi Ltd., Beijing, China), respectively.

2.2.4 Calculations and Statistical Analysis

Decomposition rates were calculated from the remaining dry mass using a single negative exponential decay model $y = e^{-kt}$, where y is the fraction of mass remaining at time t , t is the time elapsed in years and k is the annual decay constant [30]. The remaining amount of elements C, N and P on each sampling date was determined by multiplying the litter elements' (C, N and P) concentration by the litter mass and the litter mass remaining, and comparing it to the initial litter elements' (C, N and P) mass. The stoichiometric rates (C:N, C:P and N:P) were calculated on an element mass basis. Repeated-measure analysis of the variance was used to test the effects of tree species, N additions, sampling data and their interactions on elements (C, N and P) remaining and stoichiometric ratios. For a specific date, one-way analysis of variance was used to determine the chemistry addition effect on the measured parameters. Differences among means were considered significant at the $p < 0.05$ level. All statistical tests were performed using the Software Statistical Package for the Social Sciences (SPSS) version 22.0 (IBM SPSS Statistics Inc., Chicago, IL, USA).

2.3 Results

2.3.1 Decay Constant

Regardless of N additions, decay constants (k values) markedly differed between species (Figure 1). *C. acuminata* litter always decomposed faster than *M. wilsonii* litter. For *M. wilsonii* litter, the k values were significantly lower in the N addition treatments than in the control. However, N additions had no significant effect on k values of *C. acuminata* ($p > 0.05$).

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2.3.2 Litter C, N and P remaining

The amount of C remaining in both species decreased significantly as decomposition proceeded (Table 2-1; Figure 2-2a, b). After 168-day fast loss, C loss in *M. wilsonii* gradually slowed down and retained 24%–32% after one year of decomposition. Similarly, C loss of *C. acuminata* litter occurred rapidly and left 11%–17% until the end of the experiment (Figure 2-2a,b). N treatments had no significant effect on litter C loss ($p = 0.139$, Table 2-1).

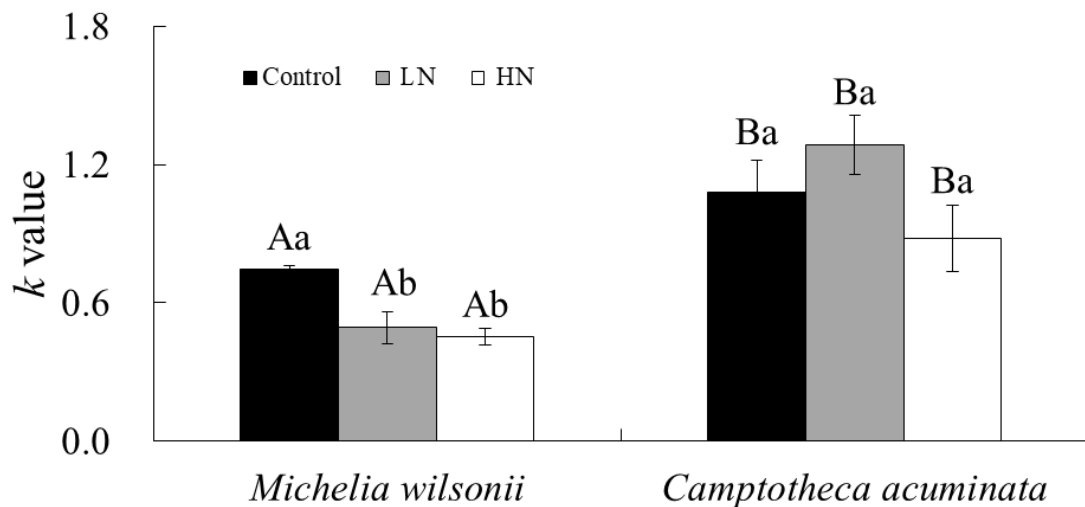


Figure 2-1. The decomposition constant (k , year⁻¹) of *M. wilsonii* and *C. acuminata* over 1-year decomposition under three N treatments. Values are expressed as mean \pm SE. Different lowercase letters indicate significant differences between N additions for the same species; different capital letters denote significant differences between tree species for the same N addition. Control: no N addition (0 kg N ha⁻¹ yr⁻¹); HN: high-N addition (40 kg N ha⁻¹ yr⁻¹); LN: low-N addition (20 kg N ha⁻¹ yr⁻¹).

For *M. wilsonii*, the remaining N was higher in the N treatment plots than in the control plots during the late stage, especially after 284 and 351 days (Table 2-1; Figure 2-2c,d). By the end of the experiment, the remaining N for *M. wilsonii* was 68%, 79% and 106% for the control, LN and HN plots, respectively (Figure 2-2 c,d). However, N addition did not significantly affect *C. acuminata* N release. The remaining N for *C. acuminata* was 61%, 56% and 70% for the control, LN and HN plots, respectively (Figure 2-2c,d). Regardless of N treatments, *M. wilsonii* N loss

2. N ADDITIONS RETARD NUTRIENT RELEASE FROM FOLIAR LITTERS

rates were significantly slower than those of *C. acuminata* after one year of incubation (Table 2-1; Figure 2-2c,d). Statistical analysis indicated that the effect of N addition on the remaining N in litter was dependent on litter type and decomposition period (Table 2-1).

Both litter types showed different patterns in P release throughout the experimental period (Figure 2-2e,f; Table 2-1). The P content of *M. wilsonii* litter clearly accumulated in the late decomposition stage (Figure 2-2e). However, the *C. acuminata* P content was always released during the decomposition process (Figure 2-2f). After one year of decomposition, the P remaining in *M. wilsonii* litter was 48.2%, 82.7% and 119.4%, in the control, LN and HN plots, respectively. However, the P remaining in *C. acuminata*, was only 38.8%, 24.6% and 51.9% in the control, LN and HN plots, respectively. The ANOVA analysis showed that N treatments, species, decomposition stages and their interactions all had significant influences on the P remaining (Table 2-2).

Table 2-1. Results of repeated-measure ANOVA showing the effects of sampling dates (T), tree species (S), N treatments (N) and their interactions on element (C, N and P) remaining and their C: N: P stoichiometry.

	C Remaining		N Remaining		P Remaining	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
S	45.90	< 0.001	52.22	< 0.001	68.98	< 0.001
N	2.34	0.139	4.69	0.031	9.04	0.004
T	182.18	< 0.001	32.81	< 0.001	39.36	< 0.001
S × T	3.78	0.027	24.65	< 0.001	35.38	< 0.001
N × T	2.13	0.090	6.86	0.006	11.92	0.001
N × S	0.43	0.659	0.95	0.415	1.21	0.333
N × S × T	1.37	0.266	5.51	0.013	14.36	< 0.001

2. N ADDITIONS RETARD NUTRIENT RELEASE FROM FOLIAR LITTERS

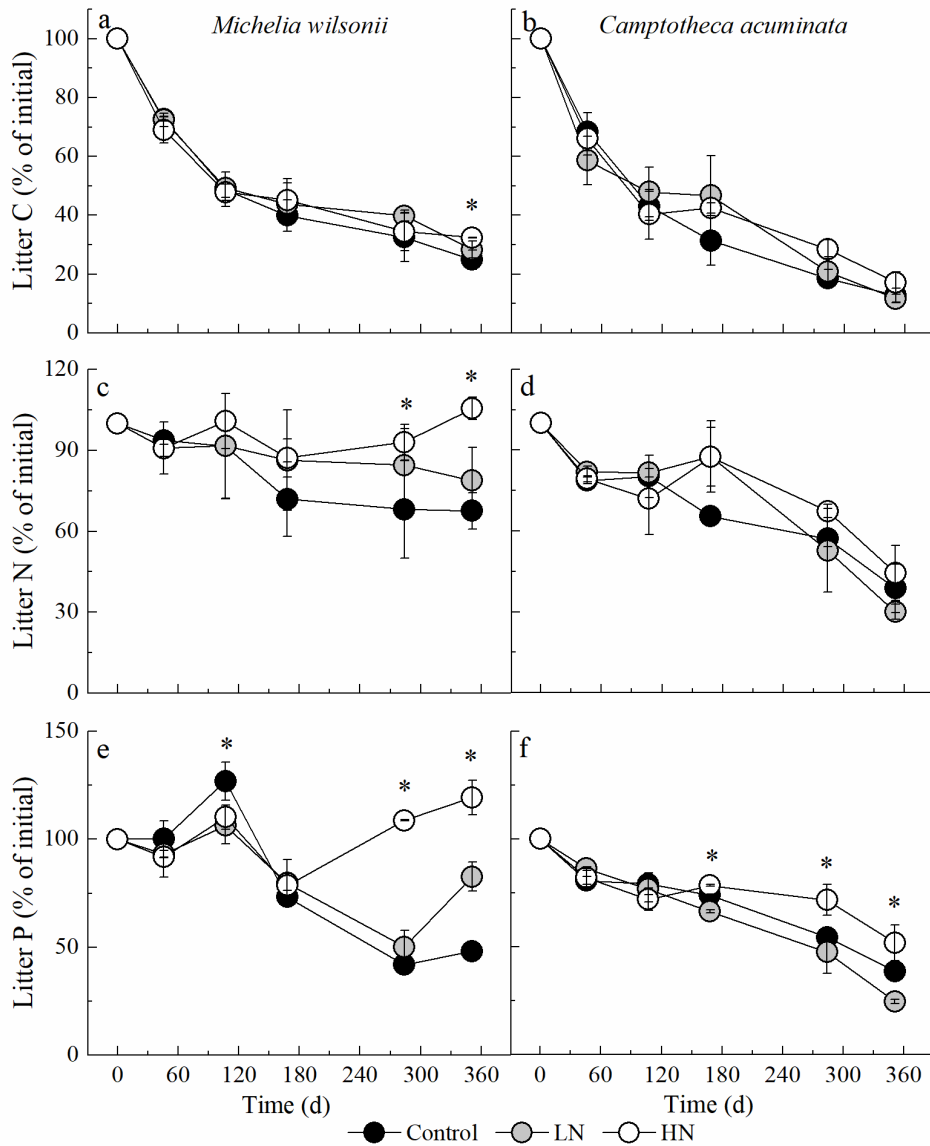


Figure 2-2. C, N and P remaining of *M. wilsonii* and *C. acuminata* over 1-year decomposition under three N treatments. Values are expressed as mean \pm SE. * Indicates significant differences among N additions. Control: no N addition ($0 \text{ kg N ha}^{-1} \text{ yr}^{-1}$); HN: high-N addition ($40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$); LN: low-N addition ($20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$).

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2.3.3 Stoichiometric Dynamic

Table 2-1. Continued

	C: N		C: P		N: P	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
S	173.58	< 0.001	257.68	< 0.001	68.21	< 0.001
N	1.12	0.359	4.13	0.043	3.29	0.073
T	81.73	< 0.001	55.80	< 0.001	8.63	0.004
S × T	3.25	0.039	15.38	< 0.001	3.32	0.062
N × T	0.77	0.589	6.49	< 0.001	4.18	0.030
N × S	2.82	0.099	0.24	0.210	0.20	0.237
N × S × T	0.83	0.542	5.92	< 0.001	8.52	0.003

Regardless of N treatment, the N: P ratios in *M. wilsonii* were obviously higher than those of *C. acuminata* during the one-year incubation (Figure 2-3e,f). ANOVA results indicated that the effects of N additions on the N: P ratio were dependent on tree species and sampling interval (Table 2-1).

Irrespective of N treatment, the C: P ratio of *M. wilsonii* litter remarkably declined during the first 105 days of decomposition but tended to increase after 286 days. N treatments significantly decreased C: P ratios in 351 days, compared to control plots (Figure 2-3c). However, the *C. acuminata* C: P ratio generally decreased over the one-year decomposition (Figure 2-3d). The ANOVA analysis showed that tree species, N additions, sampling dates and their interactions all had a significant impact on C: P ratio (Table 2-1).

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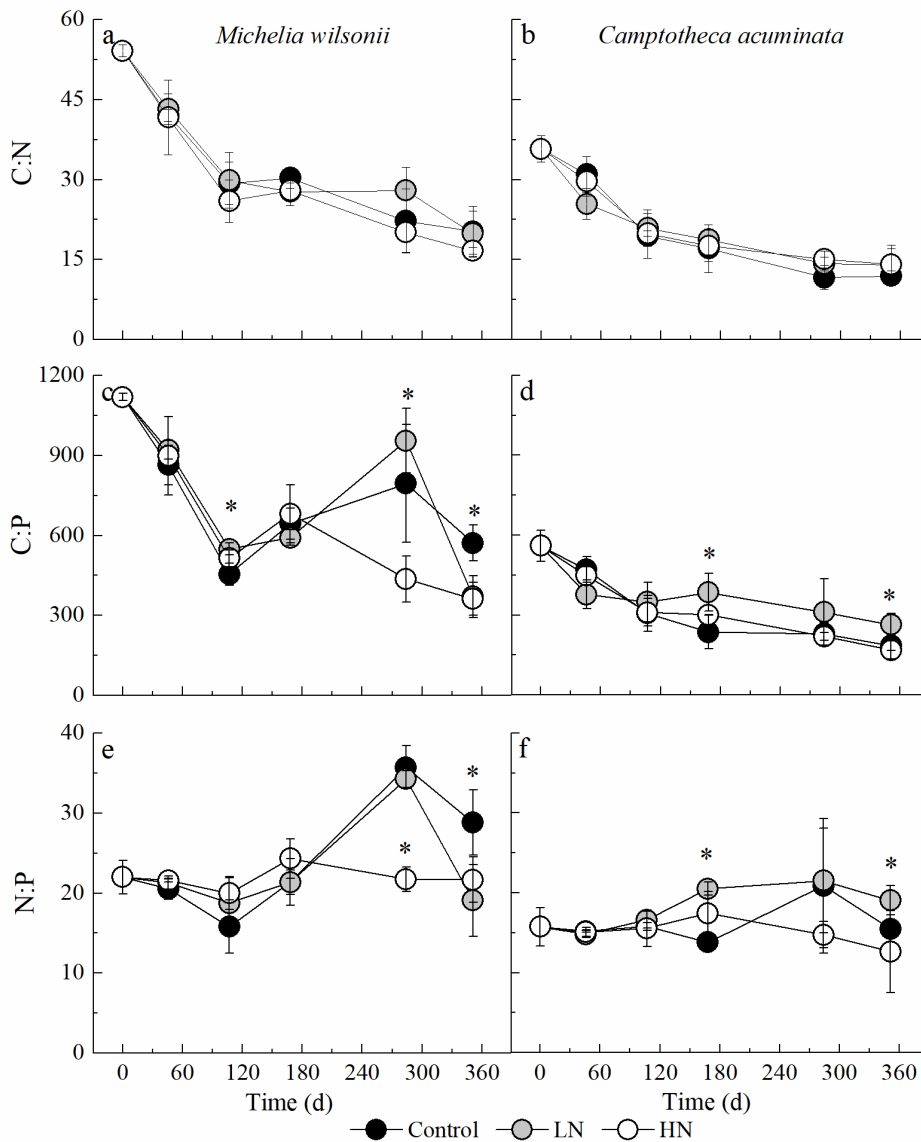


Figure 2-3. C, N and P stoichiometric ratios of *M. wilsonii* and *C. acuminata* over 1-year decomposition under three N treatments. Values are expressed as means \pm SE. * Indicates significant differences among N additions. Control: no N addition ($0 \text{ kg N ha}^{-1} \text{ yr}^{-1}$); HN: high-N addition ($40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$); LN: low-N addition ($20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$).

2.4 Discussion

The results of this study showed significant differences in litter decomposition and nutrient release between tree species. Generally, litter with

2. N ADDITIONS RETARD NUTRIENT RELEASE FROM FOLIAR LITTERS

high initial nutrient content and low C: N ratio were suggested to have higher decomposition rates (Marklein and Houlton, 2012). In our study, nutrient content was higher, but stoichiometric ratios were lower in *C. acuminata* litter than in *M. wilsonii* litter. Consequently, the decomposition rate of *C. acuminata* litter was often faster than that of *M. wilsonii* litter, irrespective of the N regime.

However, N additions had different effects on the decay rate of the two types of litter. N additions decreased the decomposition rate of *M. wilsonii* litter, but did not have an effect on *C. acuminata* litter. A previous study also reported that extremely high N additions inhibited litter decomposition rate in subtropical forests (Zhou et al., 2017). Knorr et al. (2005) concluded that ambient N deposition and N addition levels are two important factors regulating litter decomposition. Litter decomposition may be inhibited when N addition rates are 2–20 times higher than the ambient N deposition amount. In the present case, N addition levels were roughly between 0.5 and 1 times higher than the background N deposition. Our fertilization rate was relatively low compared to other simulated N deposition experiments. On the other hand, elevated N may increase soil P limitation in a site, and the P effect may override the N effect (Aerts, 1997). Therefore, litter P content might regulate the decomposition rate in high ambient N deposition and P-poor ecosystems. Thus, N additions exhibited a greater suppression on P-low *M. wilsonii* litter compared to high-P *C. acuminata* litter.

Nutrient release in decomposing litter is positively regulated by total N content or stoichiometric ratios (e.g., C: N and C: P) (Moore et al., 2006). Previous studies reported that N in decomposing litter starts to release when the C: N ratio of the litter is <40 (Parton et al., 2007). The results in our study noted the initial C: N ratio of *M. wilsonii* and *C. acuminata* was 54 and 36, respectively. Net N release of both tree species occurred during the entire experiment. The rate of N release was greater in N-rich *C. acuminata* than in N-poor *M. wilsonii*. This may be because the *M. wilsonii* C: N ratio is much higher than that of *C. acuminata*. N additions slowed down the net N release in decaying litter. In addition, low-N litter *M. wilsonii* could be more easily affected by external N addition relative to high-N litter *C. acuminata*. Litter N mineralization may also be mediated by initial litter N content (Tu et al., 2014b). Simulated N deposition suppressed the net N release of

2. N ADDITIONS RETARD NUTRIENT RELEASE FROM FOLIAR LITTERS

foliar litter in a natural evergreen broad-leaved forest and in a bamboo forest with a high background N deposition area (Kuperman, 1999). Moreover, the suppression of N addition on litter N mineralization was stronger in N-poor *Liquidambar formosana* litter than in N-rich *Alnus cremastogyne* (Zhou et al., 2018a). This study also found that the effect of N addition on litter N release differed between contrasting litters, with *M. wilsonii* being stronger than *C. acuminata*. It is important to note that N was even immobilized in the *M. wilsonii* litter in the HN treatment by the end of the experiment. Net N immobilizations generally occur as decomposers access N exogenous to the litter and convert it to microbial biomass or exo-enzymes (Zheng et al., 2017). In this region, microbes may not meet their basic N requirements. N addition treatments could, to some extent, provide more external N for biological enrichment, implying that the N release in decomposing litters may be partly offset by microbial immobilization.

Similar to N release, the P pattern in decomposing litter is primarily regulated by litter C: P ratios (Zheng et al., 2017; Zhou et al., 2017). The immobilization of litter P has been seen to occur when the C: P ratio is greater than 700 (Vivanco and Austin, 2011). The initial C: P ratio for *C. acuminata* litter was 560. Net P release occurred in *C. acuminata* litter under all the N additions throughout the experimental period. However, the initial C: P ratio for *M. wilsonii* litter was 1192. As a result, microbes often immobilized more P in the litter. In addition, HN addition resulted in the net P immobilization or inhibitory effect of litter P in both litter types by the end of the experimental period. P input is usually minimal in natural ecosystems, therefore, N additions may, to some extent, strengthen the P limitation of the ecosystems. Litter P could be rapidly recycled internally during the decomposition processes, which could in turn hinder P release to the soil (Chen et al., 2013). Our study found that N additions tended to favor the accumulation of P. Some studies have also found an accumulation of P with N deposition (Gong et al., 2020). The litter P accumulation induced by N deposition might attribute to a relative shortage of P associated with the stoichiometric constraint theory (Yuan and Chen, 2015), but further supporting evidence is necessary.

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Irrespectively of tree species and N additions, the C: N ratio generally decreased as litter decomposition progressed. This result is in line with the observations obtained in many other tree species (Cotrufo et al., 1995; Finn et al., 2015; Manzoni et al., 2010). The C: P and N: P ratios pattern was different between two contrasting tree species during the decomposition process. This is because the nutrients release pattern differed between *C. acuminata* and *M. wilsonii* during decomposition. In addition, previous studies have also found that simulated N deposition altered the C, N and P stoichiometry (Hobbie, 2008; Zhu et al., 2016). As mentioned above, litter C release was similar among N addition treatments, but litter P release declined with increasing N additions. To alleviate the N-induced negative effect on litter P release, the litter P demand will be increased under N additions (Chen et al., 2013). Therefore, N additions, especially under the HN treatment, tended to decrease C: P ratios in the late period of decomposition. On the other hand, N-inhibited magnitude in litter P was greater compared to that in litter N during the late period. N additions also tended to decrease litter N: P stoichiometry in the late period of decomposition.

2.5 Conclusions

This study investigated the litter decomposition and nutrients release of two contrasting litter types following gradient N additions in a subtropical forest with high N background. The decay rate and the mineralization of N and P was faster in nutrient-rich *C. acuminata* litter than in nutrient-poor *M. wilsonii* litter, regardless of N regime. The effect of N addition had negative effects on the decomposition rate as well as N and P release in *M. wilsonii* litter during the late decay phase. For *C. acuminata*, N additions did not affect N release, but retarded P release in the late stage. Overall, the effect of N addition on the remaining N and P was stronger in *M. wilsonii* litter than in *C. acuminata* litter, probably due to the elevated C: N and C: P ratios during decomposition. Increasing N deposition may slow down the nutrient release from decomposing litter in the subtropical forests where significant N deposition occurs. Additionally, N-induced effects may, to some extent, be dependent on the initial quality and the decay stage.

3. Root diameter controls the accumulation of humic substances in decomposing root litter

Modified on the basis of the manuscript

Qun Liu, Liyan Zhuang, Rui Yin, Xiangyin Ni, Chengming You, Kai Yue, Bo Tan, Yang Liu, Li Zhang and Zhenfeng Xu

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3. ROOT DIAMETER CONTROLS HUMIC SUBSTANCES ACCUMULATION

3.1 Introduction

Organic matter accumulated on the soil surface as humus is of primary importance for long-term soil fertility in forest ecosystems (Prescott et al., 2000b). Humification is the biogeochemical transformation of plant detritus into more recalcitrant humic substances, which largely regulate soil carbon (C) sequestration, soil aggregate formation and nutrient storage (Berg and McClaugherty, 2014). Plant roots and leaves are two crucial sources of soil organic matter. Studies have explored the accumulation of humic substances in decomposing foliar litters (Ciarkowska and Miechówka, 2017; Ni et al., 2014). Recent evidences indicate that plant roots may be more important in accumulating stable soil organic matter than leaves in some forest ecosystems (Mambelli et al., 2011; Sun et al., 2018). However, the humification patterns of plant roots and their controls are not as well understood as those on foliar litters, especially in cold forest ecosystems.

Substrate quality is considered to be one of the most important drivers of litter humification (Cotrufo et al., 2013). In terrestrial ecosystems, the rates of root decomposition mainly depend on root chemistry (Silver and Miya, 2001). Root diameter has been supposed as a key agent of root decomposition because it integrates physical-chemical properties associated with root development (Fahey and Arthur, 1994). For example, small-diameter roots generally have higher nutrient contents [e.g., nitrogen (N) and phosphorus (P)] and less structural carbohydrates (e.g., lignin and cellulose) as compared with large-diameter roots (Ludovici and Kress, 2006; Silver and Miya, 2001). Small-diameter roots are likely to be utilized more efficiently by microbes relative to large-diameter roots (Cotrufo et al., 2013; Sun et al., 2013). Therefore, root humification may decrease with increasing root diameter. However, few studies combined root diameter as a factor to explore the pattern of root humification (Wang et al., 2014). Therefore, we aimed to fill this gap and assess the accumulation of humic substances in decomposing root litters.

High-altitude forest ecosystems contain large amounts of soil carbon stocks, which are especially vulnerable to climate change (Scowcroft et al., 2000; Xu et al., 2015). Climate (e.g., temperature and moisture) has great potential to regulate

3. ROOT DIAMETER CONTROLS HUMIC SUBSTANCES ACCUMULATION

litter humification by influencing decomposers (Prescott et al., 2000b; Tan et al., 2013). Current studies have shown that experimental warming often has accelerated the rates of litter decomposition and nutrient release (e.g., (Berger et al., 2015; Xu et al., 2015), which in turn may favor the humification of plant litters. However, few studies have focused on the accumulation of humic substances of root litters, although many artificial warming experiments have examined the decomposition of foliar litters (Yue et al., 2015). Environmental gradients (e.g., altitude and latitude) are often used for climate change studies (Berger et al., 2015). How ongoing climate change affects long-term soil carbon sequestration through humification of plant roots still remains unclear. Therefore, it is very crucial to synchronously examine root humification along natural gradients.

Here, a two-year field experiment was conducted to investigate the mass remaining and humification of root litter of three root diameters (0-2 mm, 2-5 mm and 5-10 mm) of two common tree species (*Picea asperata* and *Abies faxoniana*) at two elevations (3037 m and 3580 m) using a litter-bag method on the eastern Tibetan Plateau of China. The main objective of this study was to test the following hypotheses: (1) root humification would decrease with increasing root diameter; (2) the accumulation of humic substances would be faster at the low-elevation site (3037 m) than at the high-elevation site (3580 m).

3.2 Material and methods

3.2.1 Site descriptions

This experiment was carried out at the Long-term Research Station of Alpine Forest Ecosystem of Sichuan Agricultural University (31°14'-31°19'N, 102°53'-102°57'E, 2458-4619 m a.s.l), which is located on the eastern Tibetan Plateau of China. Annual mean temperature ranges from 2 °C to 4 °C and mean annual precipitation is about 850 mm (Zhuang et al., 2018). In general, the ground is covered under seasonal snow from mid-November to early April. The soil is classified as a Cambic Umbrisols according to the IUSS Working Group (Group, 2007). Minjiang fir (*Abies Faxoniana* Rehd.) and dragon spruce (*Picea asperata* Mast.) are two dominant tree species in this area. More details about the study sites can be found in our previous study (Li et al., 2017).

3. ROOT DIAMETER CONTROLS HUMIC SUBSTANCES ACCUMULATION

Soil temperature at the depth of 10 cm was measured every 2 h using DS1923-F5 Recorders (iButton DS1923-F5, Maxim/Dallas Semiconductor, Sunnyvale, USA) at the two elevation sites (3037 m and 3580 m) during the experimental periods (Figure A-1). Soil water content (SWC) at the depth of 10 cm was determined by a Theta probe (Figure A-2). Daily mean soil temperature (MT), positive accumulated temperature (PAT), sum of daily mean temperature above 0 °C) and negative accumulated temperature (NAT, sum of daily mean temperature below 0 °C) were calculated during the winter and growing season (between two successive sampling dates), respectively (Table A-1). There were no significant differences in basic soil properties between two elevation sites in July 2013 (Table A-2).

3.2.2 Root collection and litterbag experiment

In July 2013, root samples were carefully excavated from the topsoil (20 cm depth) within approximately 2 m distance of the target tree stem from a fir-spruce mixed forest adjacent to 3037 m study site. For each species, roots were gently separated from soil particles and other materials by washing and brushing with deionized water. For each species, roots were gently separated from soil particles and other materials by washing and brushing with deionized water. The cleaned roots were divided into 0-2 mm (fine roots), 2-5 mm (medium roots) and 5-10 mm (coarse roots) diameter classes (Camiré et al., 1991). According to diameter data of root orders of two conifers, fine roots (0-2 mm) approximately contain the first 6 order roots (McCormack et al., 2015; Zhuang, 2016).

About 5.000 ± 0.010 g root segments were sealed into 20 cm × 20 cm polyester litterbags. The mesh sizes of litterbags were 1.0 mm on the top and 0.1 mm on the bottom. Six plots (5 m × 5 m) were randomly established at each site (3037 m and 3580 m). For each root class, duplicate sets of litterbags were deployed horizontally at a soil depth of 10 cm in each subplot late in the growing season (mid-October) 2013. Meanwhile, one litterbag of each root diameter class of two tree species was randomly retrieved from each plot for determination of initial water content of air-dried roots and root chemistry after litterbags establishment. The initial water content of root samples was used to correct the initial dry mass of roots.

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One litterbag of each root class of the two tree species was randomly retrieved from each plot on early spring 2014 (mid-April), late autumn 2014 (mid-October), early spring 2015 and late autumn 2015. In the laboratory, extraneous matter such as other plant materials, mineral soil particles and soil animals were handpicked from the decomposed litters. The cleaned samples were oven-dried at 65 °C for 48 hours to determine litter mass remaining at each sampling time. Root samples were pulverized and passed through a 0.15 mm sieve. Sieved root samples were used for chemical analyses.

3.2.3 Chemical Analyses

The organic C, N and P concentrations were determined using the H₂SO₄-K₂Cr₂O₇ oxidation method, the Kjeldahl acid-digestion method and the phosphomolybdenum yellow spectrophotometry method, respectively (Xu et al., 2015). The lignin and cellulose concentrations were determined according to a modified acid detergent solution method (Vanderbilt et al., 2008).

Humic substances (HS) were extracted with 100 ml mixed solutions of 0.1 M NaOH + 0.1 M Na₄P₂O₇ using 1.00 g air-dried root (Adani and Ricca, 2004; Ni et al., 2015). Humic acid (HA) and fulvic acid (FA) were separated with 0.5 M H₂SO₄ at 80 °C, and the separated humic acid was dissolved with hot 0.05 M NaOH solution, and fulvic acid was determined by the difference between HS and HA. Both humic substances and humic acid were filtered through a 0.45 µm filter paper and then analyzed using a TOC analyzer (multi N/C 2100, Analytik Jena, Thüringen, Germany).

3.2.4 Calculations

Mass remaining was calculated as:

$$\text{Mass remaining (\%)} = M_t/M_0 \times 100\% \quad (1)$$

where M₀ and M_t are the oven-dried mass of initial litter and remaining residues, respectively, at times *t*;

Fulvic acid concentration (FA) was calculated as (Gigliotti et al., 1999):

$$FA \text{ (g kg}^{-1}\text{)} = HS - HA \quad (2)$$

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where HS and HA denote the concentrations of humic substances and humic acids, respectively;

Humification degree (HD) was calculated as (Ni et al., 2015):

$$HD (\%) = HS/OC \times 100\% \quad (3)$$

where HS and OC indicate the concentrations of humic substances and organic carbon, respectively.

3.2.5 Statistical analyses

Repeated-measures analysis of variance (ANOVA) was used to evaluate the effects of root diameter, tree species and elevation on root mass remaining, the concentrations of humic substances, humic acid, fulvic acid and humification degree over time. A step-wise regression analysis was conducted to examine the influences of initial litter quality (the concentration of C, N, P, lignin and cellulose and stoichiometric ratio) and environmental factors (SWC, MT, NAT and PAT) on humic substances, humic acid, fulvic acid and humification degree during winter and growing season over the two years of decomposition. For each sampling time, differences in all variables among root diameters were evaluated using one-way ANOVA following multiple comparisons with Tukey test if the one-way ANOVA results were significant. The statistical tests were considered significant at the $P < 0.05$ level. All analyses were performed in SPSS 17.0 (IBM SPSS Statistics Inc., Chicago, IL, USA).

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3.3 Results

Table 3-1. Results of repeated measures ANOVA showing the F values for effects of diameters, elevation, species, time, and their interactions on mass remaining (MR), humic substances (HS), humic acid (HA), fulvic acid (FA) and humification degree (HD).

Factor	MR	HS	HA	FA	HD
Diameter (<i>D</i>)	17.30***	132.36***	106.29***	51.19***	147.86***
Elevation (<i>E</i>)	7.70*	1.29	3.75	0.18	5.92*
Specie (<i>S</i>)	6.25*	1.52	0.01	1.26	0.01
Time (<i>T</i>)	438.89***	445.37***	116.88***	545.55***	453.50***
<i>D</i> × <i>E</i>	0.73	0.44	0.17	0.22	1.22
<i>D</i> × <i>S</i>	1.58	13.68***	4.93*	7.12**	22.84***
<i>D</i> × <i>T</i>	3.51**	4.11***	6.05***	6.37***	5.06***
<i>E</i> × <i>S</i>	0.42	0.36	0.18	0.44	1.27
<i>E</i> × <i>T</i>	2.13	31.60***	5.95***	33.72***	34.10***
<i>S</i> × <i>T</i>	0.91	1.71	0.97	2.26	4.67*
<i>D</i> × <i>E</i> × <i>S</i>	0.10	0.89	0.31	1.01	1.06
<i>D</i> × <i>E</i> × <i>T</i>	1.00	0.55	1.18	0.62	0.78
<i>D</i> × <i>S</i> × <i>T</i>	0.99	3.39**	2.33*	2.92*	4.53***
<i>E</i> × <i>S</i> × <i>T</i>	0.47	2.03	0.21	2.32	3.23*
<i>D</i> × <i>E</i> × <i>S</i> × <i>T</i>	0.40	0.50	2.33	0.60	0.70

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

3.3.1 Mass remaining

Tree species and root diameter alone had significant influences on root mass remaining (Figure 3-1 a-d; Table 3-1, all at least at $P < 0.05$). In general, mass remaining of the two conifer trees tended to increase with an increase of root diameter, especially at the 3037 m (Figure 3-1 a-d). Root mass remaining at the 3037 m was slightly lower than that at the 3580 m by the end of the experiment (Figure 3-1; Table 3-1, $P < 0.05$). After 2-year decomposition, the mass loss of

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spruce and fir root litters was 1.6-6.2% and 1.6-4.0% greater, respectively, at the 3037 m than at the 3580 m (Figure 3-1 c, d).

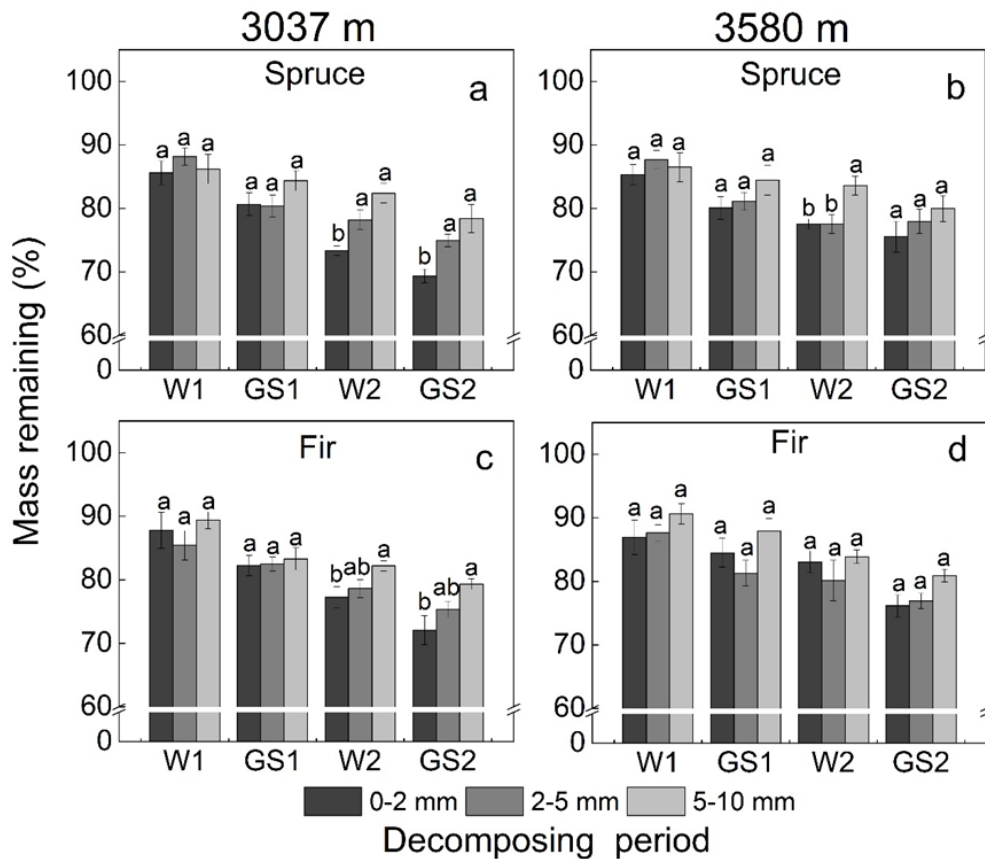


Figure 3-1. Mass remaining (mean±SD, n=6) in different root diameters for spruce and fir at two elevations during the two-year decomposition. Different lower case letters indicate significant differences between diameters for same species. W1: the first winter, GS1: the first growing season, W2: the second winter, GS2: the second growing season.

3.3.2 Humic substances concentration

Regardless of root diameter, tree species and elevation, the concentration of humic substances had a significant decrease as decomposition progressed (Figure 3-2 a-d, Table 3-1, $P < 0.001$). In addition, the concentration of humic substances tended to decline with increasing root diameter (Figure 3-2 a-d, Table 3-1, $P < 0.001$). However, both species and elevation as single factor had no significant effects on humic substances concentration (Table 3-1).

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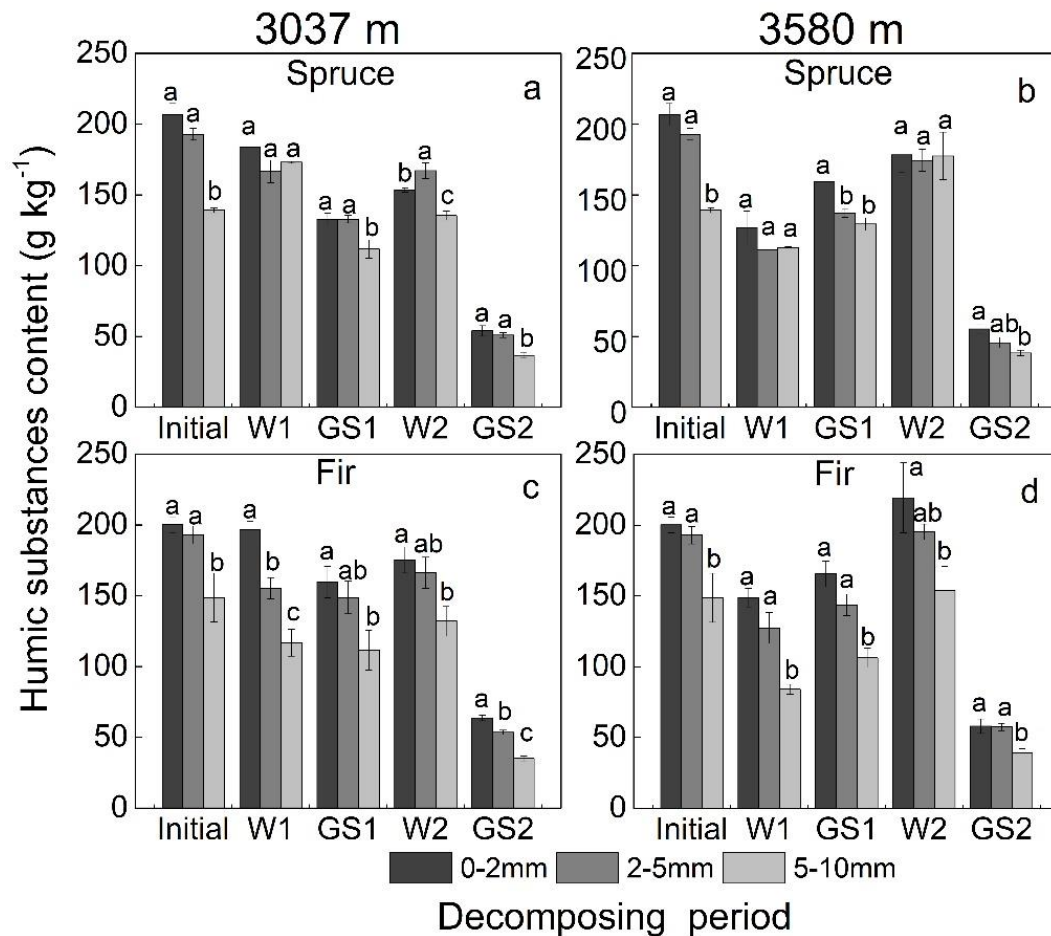


Figure 3-2. Humic substances content (mean \pm SD, $n=6$) in different root diameters for spruce and fir at two elevations during the two-year decomposition. Different lower case letters indicate significant differences between diameters for same species. Initial: the initial values, W1: the first winter, GS1: the first growing season, W2: the second winter, GS2: the second growing season.

3.3.3 Humic acid concentration

Regardless of tree species and elevation sites, humic acid concentration of all diameter classes decreased slightly in the first winter, and then increased dramatically in the following seasons (Figure 3-3 a-d). In addition, humic acid concentration tended to decrease with increasing root diameter (Figure 3-3 a-d; Table 1, $P<0.001$). However, either species or elevation as single factor did not affect concentration of humic acid (Table 3-1).

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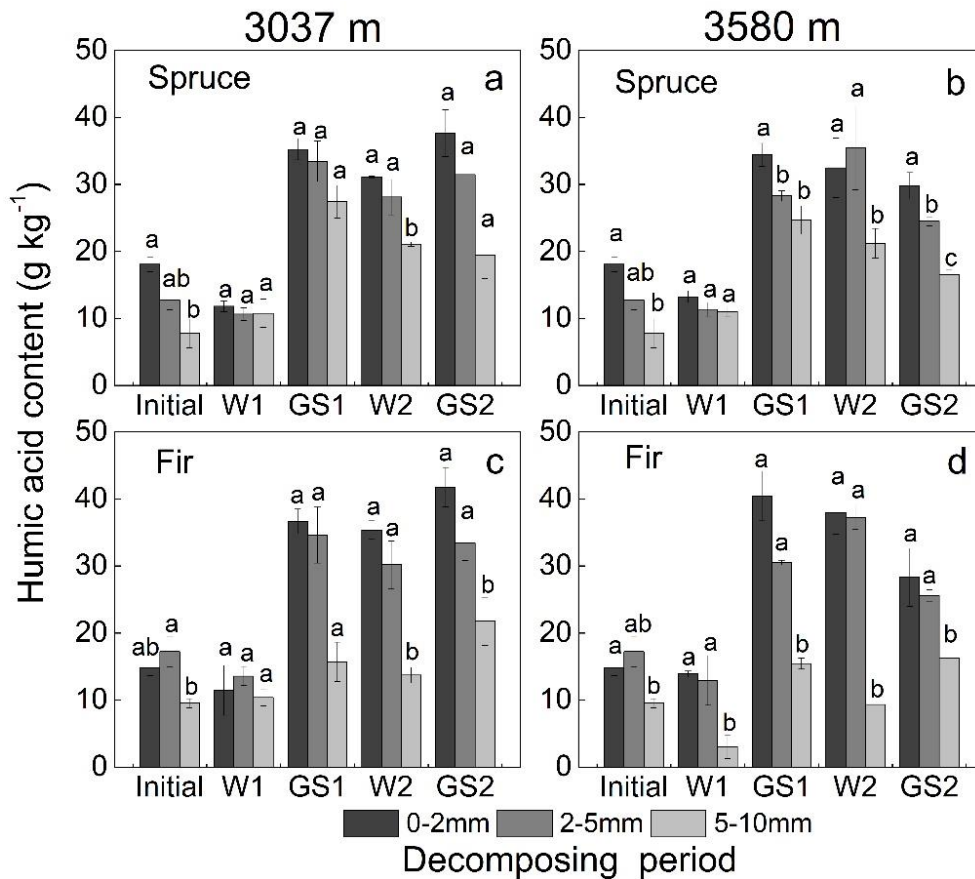


Figure 3-3. Humic acid content (mean±SD, n=6) in different root diameters for spruce and fir at two elevations during the two-year decomposition. Different lower case letters indicate significant differences between diameters for same species. Initial: the initial values, W1: the first winter, GS1: the first growing season W2: the second winter, GS2: the second growing season.

3.3.4 Fulvic acid concentration

Regardless of tree species and elevation sites, humic acid concentration of all diameter classes decreased slightly in the first winter, and then increased dramatically in the following seasons (Figure 3-4 a-d). In addition, humic acid concentration tended to decrease with increasing root diameter (Figure 3-4 a-d; Table 3-1, $P < 0.001$). However, either species or elevation as single factor did not affect concentration of humic acid (Table 3-1).

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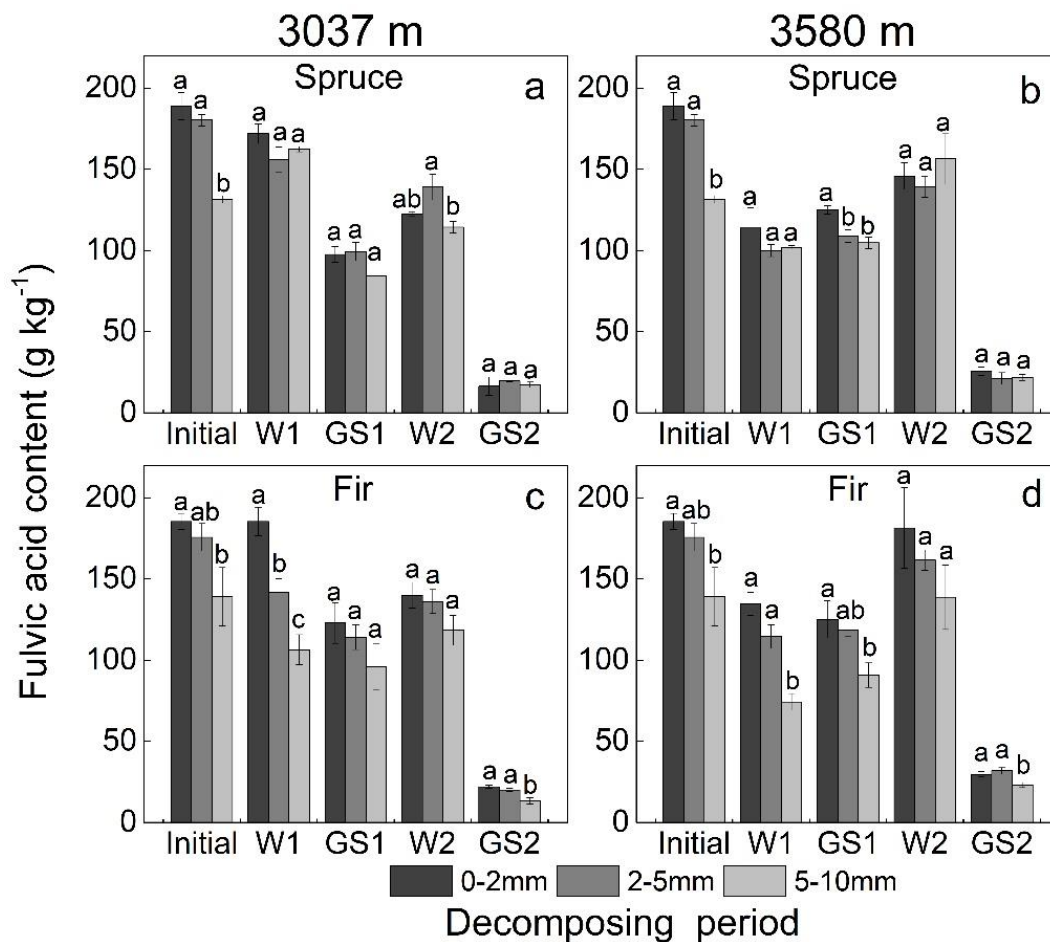


Figure 3-4. Fulvic acid content (mean±SD, n=6) in different root diameters for spruce and fir at two elevations during the two-year decomposition. Different lower case letters indicate significant differences between diameters for same species. Initial: the initial values, W1: the first winter, GS1: the first growing season, W2: the second winter, GS2: the second growing season.

3.3.5 Humification degree

In general, the degree of humification of the three root diameter classes decreased as decomposition progressed (Figure 3-5 a-d). In addition, humification degree was affected significantly by elevation and diameter (Table 3-1, all at least at $P < 0.05$, Figure 3-5 a-d). The humification degree of two tree species tended to decline with increasing root diameter at two elevations (Figure 3-5 a-d). However, no significant differences were detected in humification degree between two tree species (Table 3-1). After 2-year field incubation, the humification degree

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exhibited an order of fine root > medium root > coarse root regardless of tree species and elevation sites (Figure 3-5 a-d).

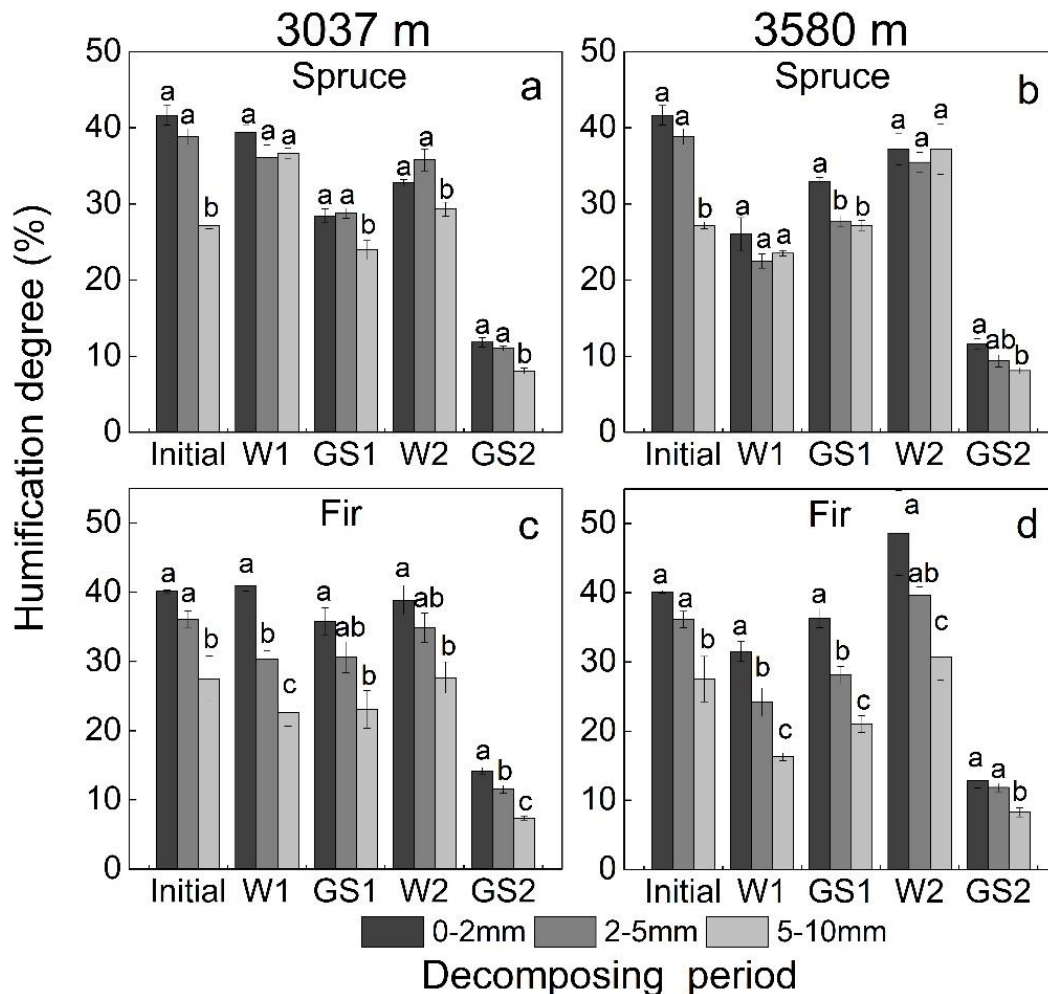


Figure 3-5. Humification degree (mean \pm SD, n=6) in different root diameters for spruce and fir at two elevations during the two-year decomposition. Different lower case letters indicate significant differences between diameters for same species. Initial: the initial values, W1: the first winter, GS1: the first growing season, W2: the second winter, GS2: the second growing season

3.3.6 Factors affecting root humification in different seasons

Across three diameter classes of two species at two elevations, stepwise linear regression analysis showed that **the concentration of humic substances and fulvic acid and humification degree** were correlated with initial C/P ratio and temperature in the first winter (Table 3-2). However, cellulose concentration was the dominant factor affecting the concentration of humic substances and

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fulvic acid during the first growing season (Table 3-2). In addition to root cellulose, the concentrations of humic substances, humic acid and fulvic acid were also affected by temperature and C content in the second winter. During the second growing season, cellulose content was significantly associated with the concentration of humic substances and humic acid. Moreover, fulvic acid concentration was comprehensively influenced by cellulose and positive accumulated temperature (PAT, Table 3-2).

Table 3-2. Dominant factors and determination coefficients (R^2), in parentheses, for step-wise regression analyses content of humic substances (HS), humic acid (HA) and fulvic acid (FA), and humification degrees (HD). affected by initial quality and environmental factors in winter and growing season of two years, respectively. Initial quality: orange carbon (C), total nitrogen (N), total phosphorus (P), C/N, C/P, Lignin, Cellulose, Lignin/N; SWC: soil water content; MT: daily mean temperature; PAT: positive accumulated temperature; NAT: negative accumulated temperature. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

First winter				
	HS	HA	FA	HD
	C/P (0.33)	P(0.12)	C/P (0.30)	C/P (0.36)
	MT (0.52)		MT (0.54)	MT (0.48)
<i>F</i>	16.7***	0.7	14.8***	19.2***

Table 3-2. (continued)

First growing season				
	HS	HA	FA	HD
	Cellulose (0.62)	C/P (0.63)	Cellulose (0.41)	Cellulose (0.64)
		Lignin (0.69)		
<i>F</i>	22.4***	36.9***	23.6***	60.2***

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Table 3-2 (continued)

Second winter				
	HS	HA	FA	HD
	Cellulose (0.30)	Cellulose (0.59)	Cellulose (0.12)	Cellulose (0.34)
	MT (0.37)	C (0.65)	SWC (0.50)	
<i>F</i>	9.2**	30.5***	9.8**	17.6***

Table 3-2 (continued)

Second growing season				
	HS	HA	FA	HD
	Cellulose (0.78)	Cellulose (0.54)	Cellulose (0.18)	Cellulose (0.78)
			PAT (0.54)	
<i>F</i>	26.2***	39.9***	11.6**	118.1***

3.4 Discussion

Diameter-associated variations in root physicochemical and morphological traits may have great potentials to affect mass loss and humic substances in decomposing roots. In line with the first hypothesis, our results found that the mass loss and accumulation of humic substances generally decreased with increasing root diameter over the 2-year decomposition process. Negative effects of root diameter on mass loss were observed in other tree species, such as spruce, pine and poplar (Majdi, 2004; Mao et al., 2011). In a specific ecosystem, root humification is mainly driven by root quality, such as N concentration, C/N ratio and refractory materials (Berg and McClaugherty, 2014). High quality root litters characterized by higher nutrient contents and lower stoichiometric ratios could be favorable to the formation of humic substances than poor quality root litters. Fine roots often had higher nutrient contents and lower stoichiometric ratios as compared to larger diameter roots (Makita et al., 2015; Zhuang et al., 2018). Our previous study found that the nutrient concentrations (e.g., N and P) increased but stoichiometric ratios (e.g., C: N and C: P) decreased with increasing root diameter

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for the two tree species (Liu et al., 2019). In present study, C/P ratio was a key driver of root humification in the first winter but cellulose content was the dominant factor regulating root humification in the following seasons. In addition, compared to larger diameter roots, smaller diameter roots with less secondary tissues may, to some extent, favor soil microbial complexation of stable humic substances (Chapin III et al., 2011; Hishi and Takeda, 2005). Lastly, specific root areas of two tree species decrease with increasing root diameter (Zhuang, 2016). Obviously, fine roots (0-2 mm) were more accessible to microbes and soil fauna compared to medium (2-5 mm) and coarse roots (5-10 mm), which may be partially beneficial for the formation of humic substances in finer roots.

In general, temperature is one of key factors that regulate litter humification, especially in cold biomes. Warming could stimulate the formation of humic substances through affecting the activity and composition of soil organisms (Prescott et al., 2000b). Contrary to the second hypothesis, however, no significant differences in the accumulation of humic substances were observed between the two elevation sites. Along an altitudinal gradient, climatic factors can co-vary with edaphic factors. For example, some studies have shown that the effect of temperature was overridden by soil moisture or other site factors (i.e., soil fertility) in climate-gradient studies (Murphy et al., 1998; Scowcroft et al., 2000). In this study, however, no obvious differences were found in soil moisture and soil properties between the two sites. In the subalpine forest ecosystems on the eastern Tibetan Plateau, the duration of seasonal snow cover is approximately 4-6 months, depending on elevation (Li et al., 2017). Previous studies have found that snow depth and freeze-thaw cycles increase with an increase in elevation in the study area (Zhu et al., 2012). In addition, recent studies have also found that seasonal snow cover combined with freeze-thaw cycle favor litter decomposition and accumulation of humic substances in our study area (Ni et al., 2014; Ni et al., 2015; Wei et al., 2013). Thus, the expected temperature effects on accumulation of humic substances may, to large extent, be offset by the effects of snow cover and freeze-thaw cycles associated with elevation.

The accumulation of humic substances largely varied with plant species during the decomposition process (Berg and McClaugherty, 2014). For example,

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Ni et al. (2014) demonstrated that humic substances accumulated faster in birch foliar litter relative to cypress and larch litters after the 1-year decomposition. However, irrespective of elevation and diameter, the concentration of humic acid and fulvic acid did not differ between the two conifers. This is due to the fact that both Minjiang fir and dragon spruce are evergreen coniferous tree species, with similar content of compounds (Liu et al., 2019). There was a similar linear relationship between mass remaining and humic substances for both tree species, implying a similar pattern in accumulation of humic substances (Figure 3-6). By contrast, the study on foliar litter humification of Minjiang fir certified that root humification degree of this tree species was relatively high in this study area (Ni et al., 2015). Unlike foliar humification, root humification could also be partly affected by living roots and exudates. Therein, root exudates could provide readily available C for microbes, which in turn may promote the formation of humic substances (Cotrufo et al., 2013). Therefore, we assume that plant roots of subalpine forests may be more important to accumulate soil organic matter as compared to aboveground leaves, but additional supporting evidence is needed.

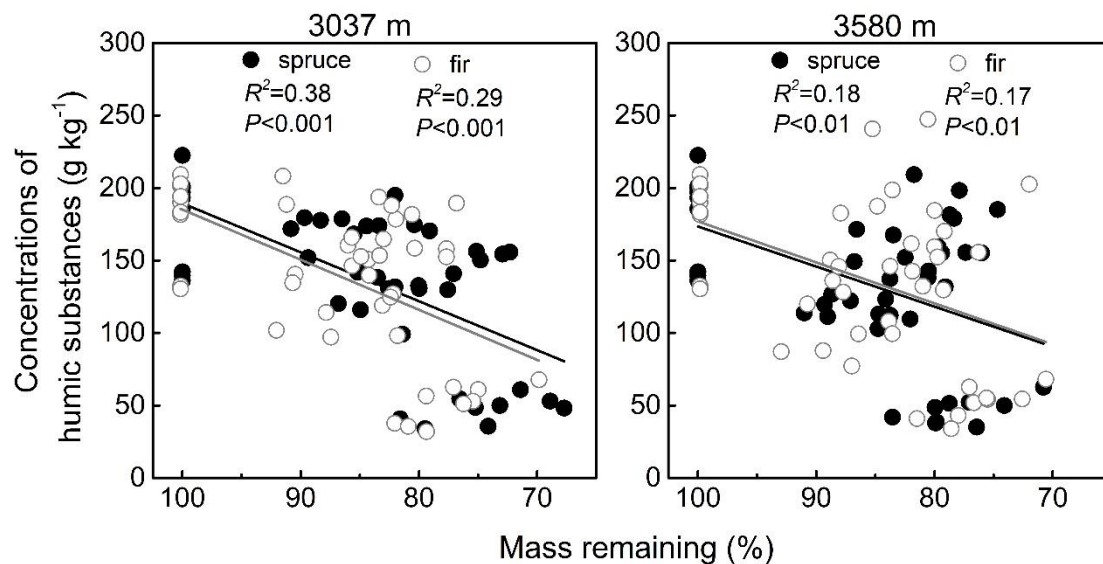


Figure 3-6. Linear relationship between mass remaining and humic substances concentration of spruce and fir at two elevations over the experimental period.

The accumulation of humic substances varied between winter and growing season. Stepwise regression analysis indicated that C: P was a key driver of root humification in the first winter but cellulose content was the dominant factor of

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root humification in the following seasons. During the first winter, rapid releases of labile materials associated with frequent freeze-thaw could provide high-quality substrates for organisms to form humic substances (Baptist et al., 2010; Bokhorst et al., 2013). However, after the first winter, root humification was dominated by cellulose and lignin-like products associated with microbial metabolism (Cotrufo et al., 2013; Prescott, 2010). On the other hand, humic acid content tended to accumulate but fulvic acid content tended to degrade over the growing season. Frequent precipitation during the growing season may lead to fulvic acid loss by leaching due to its strong mobility (Ciarkowska and Miechówka, 2017; Elliott, 2013). Moreover, fulvic acid with small molecular weight could be transformed into humic acid with more complex structure as decomposition progressed (Frouz et al., 2011a; Zhang and Forkin, 1994).

3.5 Conclusions

This study investigated the diameter-based variations of root mass remaining and humification patterns in two common tree species (*Picea asperata* and *Abies faxoniana*) at two elevations (3037 m and 3580 m) on the eastern Tibetan Plateau. Regardless of species and elevation, the mass loss and concentrations of humic substances of root litters generally decreased with increasing root diameter. The accumulation of humic substances was significantly associated with root C: P ratio and daily mean temperature in the first winter but with root cellulose content in the following seasons. Moreover, for the accumulation of humic substances, diameter-induced variations were much stronger than altitudinal and interspecific differences in decomposing root litters. As a result, short-term warming could not directly affect the accumulation of humic substances in decomposing roots. Our observations underscore the ecological importance of seasonal snowpack and diameter-associated root processes in subalpine forests. These findings improve our understanding the accumulation of humic substances in decomposing roots in this region experiencing snow-covered winter.

4. Home-field advantage of litter decomposition faded 8 years after spruce forest clearcutting in Western Germany

Modified on the basis of the manuscript

Liyan Zhuang, Andrea Schnepf, Kirsten Unger, Ziyi Liang and Roland Bol

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4. DECOMPOSITION HFA FADED AFTER SPRUCE CLEARCUTTING

4.1 Introduction

Forest cover change contributes to complex feedbacks on forest ecosystems along chronosequences (Farber et al., 2006) and results in the disruption of ecological processes, including microclimate and soil nutrients mineralization (Achilles et al., 2021; Both et al., 2017; Mayer et al., 2020). Clearcutting, changing the dominated species, and forest growth dynamics leave behind a significant shift in ecosystem-scale species communities, influencing the decomposition pattern during regeneration. Such as, nutrient-rich litter or logging residual in early successional stages is associated with faster decomposition and turnover rates, while slower organic matter recycling and infertile soil had usually found under older forests (Trap et al., 2011; Xuluc-Tolosa et al., 2003). The change in the decomposition process determines organic matter sequestration and hence forest growth (Zhang et al., 2018c). A better understanding of litter decomposition and nutrient cycling is necessary for an effective management strategy to promote forest regeneration, especially after deforestation or decades of regeneration (Allison et al., 2013).

In the last century, large forest areas in central Europe were converted into monocultures of fast-growing spruce. Spruce monocultures are generally known for their low biodiversity and soil deterioration due to acidification and nitrogen leaching (Spiecker, 2004; Wilpert, 2022). To maintain the ecological, sociological, and cultural functions of the forest, the conversion of existing Norway spruce into more natural broadleaved and mixed forests is the main silvicultural aim in Germany and other European countries (Otto, 1995; Wulf, 2003). Some studies have shown that spruce decomposition was accelerated in its originated coniferous stands relative to away from it (Asplund et al., 2018b; Berger and Berger, 2012; Spiecker, 2004; Vesterdal, 1999). It is usually considered that soil decomposer organisms may adapt to break down particular substrate in individual ecosystems, thereby accelerating the decomposition of litter from which it is derived (i.e., home) than away from that plant (Fanin and Bertrand, 2016; Liu et al., 2019), which has been termed the home field advantage (HFA) of litter decomposition (Gholz et al., 2000).

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Moreover, the data review analysis from Ayres et al. (2009) concluded that HFA is widespread in forest ecosystems and suggested that ~30% of the variability of litter decomposition at a global scale can be explained by HFA. Clearcutting brings about a high plant abundance of pioneer species (i.e., high nutrient concentration and low lignin: N ratios) and modified soil abiotic conditions (including nutrient leaching, soil temperature, moisture, and pH (Achat et al., 2015; Ishikawa et al., 2007; Kang et al., 2018; Prescott et al., 2000a), resulting in shifts in the functioning of decomposer communities, such as decreased fungal biomass and change in bacterial community structure (Kohout et al., 2018; Pennanen et al., 1999). The resultant association between individual species and site condition can affect soil properties that enhance the decomposition of its own litter, creating an HFA effect for the species-own litter (Pennanen et al., 1999). At the same time, case studies indicated that warmer and moister conditions after clearcutting drive faster litter breakdown by higher soil decomposer activity irrespective of HFA (Finér et al., 2016; Gliksman et al., 2018). Soil decomposer communities changes when a forest is clear-cut due to the shift in plant communities and soil physical condition, and then microbial differences in ability might arise through local adaption with its "new" home environment (or a 'home' litter) (Keiser et al., 2014), however, studies rarely investigate HFA after removing the dominant species as in clearcuttings. There is a need for gathering reliable scientific knowledge on the influence of clearcutting on original 'home' and 'away' litter decomposition in the new clear-cut.

There is increasing evidence that the strength of HFA is associated with the interaction between local litter quality and specialized microbes. For example, greater fungal biomass in spruce plantations could partly explain the HFA for spruce in its habitat due to the better degradation of recalcitrant fractions through fungi adaption (Paterson et al., 2008); that is, conifers should favor soil decomposition dominated by fungi and fungivorous microarthropods, in comparison to broadleaved species (Chomel et al., 2015). Moreover, across succession, soil communities have gone through a wider range of litter qualities contributing to a broader functional capacity to degrade various litter types (Keiser et al., 2014), so decomposer ability in succession may increase with

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regeneration. However, recent studies pointed out that litter quality was not an important determinant of HFA (Veen et al., 2015), while the greater dissimilarity between 'home' and 'away' litter indicated strong HFA (Veen et al., 2015).

Measurements of plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ abundance have been shown to be useful indicators of forest organic matter dynamics (Michener and Lajtha, 2008). The difference between the isotopic signature of residual litter and litter degradation or litter nutrient dynamics are considered as the inherent tracers for understanding the progression of decomposition and nutrient mineralization/immobilization (Gautam et al., 2016). Labile compounds with faster mineralization rates exhibit higher $\delta^{13}\text{C}$ values rather than $\delta^{13}\text{C}$ -depleted recalcitrant lignin (Osono et al., 2008). In addition, microbial processes enrich carbon with $\delta^{13}\text{C}$ in relation to bulk litter (Dijkstra et al., 2008). The changes in foliar $\delta^{15}\text{N}$ values are positively associated with nitrate leaching following forest clearcutting (Craine et al., 2009; Pardo et al., 2002), that is, the foliar $\delta^{15}\text{N}$ often relates to N availability, clearcutting increases nitrification and nitrate loss rate, resulting in much of the $\delta^{15}\text{N}$ -depleted nitrate leaching out, but $\delta^{15}\text{N}$ -enriched ammonium retaining. These findings have provided us with a meaningful point that the alteration of isotopic C and N signature between litter types during decomposition are useful indicators of nutrient status after disruption of the forest.

In the Eifel National Park (Wüstebach, Germany), clearcutting operations were carried out in spruce monoculture in 2013 as the first step of conversion from planted spruce monoculture to natural forest. This significantly affected soil nutrient leaching (Jiang et al., 2017; Siebers and Kruse, 2019), moisture (Rosenbaum et al., 2012) as well as soil respiration (Wiekenkamp et al., 2016). To test the validity of the HFA change long with clearcutting management, we carried out a reciprocal transplant litter decomposition on a 70-yr spruce forest and a clear-cut after short-term (8-yr) regeneration. In addition, we tested the importance of litter quality on the strength/occurrence of HFA. The difference of litter mass loss and nutrient release, as well as isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ discrimination between spruce and beech, were determined to figure out this question.

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4.2 Materials and methods

4.2.1 Site description

The study area is located in Wüstebach (50°30'15.3" N, 6°20'03.0" E), situated within the Eifel National Park of western Germany. The climate is mild and humid, with the mean annual air temperature of 7 °C and the mean annual precipitation of about 1200 mm (Havlik, 2002). Winter is moderately cold with periods of snow. Norway spruce replaced European beech as the dominant canopy species for timber production since the 1940s. In the last decades, the Park authority has started accelerating the 'natural' regeneration towards a beech forest by clear-cuts of a significant proportion of the Norway spruce monoculture (~90%) (Etmann, 2009). The ground cover vegetation in these clear-cut stands is formed mainly by young samplings of alder [*Alnus glutinosa* (L.) Gaertn], European beech (*Fagus sylvatica*) with an admixture of early pioneer species, i.e., scrubs, bushes after 8-year regeneration. Norway spruce (*Picea abies*) is the dominant tree species in the remaining uncut forest. Five subplots were selected for this study ranging from 595 m in the northern part to 628 m in the south in forest and clear-cut, respectively. Soils at the stands are classified as Cambisols and Gleysols, and Gleysols nearby stream is moister than Cambisol. For more information about soil properties, refer to Siebers and Kruse (2019) and Wiekenkamp et al. (2016).

4.2.2 Litter decomposition experiments

Between 2019 and 2020, a reciprocal litter transplant experiment was established in the forest and clear-cut. In September 2019, freshly senesced spruce needles and beech leaves were collected from 6 sampling sites at the forest and clear-cut ecosystems, respectively. Within each collection, each substrate was collected from a minimum of 6 different plant individuals to ensure the representativeness of the pool collected. According to the purpose of forest management, we assumed that spruce is the home environment for the forest, while the home environment for beech is clear-cut.

All samples were air-dried to constant mass. 2.5 g of Spruce needles or Beech leaves were filled into each polyethylene litterbag (10 × 8 cm; 0.25 mm mesh size), respectively. The mesh size permits the entry of bacteria, fungi, and micro-fauna

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[45]. In October 2019, five sampling locations were selected for clear-cuts and adjacent forests on both Cambisols and Gleysols, respectively. At each subplot, 4 litterbags of each species were placed on the soil surface after getting rid of the humus layer or grass. Litterbags were retrieved after 1, 3, 9, 12 months. Altogether, we prepared 160 litterbags (4 sampling times \times 2 stands \times 2 soil types \times 2 species \times 5 replicates) in total. Harvested litterbags were transported to the laboratory. Oven-dried and weighed after removing soil particles and other extraneous materials.

C and N contents of each sampling were measured by a CNS analyzer. The natural abundance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was measured by stable isotope ratios mass spectrometry. The total phosphorus (P), Calcium (Ca) were determined after microwave digestion with $\text{H}_2\text{O}_2\text{-HNO}_3$ using inductively coupled plasma mass spectrometry (ICP-MS). The soil temperature and moisture in Wüstebach were measured with the wireless sensor network with 600 ECH2O EC-5 and 300 ECH2O 5TE sensors.

4.2.3 Data statistics

To determine the strength and direction of home-field effects on litter decay rate, the home-field advantage index (HFAi) for mass loss and the release of C and N was calculated following Ayres et al. (2009) and adapted from Veen et al. (2015) as

$$\text{HFAi (\%)} = \left(\frac{A_{RLa} + B_{RLb}}{2} \right) / \left(\frac{A_{RLb} + B_{RLa}}{2} \right) \times 100 - 100 \quad (4)$$

where i_{RLj} represents the relative mass or nutrient loss of species i in environment j . Single sample t -tests were used to test whether the HFAi differed from 0.

HFAi stands for the additional decomposition or mineralization at home versus away environment and is a net value for both species (A and B) in the reciprocal experiment.

The mean HFA (% increase in k value at home versus away environment) for each litter type was calculated according to (Wang et al., 2013):

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$$\text{The mean HFA} = (k_{\text{home}} - k_{\text{away}})/k_{\text{away}} \times 100 \quad (5)$$

where k_{home} and k_{away} are the decomposition constants of a given species at home and in away environments, respectively.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are expressed as

$$\delta (\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (6)$$

where R_{sample} and R_{standard} represent either $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratios of sample and standard material, respectively. The stable isotope ratio values are expressed in parts per million (‰) relative to international standards. Vienna Pee Dee Belemnite (VPDB) for carbon isotope and atmospheric nitrogen for nitrogen isotopes. The analytical precisions for carbon isotopes ± 0.1 ‰ and ± 0.3 ‰ for nitrogen isotopes.

Mass remaining (%) was calculated from dry mass at sampling date divided by initial dry mass. The decomposition rate (k value, yr^{-1}) was estimated according to the exponential regression $y = e^{-kt}$, y (%) is mass remaining over time t , k is the decomposition rate by Olson (1963). Nutrients remaining (%) of each sample were estimated as nutrient content at each sampling time divided by initial nutrient content and expressed by % of the initial amount. We performed t -tests: (1) to test the significance of initial quality and residuals after one year of decomposition between beech and spruce; (2) to test k values of beech and spruce in clear-cuts and forest on Cambisols and Gleysols; (3) to examine the environmental differences between forest and clear-cut at each sampling point; and finally, (4) to determine if the HFA_i was significant between soil types. Repeated measure ANOVAs were used to compare the significance of soil types, stands, and species on various nutrients remaining over time. Three-way ANOVAs were calculated to compare the three factors: soil types, stand, and species on nutrient remaining. A series of stepwise regressions were conducted to detect the variance relationship, like nutrients and stoichiometry on mass loss between soil types, stands, and species. All statistical analysis was performed using SPSS22.0 for the Windows software package.

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4.3 Results

4.3.1 Environmental difference between stands and soils

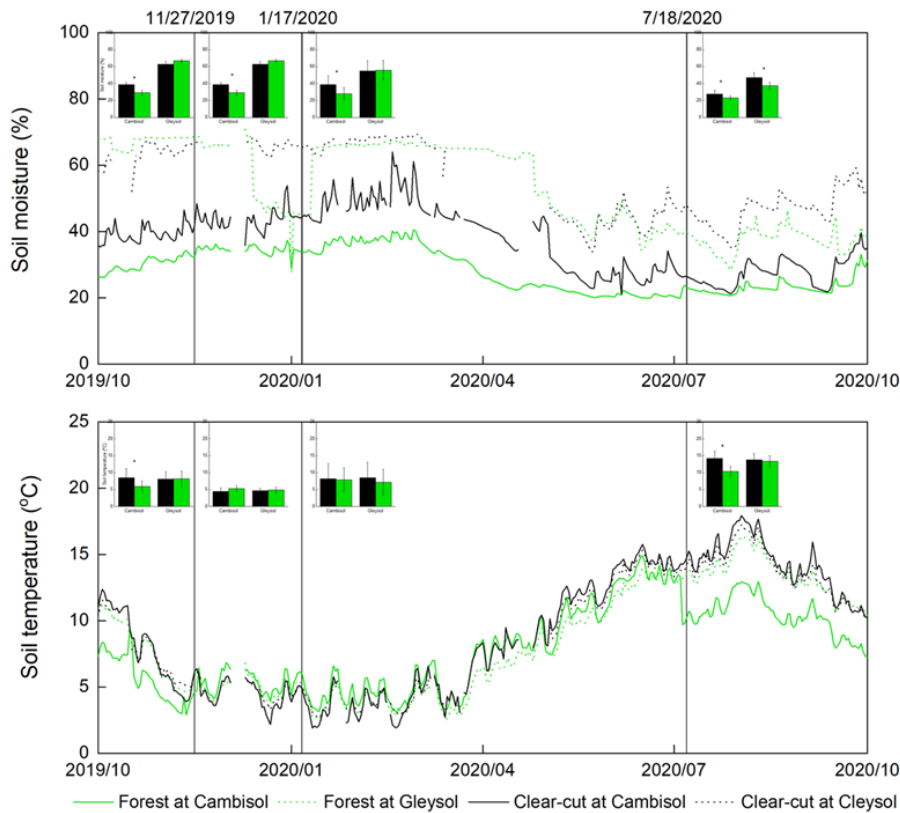


Figure 4-1. The soil moisture (%) and temperature (°C) dynamics in the top layer during one year of decomposition. Bar charts indicate mean values with error bars at each sampling time. The green bar indicated forest; the black bar indicated clear-cut.

Soil types and forest management greatly influence soil environmental conditions (Figure 4-1). On average, the soil moisture content was significantly higher in clear-cut than in the forest at both soil types, ranging from 36.6–55%, and Cambisols showed a larger difference in soil moisture by 8.7% than Gleysols by 2.7%, comparing between clear-cut and forest. At both soil types, the temperature at the forest floor was approximately 1 °C higher in clear-cut than in the forest. The results of the *t*-test revealed that the soil moisture and temperature conditions were mostly higher in clear-cut than forest with times, particularly at Cambisols.

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4.3.2 Initial litter quality and litter nutrients after one year of decomposition

Table 4-1. Nutrient concentrations and compound ratios of beech and spruce litter before and after one year of decomposition.

	Initial Litter Quality	
	Beech	Spruce
C (%)	47.1 ± 0.2a	48.4 ± 0.1b
N (%)	2.1 ± 0.1a	1.2 ± 0.0b
P (mg kg ⁻¹)	278.4 ± 10.4a	254.9 ± 8.6b
C: N	22.4 ± 0.5a	39.0 ± 1.3b
Ca (mg kg ⁻¹)	2.18 ± 0.04a	1.67 ± 0.01b

Table 4-1. (continued)

	Residual Quality after 1 Year of Decomposition			
	Forest		Clear-Cut	
	Beech	Spruce	Beech	Spruce
C (%)	48.2 ± 0.8a	49.5 ± 0.6b	46.1 ± 0.6a	47.9 ± 0.5b
N (%)	3.0 ± 0.1a	1.9 ± 0.8b	2.8 ± 0.1a	1.6 ± 0.1b
P (mg kg ⁻¹)	105.2 ± 6.3a	81.0 ± 8.9b	104.5 ± 6.0a	61.5 ± 4.9b
C: N	20.2 ± 0.6a	34.4 ± 0.7b	20.8 ± 0.8a	35.1 ± 0.4b
Ca (mg kg ⁻¹)	1.02 ± 0.09a	0.74 ± 0.08b	1.20 ± 0.05a	0.79 ± 0.06b

The lower-case letter indicates the significance between species at the same stands. Different lowercase letters indicate significant differences between beech and spruce in each site ($p < 0.05$).

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Initial litter quality differed between species. European beech had significantly better initial quality than Norway spruce for C, N, P, and Ca, as well as lower C: N and C: P ratios (Table 4-1). After one year of decomposition, nutrients concentration and C stoichiometry were significantly different between species and stands. Most nutrient concentrations decreased, except for the N and C: P ratio. Furthermore, C concentration increased in the forest but decreased in clear-cuts for both species during decomposition.

4.3.3 The effect of home-field advantage on litter decomposition rates

A significant home-field advantage was shown for the two soil types in this experiment (HFAi = 11 at Cambisols and HFAi = 4 at Gleysols, Table 4-2). A pattern of the higher decomposition rate of the spruce in the original spruce forest after one year of decomposition followed by k values (Figure 4-2c,d). However, there was no promotion between forest and clear-cut stands in the initial three months. Spruce has a lower 3-month k value in forest than in clear-cut (Figure 4-2a,b), while beech in clear-cut decomposed faster than in forest at Cambisols, but slower when decomposing in Gleysols. Moreover, after one year of decomposition, the k value of beech in clear-cut decreased but was higher than the forest stand at Cambisols, while the k value of beech in Gleysols did not differ significantly.

The k values for beech and spruce varied among stands and soil types with times. k decreased in time for both spruce and beech. The 3-month k values were on average 2- to 3-fold higher compared to the 1-year values (Figure 4-2). The decomposition rate of spruce in the first three months was significantly higher than beech in most stands except for forest stand at Cambisols (Figure 4-2 a,b). Significantly or slightly higher k value of spruce showed in forest at all plots except for clear-cut at Cambisols after one year of decomposition, when comparing with beech litter.

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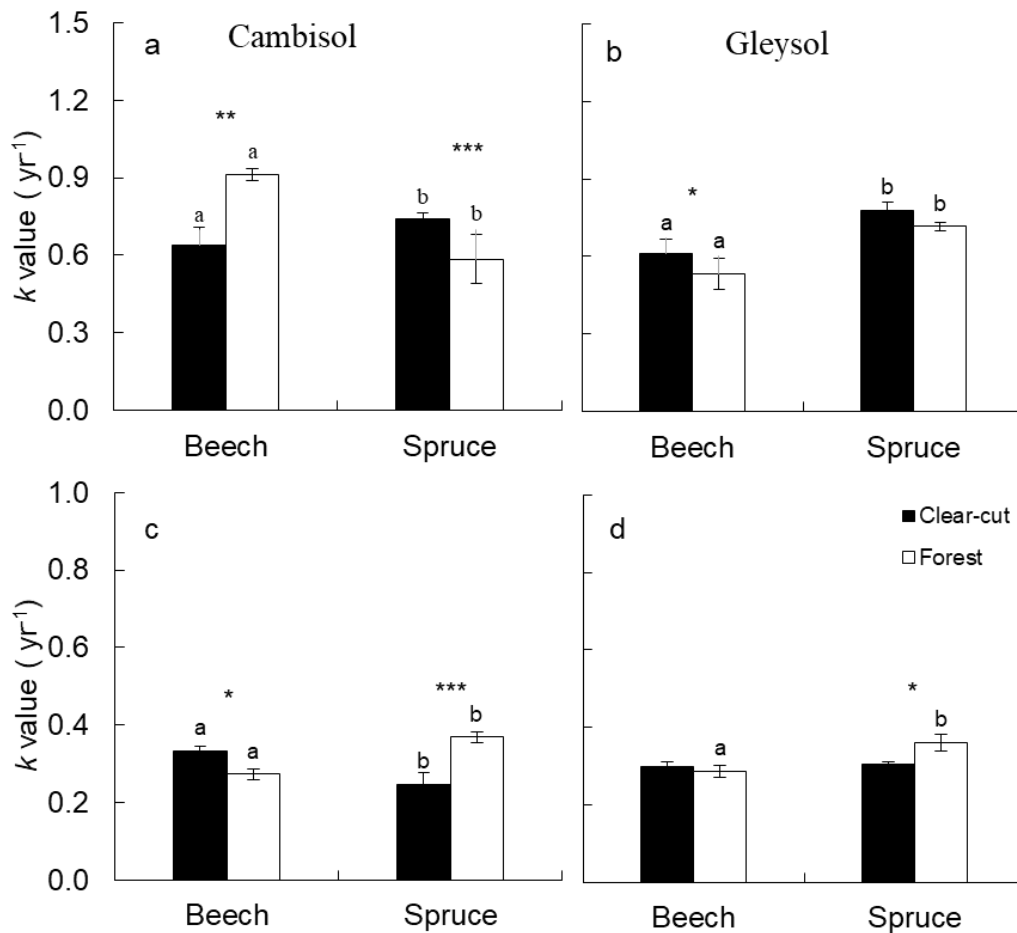


Figure 4-2. k -values (yr^{-1}) of beech and spruce in clear-cut and forest at Cambisols and Gleysols after 3 months (a,b) and one year (c,d) of decomposition. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$ indicate significance between stands with same species; lower-case letters indicated significance between species at same stands.

4.3.4 C, and N dynamics and their HFA

Our results indicate that overall C and N release increased at “home” compared with “away” (Table 4-2). The difference on C release was stronger in Cambisols (14% vs. 10% in Gleysols) for spruce decomposed in forest, while HFAi of N promoted a higher N release in Gleysols (43%) than in Cambisols (28%).

The significance of litter C dynamics varied through time and different treatments (Figure 4-3 a,b, Table 4-3). A loss of C could be observed in all substrates within the year-long decomposition. Spruce litter lost most C fraction

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in this original forest during the study period, while beech C in the forest was released rapidly in the first three months and leveled out by the times, which was 6.6% faster on average for spruce in the forest.

Table 4-2. Home-field advantage index of mass loss and C and N release on Cambisols and Gleysols.

	Cambisols	Gleysols
Mass loss	11.2 ± 0.5a	3.7 ± 1.0b
C release	14.0 ± 2.5a	10.7 ± 0.9b
N release	28.3 ± 0.9a	43.1 ± 5.4b

The lower-case letter indicates significance between stands. Different lowercase letters indicate significant differences between the two soils ($p < 0.05$).

Table 4-3. Three-way ANOVA analysis of F-value on the effect of soil types, stands, species, and their interactions on nutrient remaining over decomposition.

Effects	Remaining				
	<i>df</i>	C	N	P	Ca
Soil type	1	6.8 *	0.7	8.4 *	0.1
Stand × Soil type	1	2.9	2.1	4.3	15.6 **
Soil type × Species	1	31.6 ***	0.6	0.0	0.0
Stand × Soil type × Species	1	6.3 *	1.3	8.5*	3.2

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

4.3.5 The dynamic of litter nutrients releases during decomposition

Most nutrients indicated significant mineralization over time (Figure 4-3, Table 4-3) and observed net mineralization in all substrates following Figure 3. Both leaf litters released P rapidly one year after the start of the decomposition, losing approximately 80% of their initial amount of P (Figure 4-3 e,f, $p < 0.001$). Beech (26%) retained more P than spruce (18%) in one year period ($p < 0.05$).

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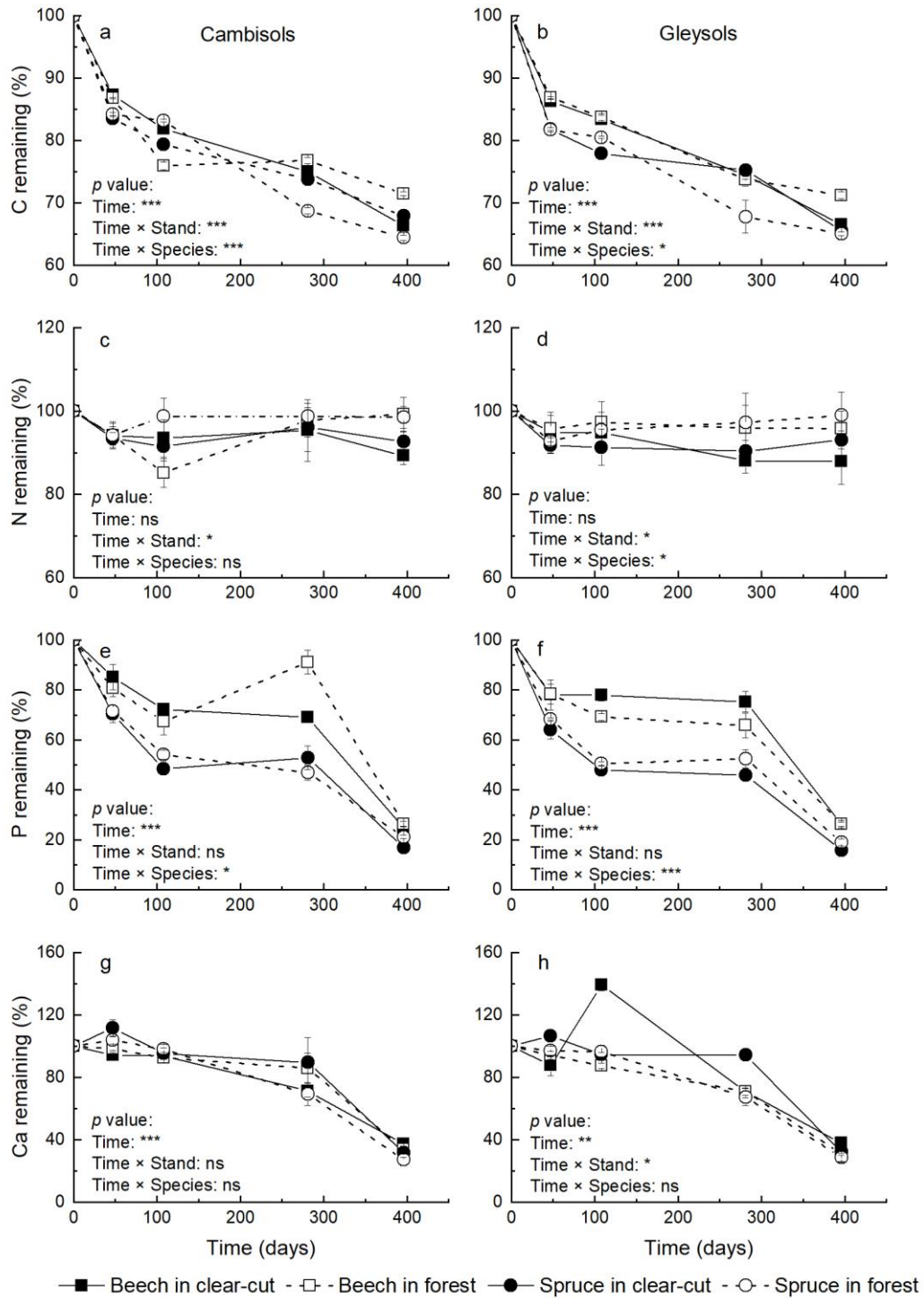


Figure 4-3. Nutrients (C, N, P, and Ca) remaining of beech and spruce in Cambisols (a,c,e,g) and Gleysols (b,d,f,h) after one year of decomposition. Error bars represent standard errors. Repeated measure ANOVA indicated significance of stand and species with time periods: ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

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Figure 4-3 e,f shows a similar pattern of P mineralization between forest and clear-cut for both species ($p > 0.05$). On average, the final Ca remaining was significantly higher in forest (70%) than in clear-cut (65%), regardless of species (Figure 4-3 g,h). Furthermore, the interaction between stands and soil types revealed that spruce Ca release was faster than beech (Figure 4-3g,h, Table 4-3).

4.3.6 Correlation between Litter Mass Loss Rate and Residual Quality

Litter decomposition rate was associated with changing substrate quality in all subplots (Table 4-4). Decomposition rate of spruce in forest increased with litter N concentration but decreased with litter Ca concentration ($R^2 = 0.97$). Decomposition of spruce in clear-cut positively changed with N but negatively correlated with P concentration ($R^2 = 0.93$). Beech decomposition rate in forests was positively related to C: N ratios ($R^2 = 0.67$) but also decreased with litter Ca concentration when decomposed in clear-cuts ($R^2 = 0.85$).

Table 4-4. Stepwise regression of the correlation between litter mass loss rate and nutrient concentrations and stoichiometry of beech and spruce under forest and clear-cut over decomposition. Data indicates significant variables related to decomposition, followed by R^2 .

	Variables	Coefficients	R^2
Spruce			
Clear-cut	N, P	0.65, -0.36	0.93
Forest	N, Ca	0.77, -0.23	0.97
Beech			
Clear-cut	Ca, C: N	-0.51, -0.49	0.85
Forest	C: N	-0.82	0.66

4.3.7 Isotopic change during decomposition

The $\delta^{13}\text{C}$ values of decomposing litters leveled off over time across litter types. The initial $\delta^{13}\text{C}$ values were -32.7‰ in beech leaves and increased by 0.13‰ on average. For spruce needles, the initial $\delta^{13}\text{C}$ value was -30.6‰ and decreased by 0.14 after 1 year of decomposition. The initial $\delta^{15}\text{N}$ values ranged from -3.3‰ in

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beech leaves and -4.7‰ in spruce needles (Figure 4-4). The $\delta^{15}\text{N}$ values for both species were finally higher in clear-cut than in forest. In the first 9 months, $\delta^{15}\text{N}$ became enriched in all subplots but then depleted in forest, while a larger decrease happened in Cambisols. Over the same period, the $\delta^{15}\text{N}$ value in clear-cut became higher throughout the experimental period in Cambisols (-3.0 and -3.7‰ for beech and spruce, respectively), but it slightly dropped since July in moister Gleysols (-3.2 and -4.1‰ for beech and spruce, respectively) (Figure 4-4). Linear regression plots of N isotopic against C concentration (%) were negatively significant among species over both stands ($p < 0.05$, Figure B-2). While the relationship of the $\delta^{13}\text{C}$ values and C: N was only linearly significant in forest for spruce ($R^2 = 0.83$, $p < 0.01$).

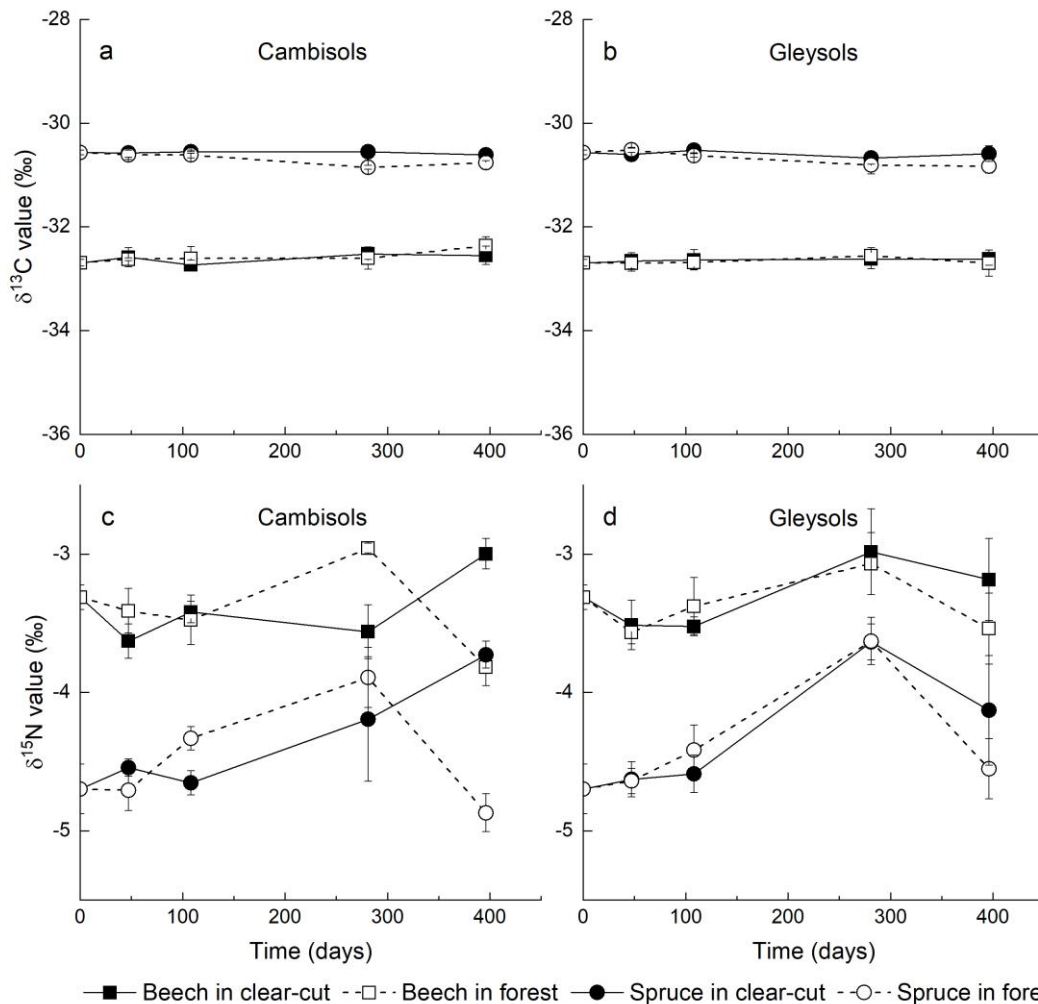


Figure 4-4. The change of isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value of beech and spruce over one year of decomposition. Error bars represent standard errors.

4.4 Discussion

4.4.1 HFA in forest and post-harvest decomposition

Our results indicated a positive effect of litter-site interaction on litter decomposition rate at the home of 11% and 4% and thus a net HFA in the spruce forest, which verified our first hypothesis. A meta-analysis has noticed that decomposition HFA is widespread in forest ecosystems, with on average 4.2% promotion in the home habitat (Wang et al., 2013). Low-quality spruce with low nutrient content and high C: N decomposed faster in spruce forest, probably due to the presence of more fungal communities well adapted for degrading recalcitrant litter (Veen et al., 2015). After 8-year clearcutting, both soil physical (soil moisture and temperature, Figure 1) and chemical conditions (Siebers and Kruse, 2019) had been markedly elevated, which can influence the development and succession of microorganisms that can assimilate substrate (Aneja et al., 2006). And thus, we found a significant suppression on spruce decomposition and a slight promotion on beech decomposition in clear-cut. On the other hand, post-harvest regeneration of understory species improves soil nutrient availability and forest sites quality, masking the original soil-litter affinity on pre-harvest forest (Zhou et al., 2018b). This could also account for the lower decomposition rate for spruce in the clear-cut and potentially masked the mean HFA for spruce after a short-term regeneration.

4.4.2 Litter chemistry regulated decomposition of Norway spruce in original forest

Decomposition and mineralization in the initial phase are generally characterized by the leaching of soluble nutrients and by decomposition of soluble and non-lignified cellulose and hemicellulose (Heim and Frey, 2004). Winter snow cover and snowmelt in this initial period physically breakdown litter tissue and accelerated nutrients release and mineralization (McDowell et al., 2010), resulting in a higher k value in clear-cut versus forest, and thus no HFA was detected in the initial 3-month decomposition.

The decomposition difference between litter types was correlated to the concentration of C and N, and C: N ratios. Our results also corroborated this hypothesis that litter N concentration served as the most critical nutrient to

4. DECOMPOSITION HFA FADED AFTER SPRUCE CLEARCUTTING

regulate the degradation of spruce, and beech was decreased with increased C: N ratios, according to the stepwise regression (Table 4). Slower N release was detected in forest, which decreased litter C: N ratios and promoted the generation of brown and white rot fungi (Rajala et al., 2011), and benefited the degradation of the lignin-rich substrate (i.e., spruce). Faster spruce Ca release strengthen the soil acidification that maintains the soil pH, sustaining the home-field effect. Although litter quality well-regulated the litter mass loss, litter quality independently did not serve as a predictor of mean HFA in this case (appendix, Figure B-1). This result is supported by evidence from Veen et al. (2015). This may be because HFA is not restricted by single litter types, but the heterogeneity of litter quality between the 'home' and 'away' habitats (Veen et al., 2015). Alternatively, the occurrence of HFA is likely system-dependent, suggesting that transplants between labile litter from nutrient-rich ecosystems and recalcitrant litter from nutrient-limited ecosystems better induce HFA (Freschet et al., 2012; St John et al., 2011). The results from this work were limited to spruce and beech only; a wider assessment between species and ecosystems is necessary for relevant controlling to determine the magnitude and the direction of HFA for plant traits.

4.4.3 Clearcutting promoted beech decomposition and nutrient release patterns

Beech leaves decomposed faster during the first year in clear-cut, which is accompanied by an increase in the mineralization rate of C and N in beech leaves and higher in immobilization in spruce needles. In addition, the less home effect of C, N release was observed after clearcutting. Thus, a transfer from spruce to beech would facilitate the potential utilization of nutrients by trees. The shift of dominated trees species by clearcutting treatment would inherently influence the regeneration in this site through litter input quality (Siebers and Kruse, 2019).

Decay rates for beech in both stands were tightly related to C: N ratios. Beech with lower C: N ratios contributed to a faster decomposition rate for beech ($k = 0.31$ on average) than spruce ($k = 0.29$ on average) in clear-cuts. Changing environmental conditions would directly affect litter mass loss after rapid shifts in plant community composition (Veen et al., 2015), contributing to the relatively

4. DECOMPOSITION HFA FADED AFTER SPRUCE CLEARCUTTING

elevated mass-loss rate for beech in clear-cuts than in spruce forests and the suppression of mean HFA effect for spruce. Moreover, removing the forest canopy elevated atmosphere C and N deposition with precipitation promotes soil nutrient availability in the short term (Siebers and Kruse, 2019) and restructures the local fungal community in soil (Kohout et al., 2018). This would further hinder the litter decomposition and nutrient turnover rate in these successional stands.

4.4.4 Soil moisture as a mediator of litter decomposition and HFA

Our results indicated that the decay of beech in clear-cuts differed between soil conditions; that is, beneath Cambisols, the decay rates of beech were significantly higher in clear-cuts than in the forest, and interestingly, it was faster than spruce in clear-cuts. However, a minor difference in clear-cut was observed when decomposing on Gleysols, as well as a decline in the HFA of decomposition and C concentration. Gleysols nearby the stream is moister than Cambisols. The microbial breakdown is likely limited with a high soil moisture level (Petraglia et al., 2019), probably resulting in insignificant decomposition between species and stands. Additionally, given the importance of the water-driven decomposition determines a weak mass loss in low-quality litter (Cotrufo et al., 2015; Mansfield and Bärlocher, 2005), contributing to a similar *k* value (from spruce) between soil types.

Across soil types, the results showed lower HFA on mass and C on Gleysol. A saturated soil environment has been identified to reduce soil microbial decomposition (Ahmed et al., 2019). Soil microbial communities of high soil moisture are generally N limited due to the less nutrient availability (Mueller et al., 2018), resulting in higher N accumulation and N release HFA in Gleysol.

4.4.5 Dynamics of the natural abundance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ during decomposition

Isotopic discrimination during litter decomposition has been observed in several studies involving selective consumption of various C compounds. Litter C concentration with $\delta^{15}\text{N}$ value, in this case, was negatively significant. This correlation signifies that $\delta^{15}\text{N}$ discrimination between litter types is due to the preferential recalcitrant fraction in substrates, which is consistent with several studies (Osono et al., 2008; Preston et al., 2009c). Microbial analysis suggests that

4. DECOMPOSITION HFA FADED AFTER SPRUCE CLEARCUTTING

^{15}N was transferred actively aboveground by saprotrophic fungi (Hobbie and Högberg, 2012) via promotion in the lignin or tannin degradation by fungi-based microbes. Suggesting that decreased ^{15}N values by retaining more litter N from forest floor than from clear-cut do contribute to higher microbial uptake and hence faster spruce litter C degradation in 'home' forest, strengthening the HFA.

In our study, we found a negligible change of $\delta^{13}\text{C}$ between stands during decomposition; residual C pools with slightly $\delta^{13}\text{C}$ distinct were needed to account for the duration of the experiment. A report from Ngao and Cotrufo (2011) indicated litter $\delta^{13}\text{C}$ discrimination appeared particularly in late stages of litter decomposition owing to the increase in the $\delta^{13}\text{C}$ of decomposition litter α -cellulose. Future long-term litter decomposition studies on the discrimination of natural abundance of isotope between species types and ecosystems are therefore recommended.

4.5 Conclusions

Spruce decomposed faster in spruce forest while beech decomposed faster in clear-cut, tightly associating with litter quality, indicating the occurrence of decomposition HFA at forest and clear-cut. Promoted decomposition and C mineralization for spruce in forest could be implied through relatively higher residual N concentration. Since the clear-cut in 2013, plant community and soil environment had shifted the historical resources from the original forest that facilitated faster beech decomposition and nutrients turnover rates due to lower C: N, thereby overriding pre-existing species HFA effects, especially at dryer Cambisols. $\delta^{15}\text{N}$ diverged after nine months at Cambisol between forest and clear-cut, suggesting that litter N decomposition correlated to soil and residual C status. This has implications for the management of upland forests that are currently still under conifers: Their regeneration to more natural forests with European beech can be promoted in short-term by intensive forest management.

5. Final discussion

5. FINAL DISCUSSION

5.1 Summary of the research objectives

i) How do the decomposition and nutrient release pattern of contrasting litter species respond to N addition in forests with already high N background deposition in Sichuan, China?

We carried out a N manipulation litterbag experiment to explore the effects of N additions (0 kg N ha⁻¹ yr⁻¹, 20 kg N ha⁻¹ yr⁻¹ and 40 kg N ha⁻¹ yr⁻¹) on decay rates and nutrients release of two contrasting species, the evergreen and nutrient-poor *Michelia wilsonii* and the deciduous and nutrient-rich *Camptotheca acuminata*, using a litterbag approach at the western edge of the Sichuan Basin of China. The decay rate and the mineralization of N and phosphorus (P) were faster in nutrient-rich *C. acuminata* litter than in nutrient-poor *M. wilsonii* litter, regardless of N regimes. N additions tended to decrease the decay constant (*k* value) in *M. wilsonii* litter, but did not affect *C. acuminata* litter. The N additions had no significant effects on carbon (C) release of both litter types. The N additions also showed negative effects on N and P release of *M. wilsonii* litter, particularly in the late decomposition stage. Moreover, for *C. acuminata* litter, N additions did not affect N release, but retarded P release in the late stage. N additions did not affect the C: N ratio in both litter types. However, N additions—especially high-N addition treatments—tended to reduce C: P and N: P ratios in both species. The effect of N addition on N and P remaining was stronger in *M. wilsonii* litter than in *C. acuminata* litter. The results of this study indicate that N additions retarded the nutrients release of two foliar litters. Thus, rising N deposition might favour the retention of N and P via litter decomposition in this specific area experiencing significant N deposition.

ii) How does C humification (sequestration) of belowground root litter respond to different elevations in an alpine forest in Tibetan Plateau, China?

We conducted a two-year litterbag experiment at two elevations (3037 m and 3580 m) on the eastern Tibetan Plateau to assess the root mass remaining and accumulation of humic substances in roots of three diameter classes (0-2, 2-5, and 5-10 mm) of two common subalpine tree species (*Picea asperata* and *Abies faxoniana*). The results indicated no significant differences between elevation based treatments in the concentration of humic substances were found. Both root

5. FINAL DISCUSSION

mass loss and concentrations of humic substance, humic acid and fulvic acid decreased with increasing root diameter. Both fulvic acid concentration and humification degree declined as root decomposition progressed but humic acid concentration exhibited an opposite trend. Our results reveal that the diameter-associated variations in the accumulation of humic substances were substantially stronger than altitudinal and interspecific differences in decomposing root litters. These findings have important implications for carbon sequestration via root humification in the subalpine forests experiencing snow-covered winter.

iii) How does clearcutting management in a German temperate forest and corresponding changed edaphic conditions affect litter decomposition, nutrient mineralization and field-litter affinity? How is this field-litter affinity (HFA)

To determine the occurrence of HFA in a forest and adjacent clear-cut, we set up a reciprocal litter decomposition experiment within the forest and clear-cut for two soil types (Cambisols and Gleysols) in temperate Germany. The forest was dominated by Norway spruce (*Picea abies*), whereas forest regeneration of European Beech (*Fagus sylvatica*) after clearcutting was encouraged. Our observation that Norway spruce decomposed faster than European beech in 70-yr-old spruce forest was most likely related to specialized litter-soil interaction under existing spruce, leading to an HFA. Elevated soil moisture and temperature, and promoted litter N release, indicated the rapid change of soil-litter affinity of the original spruce forest even after a short-term regeneration following clearcutting, resulting in faster beech decomposition, particularly in moisture- and nutrient-deficient Cambisols. The divergence between forest and clear-cut in the Cambisols of their litter $\delta^{15}\text{N}$ values beyond nine months implied litter N decomposition was only initially independent of soil and residual C status. We conclude that clearcutting modifies the litter-field affinity and helps promote the establishment or regeneration of European beech in this and similar forest mountain upland areas.

5. FINAL DISCUSSION

5.2 Synthesis

5.2.1 Litter species but also litter-soil affinity affect decomposition process

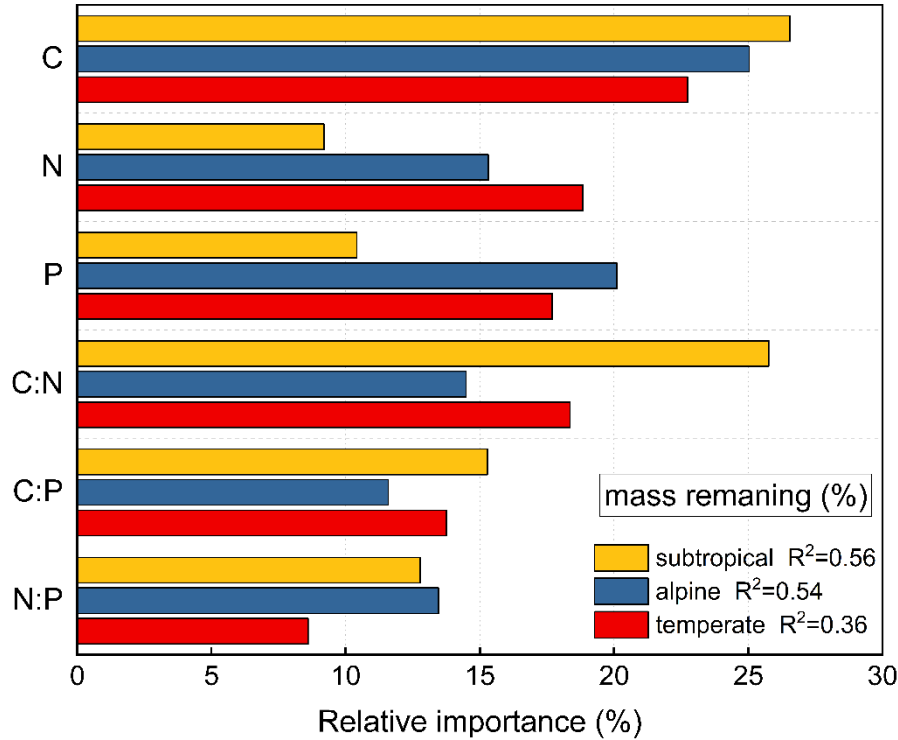


Figure 5-1. Relative importance of initial quality index affecting mass remaining rate (%) on three ecosystems

Our *in situ* decomposition experiments in subtropical and alpine forests showed that litter decomposition rates were tightly correlated with litter substrate quality, including aboveground leaf litter (*M. wilsonii* and *C. acuminata*) and belowground root litter of different diameter classes of fir and spruce (Chapter 2 and 3). That is, litter with higher nutrient concentrations and less structural carbohydrates is likely to be more leachable and more efficiently utilized by soil biotas, facilitating decomposition, as well as belowground SOM generation. In comparison between aboveground leaves and belowground roots, the mass of leaves continued to decline and released 30% by *M. willsonii* and up to 90% by *C. acuminata* throughout the 1-year long experiment period (Chapter 2), whereas the mass loss of roots slowly decreased *ca.* 20% and even remained constant for coarse root thereafter (Chapter 3). Random forest regression among

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ecosystems (Figure 5-1) indicated that litter degradation increased as N and P concentration increased in alpine forest (blue bar) and temperate forest (red bar) (Chapter 3 and 4), when in subtropical forest (yellow bar), broadleaves were mainly affected by litter C compound and C:N ratios (Chapter 2), regardless of species and litter types. In conclusion, litter C compound is the best predictor of litter decomposability in warm region. In cold region, however, nutrient concentration is more important for litter nutrient cycling and mineralization process.

Plant quality is primary source of SOM and can affect the rate of SOM stabilization associating with microbial biomass and substrate use (Cotrufo et al., 2013). High-quality litter can be selectively preserved in stabilized SOM in long-term decomposition (Wieder et al., 2014). Humification processes from all roots of the different diameters were significantly affected by substrate lignin content (Chapter 3). Lignin is generally polymerized with three main types of monolignols (sinapyl alcohol, coniferyl alcohol, and *p*-coumaryl alcohol) by extracellular enzyme (such as, peroxidase and laccase) (Bonawitz and Chapple, 2010; Liu et al., 2011a). In general, fine roots with relatively highest initial N and P concentrations and lowest C stoichiometry contributed to a higher humification degree and more stable SOM formation (HA) (Chapter 3). Increase accumulation of lignin-originated SOM entering the soil cycling can reduce the infiltration of fungal enzymes and toxin other plant cell wall (Liu et al., 2018a), which benefit to host species and its dominance in ecosystems. Several decades of lignin deposition of Norway spruce shape and strengthen its home-effect in a temperate mountain forest (Chapter 4).

Plant nutrients availability is a limiting factor for the growth of decomposition populations in forest ecosystems (Deng et al., 2017; Marklein and Houlton, 2012). High-quality litter in turns is decomposed with almost all decomposer and can improve nutrient availability in the soil (Saswati et al., 2010). The greater uptake of N and P from soil and lower biomass gained in low-quality root resulted in nutrient immobilization in alpine ecosystem (Zhuang et al., 2018). Low-quality litter of *M. wilsonii* was also found the accumulation of N and P after initial leaching period. N addition delayed this release pattern of N and P in litter

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(Chapter 2). Chemical immobilization and microbial assimilation (fungi hyphae) associated with the nutrients transformation between litter and soil (Hobbie and Hobbie, 2008). The diversity of response of litter decomposition and nutrient release to soil chemical condition and elevated N could elevate limit value and then hamper the litter sequestration on low-quality litter.

On other hand, a massive imbalance in soil available N and P resulted in soil P limitation, owing to increased N input. the magnitude of P limitation and underlying mechanisms differ between plant types and ecosystems, differently responding to climate change and forest management (Yue et al., 2018). The leaf litter of *C. acuminata* with high P and low C: N ratio indicated faster degradation and P release rate (Chapter 2). The lack of soil labile P and litter P significantly decreased the decomposition of *C. acuminata* and *M. willsonii* under high N addition (40 kg N ha⁻¹ yr⁻¹). Moreover, Litter P dynamics were directly regulated by external supply rather than internal P remobilization (Yuan and Chen, 2015). Decomposition occurred in temperate forests following disturbance, where a higher nutrient turnover period to some extent broke the forest P limitation, promoting the decomposition and succession of beech in clearcutting stands in early succession stage (the first 10 years, Chapter 4). Thus, human and natural disturbance can create a very different resources turnover rate and the composition and diversity of plant species by changing spatial and temporal distributions.

Clear-cutting can cause remarkable higher temperature and moisture, alters *in situ* formation of SOM and nutrient turnover rates, and subsequently changes in species generation, which characterized early post-disturbance succession. I verified from a meta-analysis, which depicted by 17 publications with 184 datasets about the transplant litter decomposition under the different succession stages after clearcutting (Appendix Table C-1), clearcutting operation removed the host species, resulting in decreased and switched C deposition and the disappearance of HFA effect from host species in stands of early successional stages (i.e., <10 years post-disturbance, Figure 5-2). A similar finding was reported in soil succession gradients on decomposition HFA (Veen et al., 2018). New host species following forest management were documented to have strong

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affinities to mid and mature stands (i.e., >30 years post-disturbance, Figure 5-2). Broadleaves and mixed species in ecosystems with optimal C fractions and C: N ratios have a competitive advantage over needles in terms of decomposition HFA (Figure 5-2, Appendix, Figure C-2). Thus, European beech is expected that higher ecosystem stability and resilience beyond climate change and increased N deposition would lead forests to serve as carbon sinks.

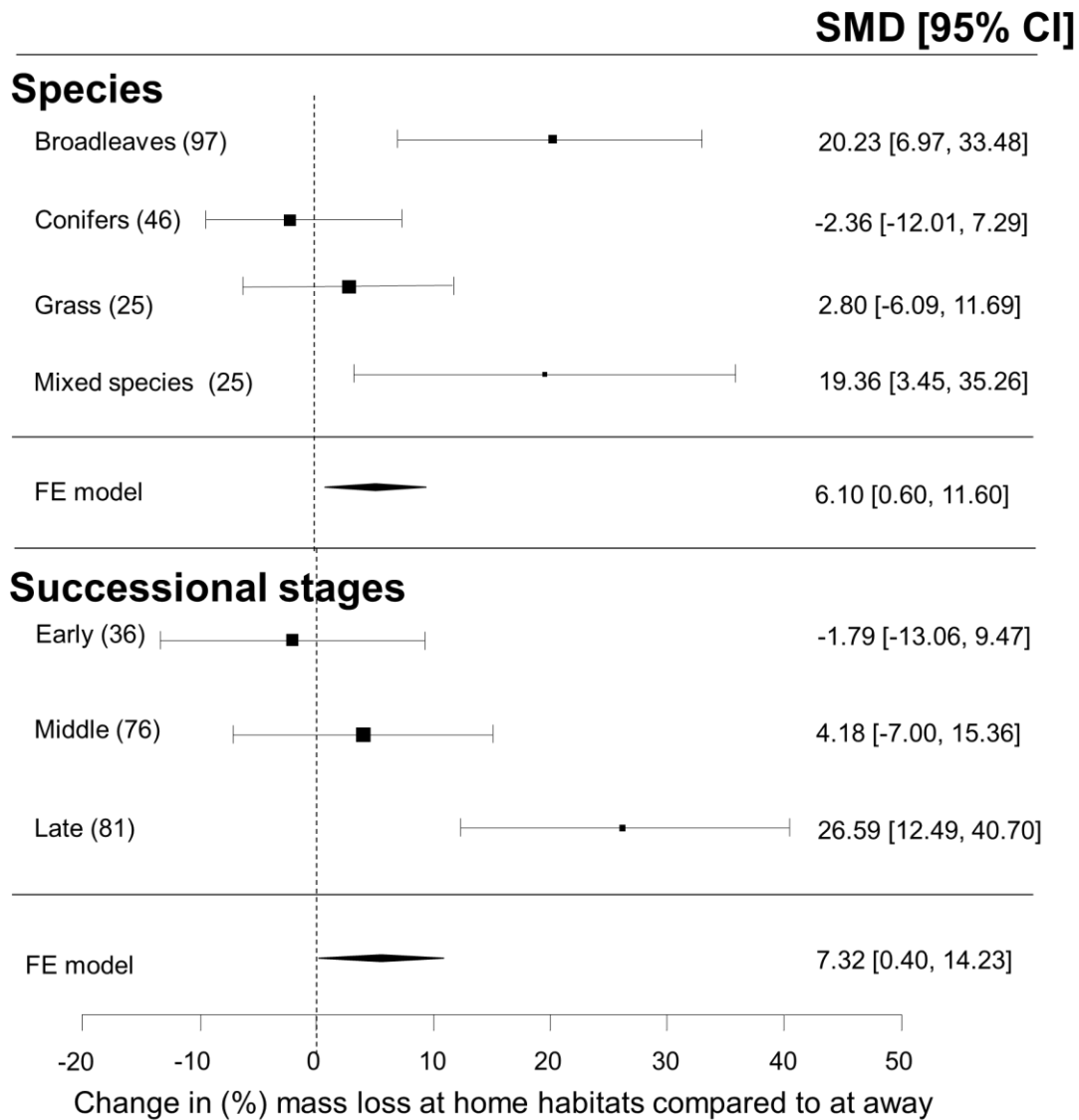


Figure 5-2. The changes (%) in the mass loss at home sites compared with those at other sites (decomposition HFA) in different species and successional stages after clearcutting management. Confidence intervals (95%) and number of cases (in parenthesis) are shown.

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Buddle et al. (2006) suggested that the re-establishment of forest to 'pre-disturbance' may require 30 years at least during the post-fire or clearcutting regeneration in the boreal forests. In Chapter 4, we assumed that soil layers in spruce forests were well established within local adaptation among soil communities after more than seven decades of regeneration. Soil layer has restored the primary habitats for spruce through long-term mineralization and humification, contributing to the decomposition HFA in spruce forests. Freschet et al. (2012) demonstrated that recalcitrant species induced HFA effects from the nutrient-limited ecosystem and labile species from nutrient-rich ecosystems. This perhaps results from the proportion of microbial generalists versus specialists (functional breadth hypothesis), which proposed that decomposers from recalcitrant species habitats have a wider functional capacity to degrade litter species at relatively fast rates, irrespective of litter quality, vice versa (Keiser et al., 2011; Van Der Heijden et al., 2008). Plant species composition is likely to have massively changed on clear-cutting stands after 8-year regeneration (Chapter 4), accompanied by improvements in soil physical and chemical conditions and soil respiration (Rajala et al., 2011; Siebers and Kruse, 2019). Thus, the original soil-specific effects on decomposition paths of the different organic molecules may be missing from or reduced at forest ground, associated with the elevated decay rate and N mineralization for European beech in clear-cut stands (Chapter 4).

5.2.2 The diversity of climate response of litter decomposition among biomes

In three ecosystems, roots degraded slowest in cold subalpine forests, and broadleaves decomposed fastest in warm, moist subtropical forests, following the CDI prediction of 0.32, 0.51, and 0.95 for subalpine forests, temperate forest, and subtropical forest, respectively (Table 5-1). This result is consistent with comparisons at global scale in various biomes, indicating that climate and litter quality hierarchically regulate plant litter decomposition on a large scale (Aerts, 2006). Furthermore, litter interaction was found between HFA_i and CDI within collected dataset (Appendix Table C-1), regardless of the different decomposition stages or successional stages (Appendix Figure C-3). This regression pointed that climatic features on-sites that are insufficient to predict the occurrence of HFA.

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Table 5-1. Calculated climate decomposition index (CDI) in different forest ecosystems.

Ecosystems	Latitude	Longitude	MAP (mm)	MAT (°C)	CDI
Alpine forest	31.23 N	102.9 E	850	3.0	0.32
Temperate forest	50.5 N	6.3 E	1200	7.0	0.51
Subtropical forest	31.02 N	103.6 E	1243	15.2	0.95

MAP and MAT indicated mean annual precipitation and mean annual temperature, respectively. The function climate decomposition index [CDI] calculated by Lloyd and Taylor (1994) and modified by Adair et al. (2008). The climate data was obtained from Visualcrossing (<https://www.visualcrossing.com/weather-history>)

The variation of humification process was observed between winter and summer time. Physical breakdown and rapid release of labile materials associated with frequent freeze-thaw in first winter could promote the formation of humic substances (Chapter 3). More importantly, Elevated summertime temperature promoted root accumulated more stable humic acid from degrading fulvic acid from cellulose and lignin-like products in alpine forests. Given the sensitivity of decomposition and the substantial limitation of temperature, fulvic acid with small molecular weight could be transformed into humic acid (more stable OM) through fungal metabolism as decomposition progressed (Frouz et al., 2011b). difference in hydrothermal conditions between the elevation-based climate gradient differentiated the mineralization and humification processes. Based on Climate change knowledge portal (CCKP) we do have a rather accurate predication of future warming trends in sensitive alpine forest. This may, for example, involve changes in winter on the duration of snow cover and the occurrence of freeze-thaw cycles, and summer time temperature and precipitation. Roots exudates provide readily available C for microbes to promote the formation of humic substances. And therefore, plant roots from cold alpine biomes are important to accumulate SOM, but additional supporting evidence is needed on warming-induced change (>1 °C experimental setting, according to CCKP prediction).

Precipitation or soil moisture, as another best predictor of decomposition. However, mass loss in near stream Gleysols was inhibited owing to the saturated

5. FINAL DISCUSSION

soil environment, indicating the suppression of microbial decomposition (Chapter 4). High soil moisture generally suggested limited nutrient availability, contributing to higher litter N immobilization and thus elevated N release HFA in Gleysols in temperate forests. When assessing subtropical forest decomposition, abundant rainfall increased physical leaching rate, mass loss rate and C mineralization rate (Chapter 2). In this thesis, intense rainfall in subtropical forest accelerated soil nutrients leaching and erosion (Ferrasol). But saturated clayey Gleysol in temperate forest have a high P-adsorption potential (Alovisi et al., 2020). Thus, the different response of soil types on water input contributed to different characteristics on litter decomposability and soil nutrient accumulation.

5.2.3 Soil chemical conditions' influence on litter decomposition

Growing evidence supporting the importance of edaphic conditions, as well as decomposer communities combining local plant litter chemistry, they are important to regulate decomposition on local scales and cross-site experiments (Fanin et al., 2019; Fanin et al., 2016; Keiser and Bradford, 2017; Veen et al., 2018). Corresponding with this viewpoint, forest floor exploration under various N treatments would have different effects on the decomposition between plant species. In my study, I found that N deposition significantly constrained the mass loss rate of nutrient-poor *M. wilsonii*, while not affecting nutrient-rich *C. acuminata* in subtropical forests. On the western edge of the Sichuan Basin, rich rainfall increases leaching rate but decreases soil P availability capacity, which fundamentally went against microbial community abundance (Li et al., 2016; Tian et al., 2019) in subtropical forests. This resulted in predictable patterns in suppression on decomposition and net N immobilization on low-quality *M. wilsonii* (Chapter 2).

We also found litter N from Norway spruce and European beech accumulated in the 1-year long decomposition in temperate forests. Meanwhile, microbial decomposition had to promote C metabolism in order to synthesize for further nutrient mining (Tian et al., 2018). Coniferous forest usually has higher soil acidity than board-leaved forest or grasslands, furthermore reducing soil P availability by binding phosphate ions with Al and Fe (Devau et al., 2009). The acidification in spruce forests may restrain microbial activity and hence phosphate activity.

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Moreover, gymnosperms (Norway spruce) have more lignin than angiosperms (European beech), which is in long-term important for the fungi to adapt and respond to N immobilization patterns in the habitat (spruce forest) and finally the performance of decomposition HFA on Norway spruce (Chapter 4).

However, clearcutting management directly changes the species community composition on the forest floor, going through a short grassland-dominated successional stage. The abiotic processes such as temperature, moisture, and UV radiation were significantly promoted and may now predominate nutrient availability and degradation (Finér et al., 2016; Keiser et al., 2021; Redding et al., 2003). This mechanism may conflict with the original litter-soil affinity and the absence of home-effect for spruce, both of which contribute to faster C and N cycling and coniferous forest management at this site (Veen et al., 2018; Xiao et al., 2019).

5.3 Conclusions

In conclusion, my study clearly demonstrated that natural events and man-made phenomena such as elevation-gradients, N addition and clearcutting as disturbance did lead to the heterogeneous changes in litter decomposition process and SOM generation. Different disturbances produced different influencing consequences on the C or nutrient loss among litter types through their effects on substrate quality and between species and their abiotic environment. The input N was an important constraint on the available litter N and P on low-quality litter. Indeed, low-quality showed high sensitivity to internal or external nutrient condition. Diameter-mediated variations were much stronger than altitudinal and interspecific differences in decomposing root litters for the transformation of complex C compounds. Moreover, the decomposition of spruce was significant regulated by N condition in original spruce forest.

Moreover, external factors affected the dynamics of litter mass loss rate and OM formation through various disturbance in ecosystems. Such as, increased beech decomposition and nutrient turnover rates would occur following clearcut areas establishment in but the HFA effect will be masked in clearcut stands in temperate forests, especially at dryer Cambisols. To a large extent, seasonal snowpack and freeze-thaw cycles associated with elevation in alpine forests offset

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the expected warming effects on the accumulation of humic substances (i.e., stable OM). Therefore, any forest management planning also needs to take into account the peculiarities of plant species in relation to edaphic conditions.

This study provided novel insight into the influencing mechanisms of various extreme environments on the degradation and nutrient mineralization pattern in types of litter and ecosystems. Such knowledge is expected to help improve our understanding of the effect of disturbances on biogeochemical cycles and forest management or natural succession. For this reason, I noted that nutrient-rich species or increasing species richness will increase their ecological capacity to buffer environmental extremes as sites become N amendment or warming. The findings of this thesis may have implications for improving our understanding of how disturbances impact biogeochemical cycles and for developing more sustainable forest management strategies in the face of global climate and societal changes.

Appendix A

Supporting information to Chapter 3

APPENDIX A

Table A-1. Daily mean soil temperature (MT), positive accumulated temperature (PAT) and negative accumulated temperature (NAT) at the two elevation sites during the specific period.

Elevation	First winter			First growing season			Second winter			Second growing season		
	MT (°C)	PAT (°C)	NAT (°C)	MT (°C)	PAT (°C)	NAT (°C)	MT (°C)	PAT (°C)	NAT (°C)	MT (°C)	PAT (°C)	NAT (°C)
3037 m	1.6	424	-81	10.8	1756	0	1.1	310	-98	10.3	1570	0
3580 m	0.3	202	-138	8.4	1376	0	-0.5	150	-248	7.8	1191	0

APPENDIX A

Table A-2. Basic properties of two elevations sites in the southwestern China.

Variables	3580 m	3037 m
Dominant tree species	fir and cypress	spruce and fir
Forest coverage	0.9	0.8
Soil properties (0-10 cm)		
Organic carbon (g kg ⁻¹)	161.4	157.6
Total nitrogen (g kg ⁻¹)	10.3	9.5
Total phosphorus (g kg ⁻¹)	1.1	1.2
Bulk density (g cm ⁻³)	0.8	0.9
pH	5.6	5.9

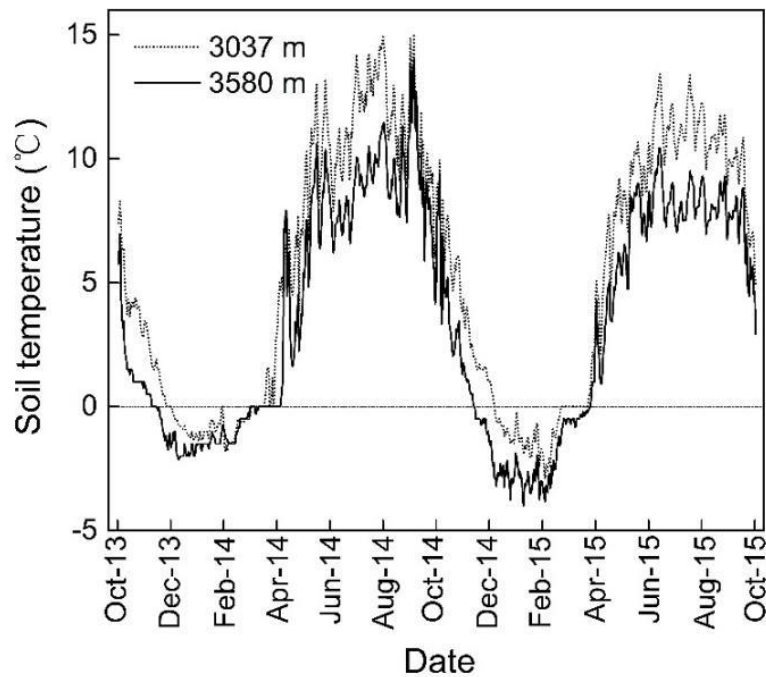


Figure A-1. Dynamics of daily mean soil temperature of 10 cm in two elevations from October 2013, to October 2015 (a total of 731 days of decomposition in the field).

APPENDIX A

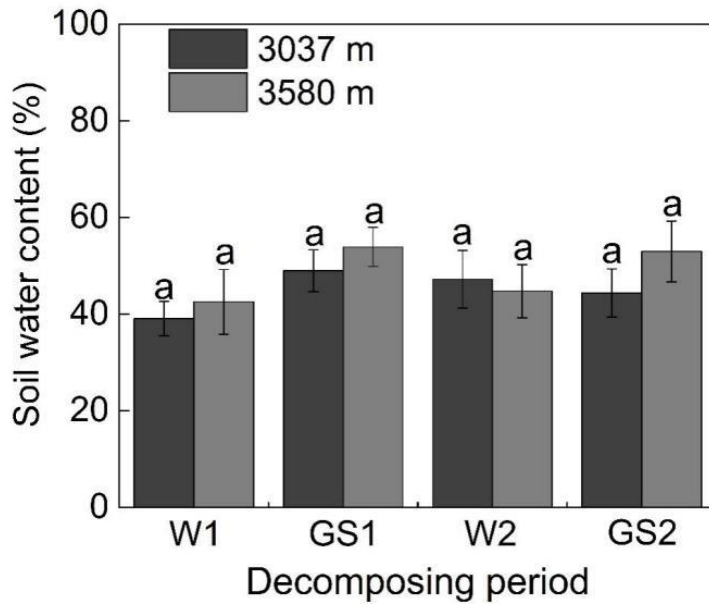


Figure A-2. Soil water content at the depth of 10 cm within two elevations. Different lower case letter indicate significant differences between altitudes. W1: the first winter, GS1: the first growing season, W2: the second winter, GS2: the second growing season.

Appendix B

Supporting information to Chapter 4

APPENDIX B

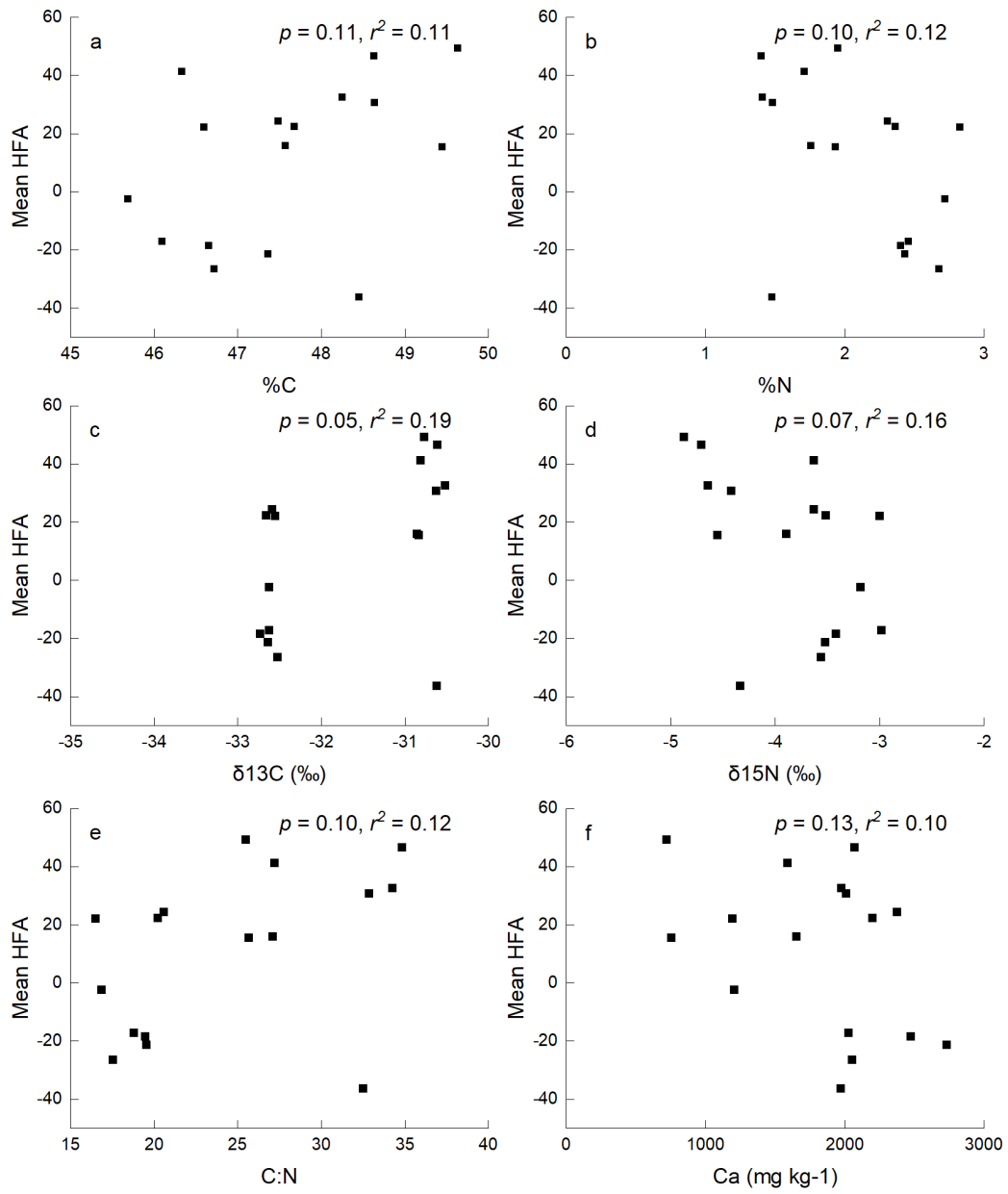


Figure B-1. The relationship between total C, N concentrations, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C: N ratios, Ca and mean HFA.

APPENDIX B

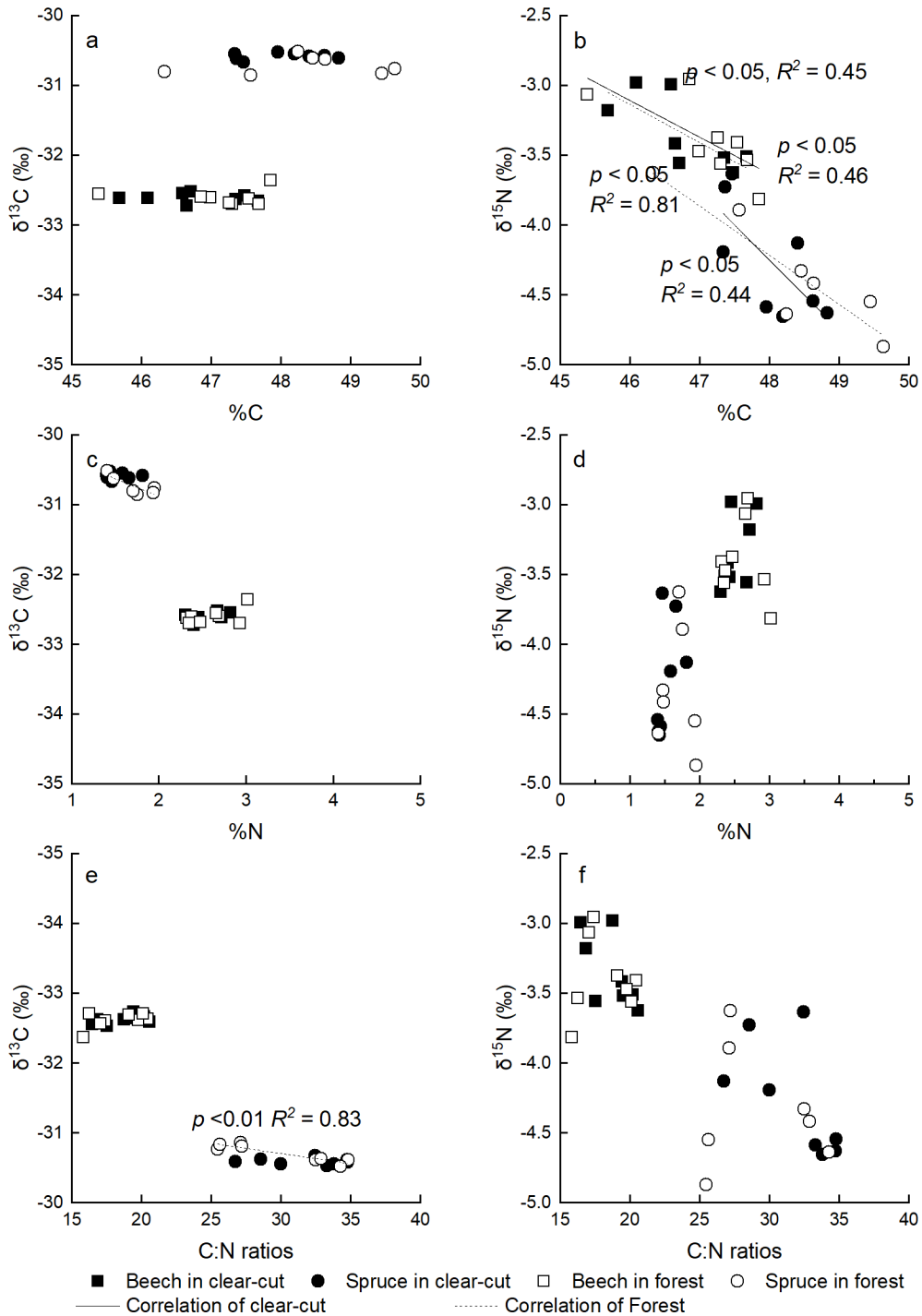


Figure B-2. the relationship between the initial litter C, N and C: N ratios on the isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value.

Appendix C

Supporting information for Chapter 6

APPENDIX C

Table C-1. The reference data collected from ecosystems occurred HFA effects in different successional stages after clearcutting harvest, as well as calculated climatic decomposition index (CDI).

Location	Latitude	Longitude	MAP (mm)	MAT (°C)	CDI	Reference
Sabah, Malaysia.	4.81N	116.9E	3800	24.2	1.95	[1].
Campeche, Mexico	17.75N	89.25W	945	22	0.55	[2].
Mauna Kea volcano, Hawaii	20.46N	157.50W	2200	15.1	1.27	[3].
Guangdong, China	22.57N	112.83E	1700	22.6	1.98	[4].
Zhenjiang, China	31.98N	119.23E	1055.6	15.2	1.20	[5].
Baotianman Nature Reserve, China	33.33N	111.77E	900	15.1	1.46	[6].
Montes de Toledo, Spain	39.52N	4.27W	469	12.9	0.58	[7].
Liao River Source Nature Reserve, China	40.04N	118.37E	550	7.3	1.23	[8].
Rincine Forest Florence, Italy	43.86N	11.66E	1273	9.2	0.92	[9].
Xilinhot City, Inner Mongolia, China	44.17N	116.48E	308	-1.1	0.67	[10].
South Tyrol territory, Italy	46.54N	11.10E	735	10.5	0.69	[11].
Hochschwab, Austria	47.59N	15.09E	1397	4.5	0.74	[12].
Que´bec, Canada	47.80N	78.07E	918	1.2	0.59	[13].
Kreisbach, Lower Austria	47.94N	14.21E	850	8.4	0.59	[14].
Frauschereck, Upper Austria	48.09N	13.24E	1180	7.7	0.63	[15].

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Kalek, Czechia	50.59N	13.26E	1000	6.3	0.62	[16].
Veluwe, Netherland	50.91N	4.06E	859	10.6	0.66	[17].
Solling plateau, Germany	51.77N	9.57E	1032	7	0.67	[18].
British Columbia, Canada	55.76N	120.23E	467	2	0.70	[19].
Vestfold, Norway	59.33N	10.1E	205	10.2	0.60	[20].

MAP: mean annual precipitation; MAT: mean annual temperature.

- [1]. (Both et al., 2017)
- [2]. (Xuluc-Tolosa et al., 2003)
- [3]. (Rothstein et al., 2004)
- [4]. (Sun et al., 2020)
- [5]. (Ji et al., 2020)
- [6]. (Wang et al., 2015)
- [7]. (Bravo-Oviedo et al., 2017)
- [8]. (Gao et al., 2016)
- [9]. (Pastorelli et al., 2021)
- [10]. (Wang et al., 2020)
- [11]. (Bani et al., 2018)
- [12]. (Berger et al., 2015)
- [13]. (Chomel et al., 2015)
- [14]. (Berger and Berger, 2012)
- [15]. (Růžek et al., 2021)
- [16]. (Veen et al., 2018)
- [17]. (Lin et al., 2015)
- [18]. (Prescott et al., 2000a)
- [19]. (Asplund et al., 2018a)

APPENDIX C

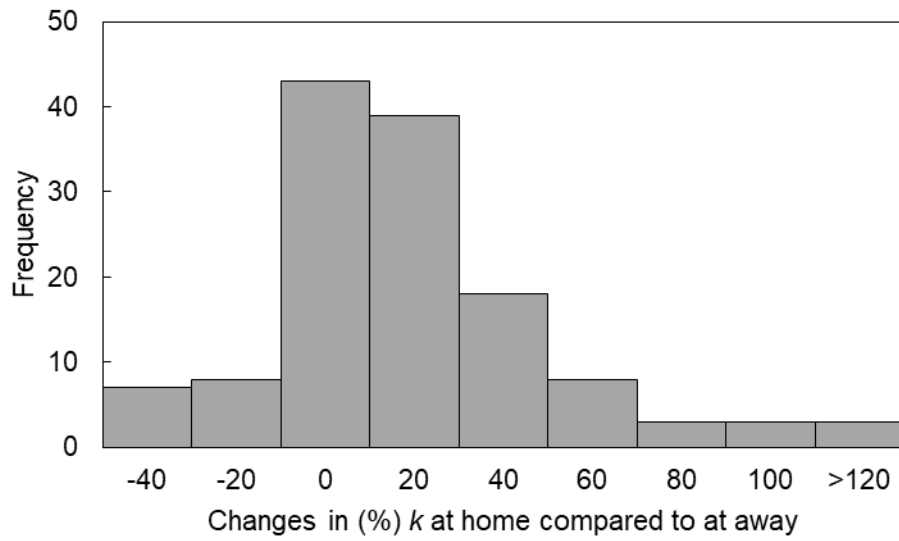


Figure C-1. The frequency distribution of litter mass loss comparison between home and away site (reference data for Figure in Chapter 5)

APPENDIX C

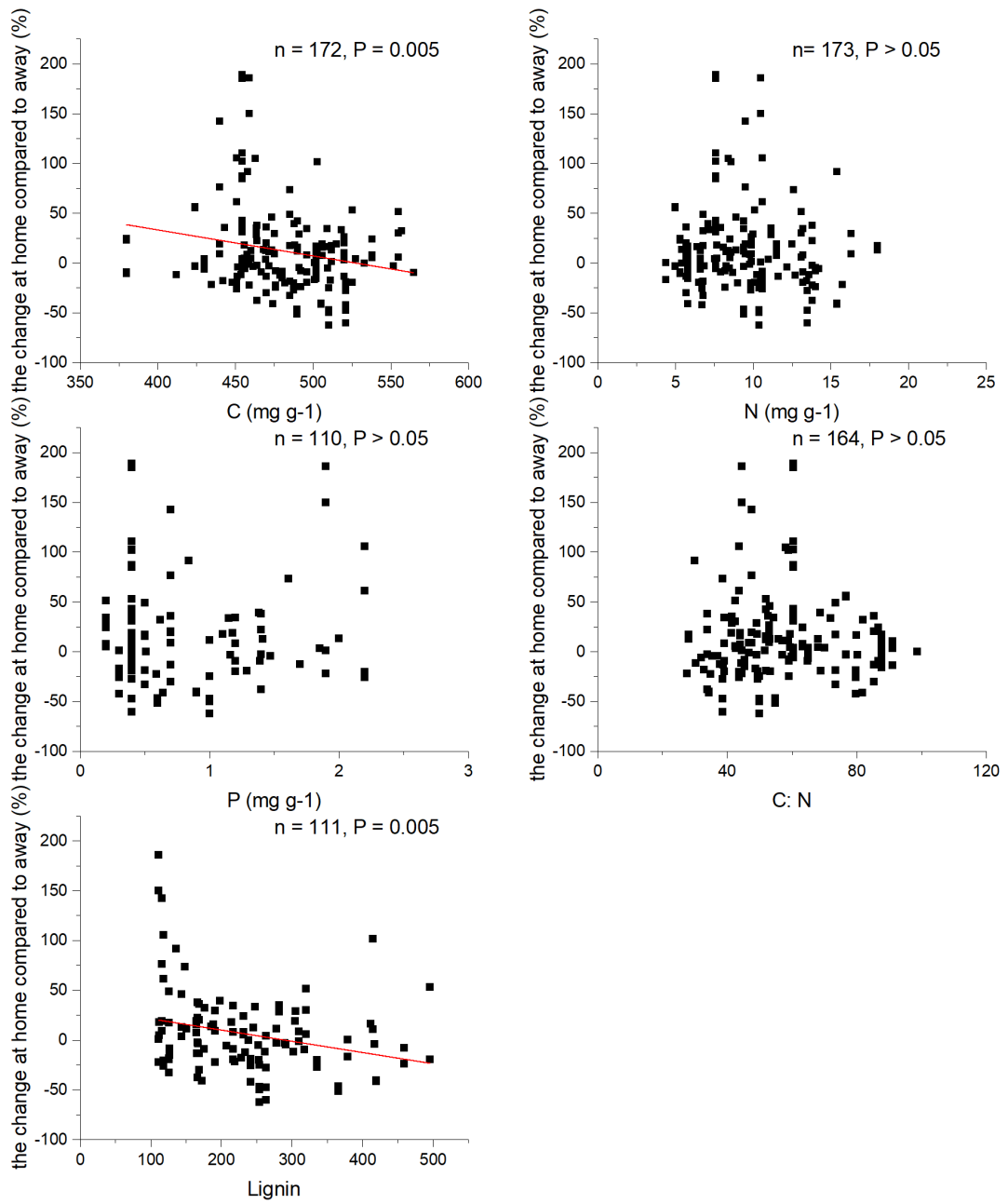


Figure C-2. Relationships between litter substrate traits (concentration of C, N, and P, and C: N ratios and lignin) and HFA effect. Red lines indicate significant linear correlations ($P < 0.05$) between litter traits and HFA effect. Sample sizes and significance were noted in each plot.

APPENDIX C

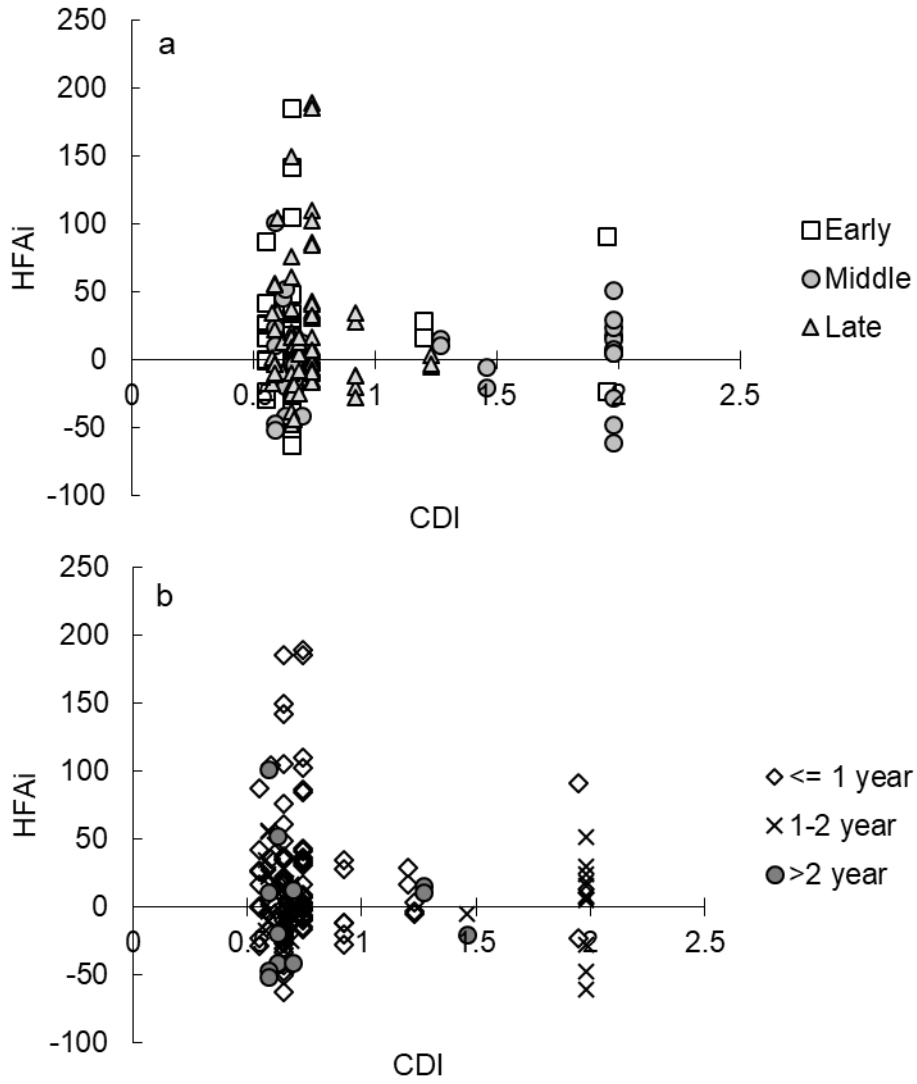


Figure C-3. The relationship between climate decomposition index (CDI) and the changes in k compared at home over away sites (HFAi)

Appendix D

The impact of clearcutting on litter decomposition – Testing the Yasso model with litterbag and standard tea bags in German Forest

Manuscript in preparation

1.1. Introduction

Through litter decomposition, more than 50% of net primary production is returned to the soil (Wardle et al., 2004) and 60 Pg C year⁻¹ is emitted to the atmosphere (Houghton, 2007). Most of these emissions originate from the decomposition of the relatively labile litter. Litter decomposition also forms more stable organic compound. The rate of decomposition varies enormously with internal litter chemistry and external climate condition (Manning et al., 2008; Zhang et al., 2008). At regional scale, litter decomposition rate is mainly regulated by plant litter quality. Litter consists mainly of labile and recalcitrant carbon, nitrogen and phosphorus fractions, requiring microbial and enzymatic degradation (Sinsabaugh et al., 2008). In other words, high-quality litter is characterized by higher N and P concentrations and lower C: N or lignin:N ratios, and can decay faster relative to low-quality litter (Micks et al., 2004; Zhu et al., 2016).

Based on a meta-analysis involving 818 plant species, Cornwell et al. (2008) indicated that plant species traits are critical predictors of their litter decomposition within a climate region. Litter decomposition experiments had been extensively conducted worldwide with amorous achievement. However, owing to site-specific and plant-specific, the comparability between studies ad sites is restrained by using local litter. Recently, Keuskamp et al. (2013) proposed a standardized plant litter to measure decomposition at local, regional and global scale. Using tea bags as standard litter to simulate the decomposition of real plant tissues on site. The collected data from worldwide can be applied to uniformed analysis on like soil C stock or CO₂ emission. This simplified litter bag experiment involves burial of green and rooibos teabags, following the measurement of mass loss after *ca.* 90 days (Keuskamp et al., 2013).

Yasso model was developed to be a simple but widely applied soil carbon model requiring a limited amount of input data, compared to the CENTURY and RothC model. Yasso takes into account differences in initial litter chemistry and the influence of climate condition on long-term decomposition processes (Liski et al., 2005). Litterbag experiments provide valuable data for testing the accuracy of prediction of decomposition from soil carbon models. According to basic climate

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and litter quality input across Canada (CIDET) (Palosuo et al., 2005), the Yasso model correctly predicted differences in decomposition rates among litter types in the early years of decomposition, but underestimated them in later years. As Yasso model is primarily original from Finland and calibrated using European litter bag data. Thus, Yasso model to estimate the litter decomposition in Wüstebach catchment would have better accuracy.

Clearcutting, a regeneration strategy to update forests from monocultures to natural forests, sharply changes the microclimate and biomass on site. Reduced input of fresh litter leads to a decline in C availability and immobilization of N into soil layer (Prescott, 1997). Currently, The majority of studies have attributed to the abiotic and biotic shifting on the forest residues or soil (Brais et al., 2004), mostly within a decade after harvesting, lacking comprehensive evidence of disturbed litter-soil continuous on forest C and nutrient stores via the change in multiple environmental conditions and species succession.

Knowledge of regulators on litter decomposition informed models used to understand how ecosystem organic matter stocks and emissions will respond to disturbances, and hence the process of feedback between the biosphere and atmosphere that might drive further natural regeneration. Therefore, it is necessary to ensure the ambient environmental convergences on regulating the decomposition and SOM accumulation. After 5-year regeneration, the clear-cut site in Wüstebach is now entering the understory re-initiation stage, and new shrubs and trees appeared. The underlying objective are those: 1) testing the standardized litter (tea) to for harmonizing local litter decomposition studies in short-term decomposition; 2) comparing the limited factors in disturbed systems between litter chemistry and climate, to address major drivers on C fraction, N, P and S dynamics after clearcutting practice; 3) simulating observed decomposition of native and standard litter with Yasso to evaluate the C compound turnover within Wüstebach catchment.

This report resulted from the Tea Composition initiative using standard litters (tea bags – Keuskamp et al., 2013) and simulated by Yasso07 model providing standardized litter decomposition measurements between forest and regeneration sites. The objective of this report was to simulate the observed

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decomposition of native and standard litter with Yasso07 to evaluate the tea bag approach for further development of pertinent simulation.

1.2. Materials and methods

1.2.1. Study area

The study is located in Wüstebach catchment, a part of the TERENO Lower Valley-Eifel field experimental observatory (50.84 N, 6.31), and covers an area of 38.5 ha, including 8.6 ha of the deforested region (22.3%, Figure D-1). The region is characterized by a mild and humid temperate climate, with the average annual precipitation of 1200 mm and the average annual temperature for 7 °C (Lehmkuhl et al., 2010). Altitude ranges from northern 595 m to southern 628 m m.a.s.l. Soils are mainly Cambisols and Planosols in hillslopes and Gleysols and Histosols in the riparian zone. The stands were predominated by Norway spruce (*Picea abies* L.) and Sitka Spruce (*Picea sitchensis*) that were planted at the end of the 1940s. Since 2013, 8.6 ha of Wüstebach catchment were deforested in order to speed up development into a natural forest of beech (*Fagus sylvatica*) and birch (*Betula pubescens*) as a potential natural vegetation cover.

1.2.2. Litter decomposition measurements

1.2.2.1. Local litter

In September 2019, most of above-ground plant tissues begins to senesce, we harvested two types of leaves from live species: Norway Spruce (original species) and Beech (later successional species). All samples were air-dried to constant mass. 2.5 g of Spruce needles and Beech leaves were filled into polyethylene litterbags (10 × 8cm; 0.25 mm mesh size), respectively, permitting entry of bacteria, fungi and microfauna (Bradford et al., 2002). In October 2019, five sampling locations were selected for CC and UC treatments. At each subplot 7 litterbags of each species were placed on the soil layer, after getting rid of humus layer or grass. Litterbags were collected after 1, 3, 6, 9, 12, 18, 24 months. Together, we prepared 140 litterbags (7 sampling times × 2 plots × 5 replicates × 2 species) in total.

Harvested litterbags were stored in refrigerator at 4 °C and transported to laboratory. Soil particles and other extraneous materials were removed from the

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harvested litter. And then freeze-dry and weigh. Mass loss (1) and k -value (2) of each sample will be calculated by the difference between the initial dry mass and harvested substrates with ash-free basis (500 °C for 4 h) (1). The remaining of C fraction (Total organic matter, water-soluble fraction, acid soluble fraction, ethanol, and acid insoluble fraction), TN, TP concentrations were measured and calculated.

$$\text{Mass loss} = (M_o - M_t)/M_o \quad (7)$$

$$M_t/M_o = e^{-kt} \quad (8)$$

Where M_o is the initial litter mass, M_t is the residual litter mass as sampling time t , k is the annual decay constant expressed in year⁻¹.

1.2.2.2. Teabag litter

Lipton green tea (EAN: 8722 7000 5552 5) and Lipton rooibos tea (EAN: 8722 7001 8843 8) were incubated and processed following the Keuskamp et al. (2013) protocol. Two types of tea were used as surrogates from high and low quality litter, respectively. At each point, a set consisting of two types of tea were buried in the soil at 8-cm depth at the beginning of every season 2018-2019, and retrieved after approx. 90 days. 75 points were selected to bury the teabag samples in both clear-cut and forest sites (Figure D-1). Harvested teabags were stored in refrigerator at 4 °C and transported to laboratory. Soil particles and other extraneous materials were removed from the harvested litter. And then oven-dry and weigh.

Environmental conditions can increase the stability of less recalcitrant compounds, reducing the mass loss of the originally hydrolyzable fraction (i.e., chemically labile). This inhibiting effect is therefore referred to as S (Equation 9), with a_g being the decomposed fraction and H_g the hydrolyzable fraction of green tea.

$$S = 1 - \frac{a_g}{H_g} \quad (9)$$

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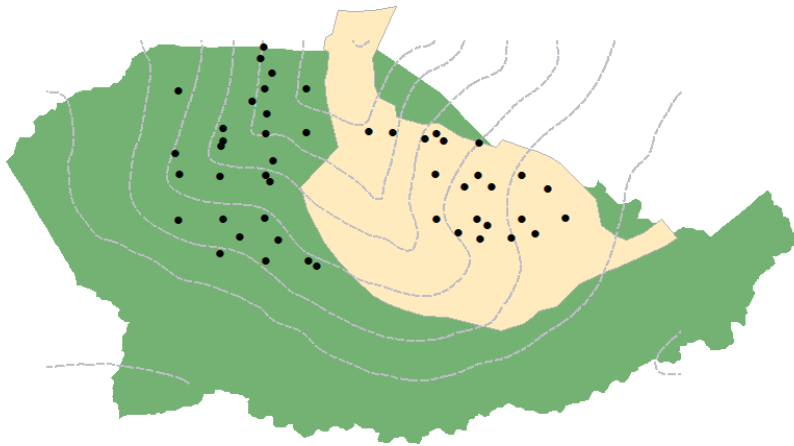


Figure D-1. Scheme for tea bag experiment, sampling points originally selected from SoilNet points where soil temperature and moisture are monitored.

1.2.3. Litter decomposition simulations

The decomposition of standard litters was simulated by using user-interface version of the litter decomposition and soil carbon model Yasso07. The Yasso model of soil carbon consists of five decomposition compartments and two woody litter compartments (Figure D-2) (Liski et al., 2005). Non-woody litter entering the soil is divided directly into the decomposition compartments of extractives, cellulose and lignin-like compounds according to its chemical composition. Each decomposition compartment has a decomposition rate that determines the proportion of its contents to be removed in a time step. Fractions of these removed quantities are transferred into the subsequent decomposition compartments having lower decomposition rates while the rest are removed from the system, that is, heterotrophic respiration or leaching while the rest forms more recalcitrant compounds (Berg et al., 1982). The decomposition rate is controlled by climate condition. In the simulations, the chemical composition of the Teabag litter was based on measurements. The mean annual temperature, precipitation and temperature amplitude were collected and calculated from data measured at the study site in 2013-2018.

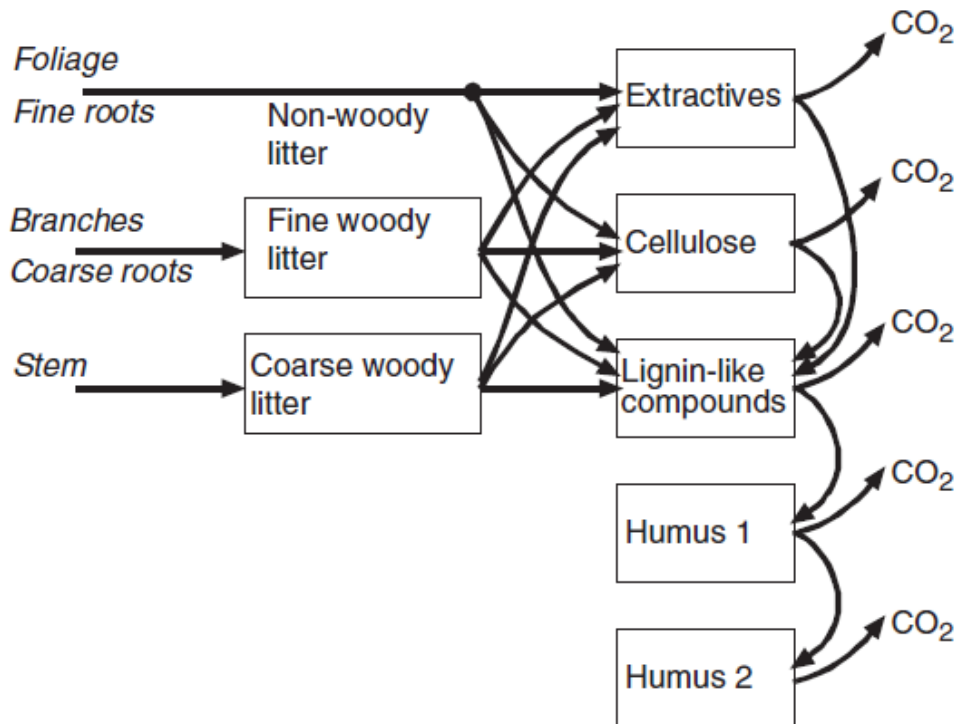


Figure D-2. Flow chart of Yasso soil carbon model. The boxes represent soil carbon compartments, the arrows carbon fluxes; only those carbon fluxes are shown that deviate significantly from zero (<http://en.ilmatieteentilaitos.fi/yasso-description>).

1.3. Results and discussion

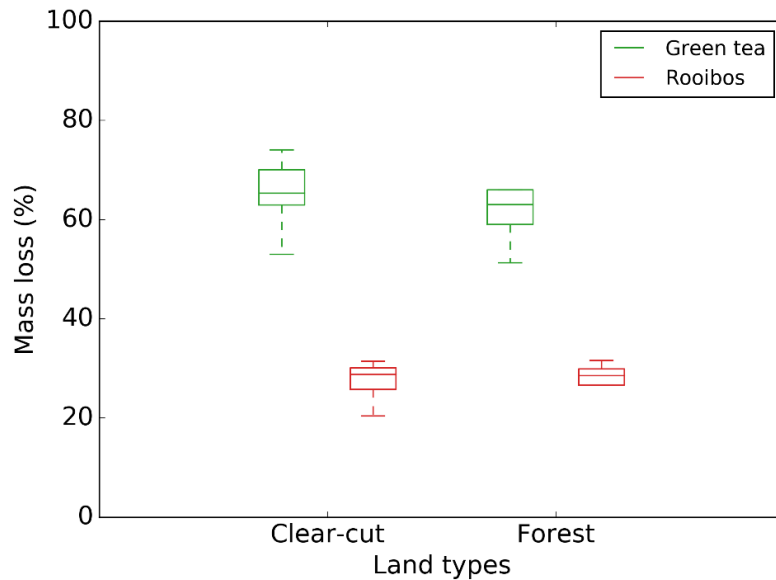
In clearcutting areas, where soil environmental condition, as well as soil pH were sharply elevated after removing the canopy species (Siebers and Kruse, 2019; Wiekenkamp et al., 2016), masking the decomposition HFA for spruce forest. Thus, the decomposition rate and nutrient release rate from beech in this new clearcutting site, were promoted, similar results also showed on standard litter in clear-cut (Figure D-3).

Owing to the difference between soil environmental conditions and soil nutrient dynamics between forest and clear-cut, we observed the significance of mass loss rates between plant types and locations, that in the original spruce forest, spruce decomposed faster than beech (Figure D-4), while in other papers (Berger and Berger, 2012; Berger et al., 2010; Pretzsch et al., 2010), beech

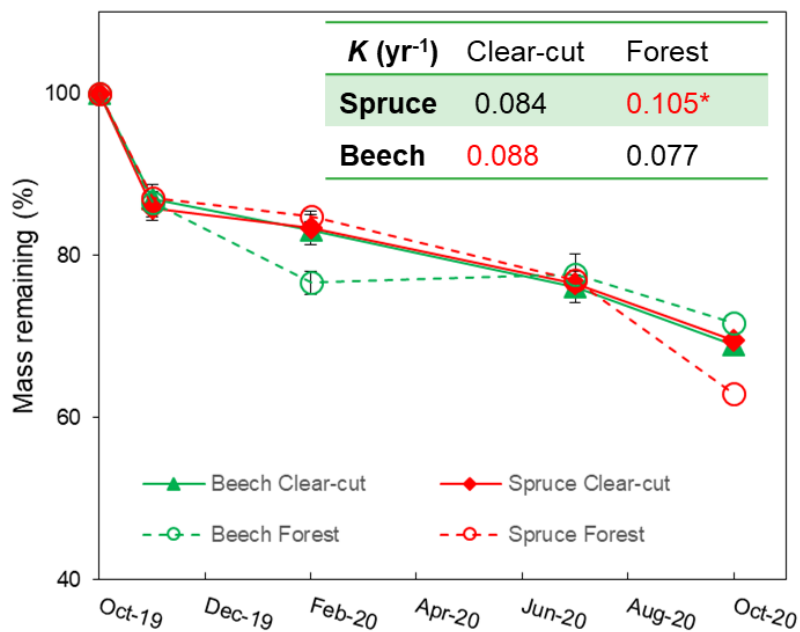
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normally had higher decomposition rates and C stock rates than spruce under the Figure D-3. Mass loss of standardized litter (green tea and rooibos tea) in clear-cut and forest.

Figure D-4. Mass remaining and k value of local litter (Norway spruce and European beech) in clear-cut and forest.



director of litter quality; At the same time, as standardized tea bag litter (Figure D-3), faster decomposed green tea, showed higher mass loss than rooibos tea, so higher mass loss rates of spruce than beech in forest to a certain extent, indicated



the Home Field advantage in the original spruce forest.

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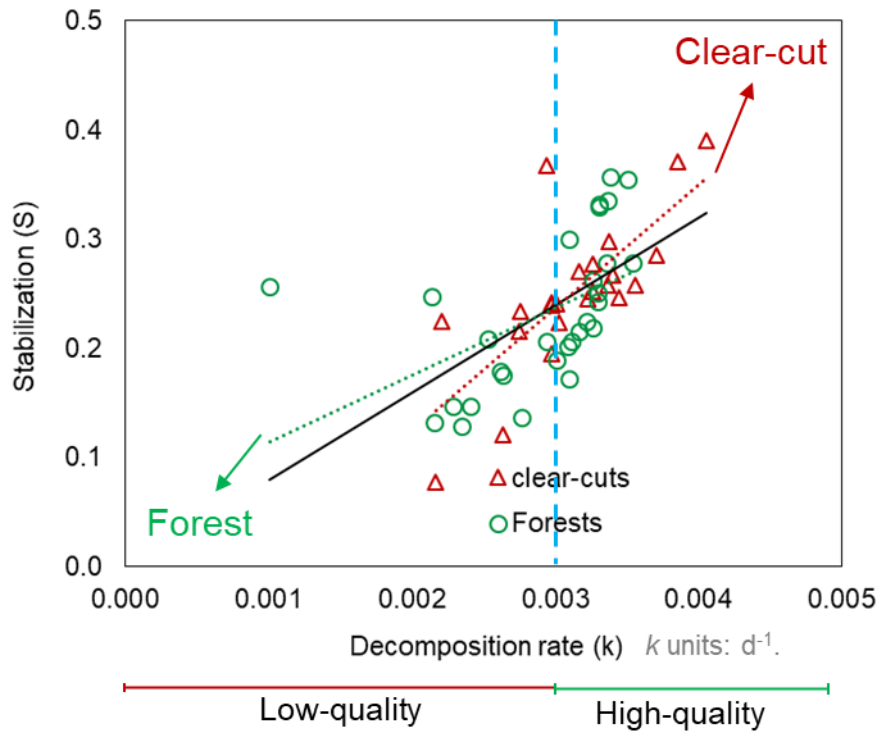


Figure D-5. *In situ* initial decomposition rate k and stabilization S for different sampling points within clear-cut and forest

After 3 months of incubation, we made a general linear regression (Figure D-5) and concluded that the stabilization factor (S) and decomposition rate (k) were linearly correlated in the studied site. Their interaction was different between site and substrate quality. Litter containing more recalcitrant compounds indicated slower decomposition rates, showing a low k value (Luo et al., 2017; Pei et al., 2019). Figure D-5 shows the same k value but lower than an intersection, which would indicate higher stabilization or stable carbon stock in forest, but easy decomposed litter would promote carbon stock rate in clearcutting area ($R^2 = 0.57$, $P < 0.005$).

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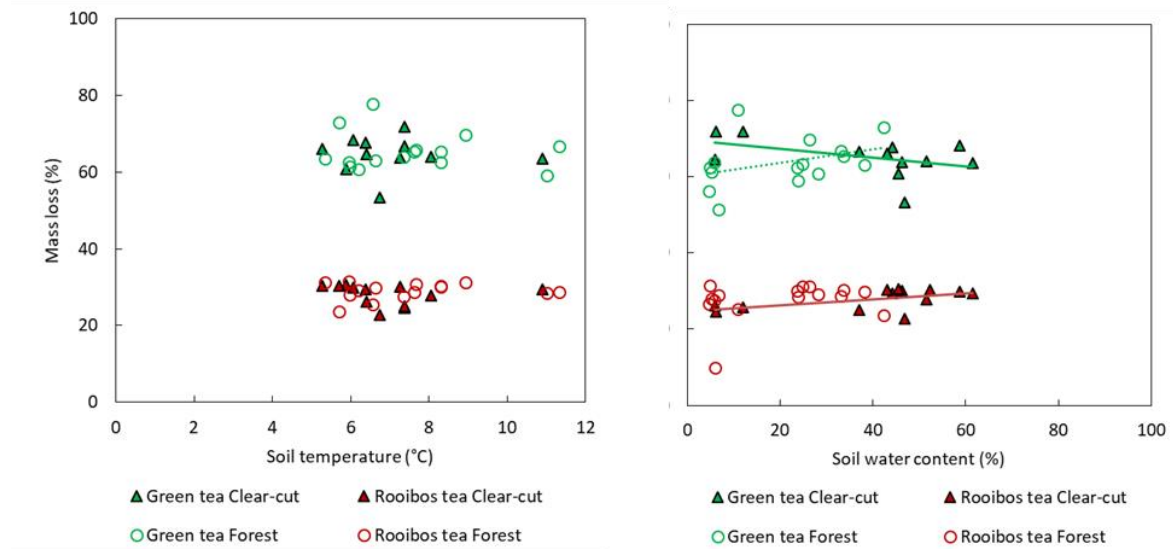
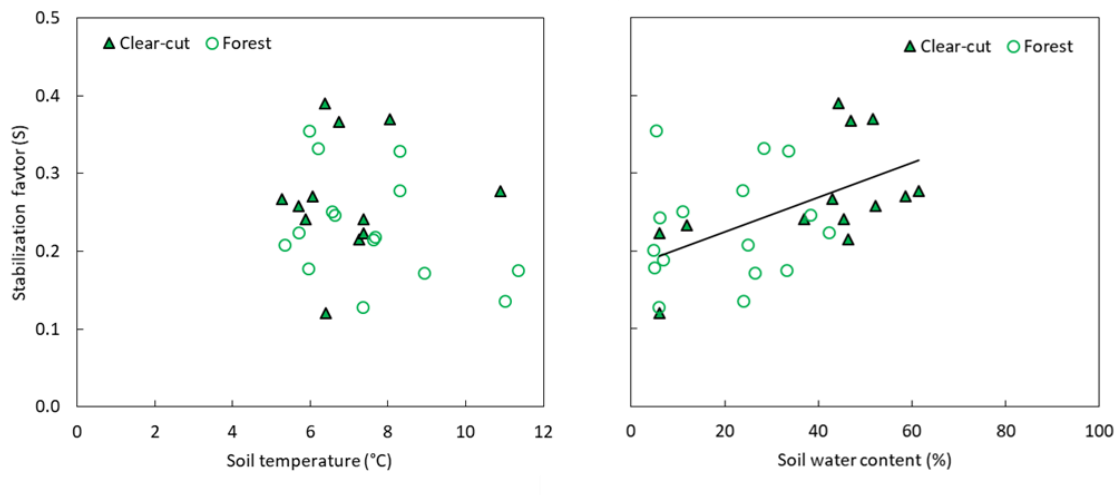


Figure D-6. Relationship between mass loss rate and environmental conditions (soil temperature and soil water content).

Regression between environmental condition and mass loss rate were indicated, tea mass loss rate was mainly associated with soil moisture in Wüstebach, but with soil temperature (Figure D-6). Litter mass loss rate increased generally with soil moisture, but inhibition appeared when soil is saturated such as in wetlands and marshes (Mueller et al., 2018; Rejmánková and Houdková, 2006). We found that the green solid line simulated by the decomposition of green tea in clear-cut, mass loss negatively responded to increasing soil moisture, such trend did not display on rooibos tea. Thus, high-quality litter is possibly more sensitive to environmental change.



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Figure D-7. Relationship between stabilization factor (S) and environmental conditions (soil temperature and soil water content).

As stabilization, we observed a positively relationship between soil moisture and stabilization in clear-cut (Figure D-7). Stabilization is normally negatively correlated with temperature and precipitation (Fanin et al., 2019). we noticed that in Wüstebach rainfall and snow in winter time induced soil frozen and freeze-thawing cycling may inhibit the release of litter fraction, resulting in a lower k value and higher stabilization value.

Table D-1. Initial chemistry of Green tea and Rooibos tea.

	Green tea	Rooibos tea
Water soluble fraction (g g ⁻¹)	0.493	0.289
Acid soluble fraction (g g ⁻¹)	0.283	0.215
Ethanol (g g ⁻¹)	0.066	0.049
Acid insoluble fraction (g g ⁻¹)	0.156	0.444

Generally, in the early stage encompasses mainly the decomposition of soluble substances and helocellulose, which is not encrusted in lignin. Further, soluble substances leach out of the litter structure and decomposed within it. The degradation in this stage is enhanced by raised contents of the main nutrients (C, N, and P). which is positively related to the degradation of nonlignified, free holocellulose. According to the simulation of Yasso07, the decomposition of two types of teabags showed the same trend with time. The trend of observed and simulated mass loss in both teas was similar (Figure D-8a). The decomposition pattern over the four years was consequence of the chemical composition of litter types. Green tea content significantly higher initial water-soluble fraction (0.49) and a lower acid-insoluble fraction (0.16) (Table D-1), decomposed significantly faster than Rooibos Tea (Figure D-8 a, b, f). Palviainen et al. (2004a) showed that the mass loss and nutrient release from needles (Scots pine and Norway spruce) were slower than broadleaf species (Silver birch). Higher decomposition rates

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among various litter types were mainly associated with low lignin and high, high hemicellulose and nutrient contents (Hobbie et al., 2010).

On the hand, we observed the buildup of humus for tea litter and gave an accumulation of humus of 10.33 (green tea) and 12.87 (rooibos tea) g m⁻². Lignified tissues may suppress acid insoluble compounds by recombining with N compounds during the decomposition, creating compounds are more recalcitrant to biological degradation (Berg et al., 2003; Berg et al., 2001; Preston et al., 2009a; Preston et al., 2009b). In this simulation, humus accumulation generally built up and reached to maximize after 8-month decomposition between both species, while the decomposition rate is almost a constant *zero* (Figure D-8a, f), which may be ruled by different conditions and have different optima. Diversity in litter quality should be a primary influencing factor for the variable amounts of organic matter (humus) in inter-site degradation (Berg et al., 2003; Berg et al., 2001).

Decomposition is also a process of production and emission of carbon dioxide. Both litter emerges CO₂ during decomposition, and the yield of CO₂ decreased dramatically with time (Figure D-9), which is positively related to C compound degradation. In contrast, humus, composed of the recalcitrant products of decomposition, is accumulated in this period. Humification, as critical components for soil organic matter (Lindner et al., 2010), regulates soil carbon sequestration, soil aggregate formation and nutrient storage (Prescott et al., 2000b). Harmonized data got from standardized litter simulation would provide a prerequisite for

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further developing Yasso07 model simulation for the estimation of the C stock and CO₂ emission in ecosystem litter pools.

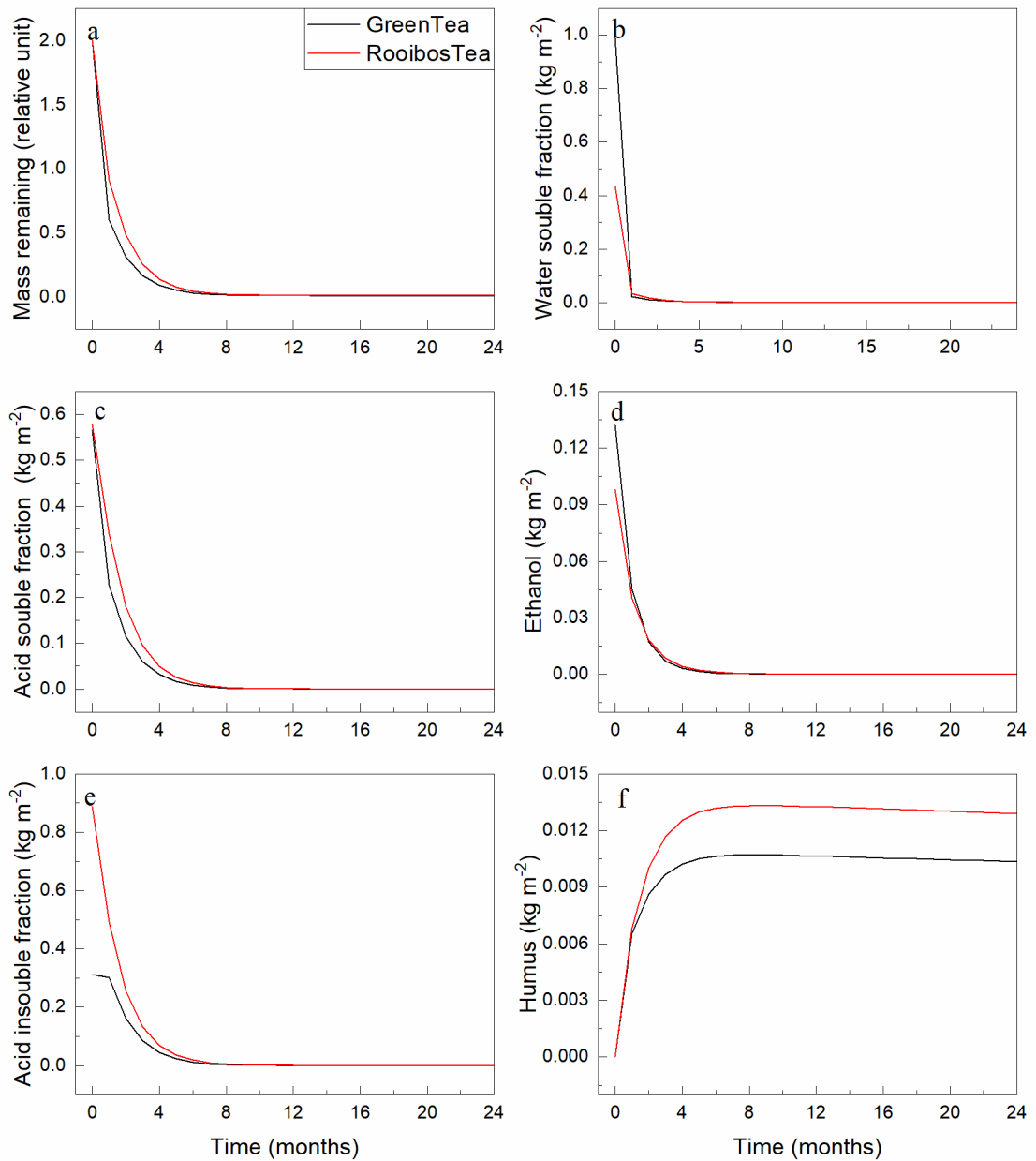


Figure D-8. Simulated mass loss and C stocks after clearcutting for standard litter (Green Tea and Rooibos Tea).

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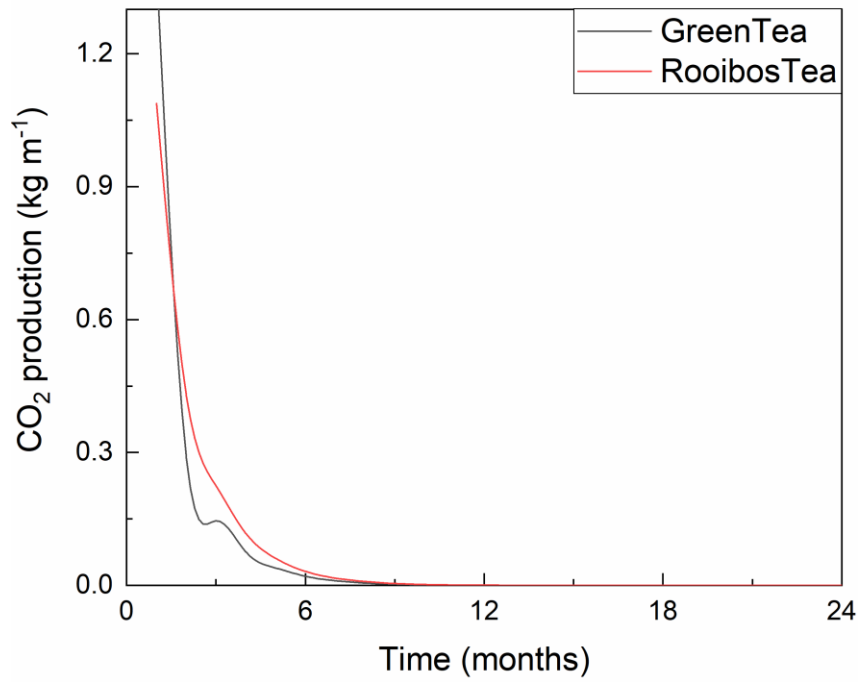


Figure D-9. Simulated litter CO₂ production after clearcutting

Appendix E

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Figure E-1. Relative mass loss rate of green tea, rooibos tea and herbal tea in forest and clear-cut.

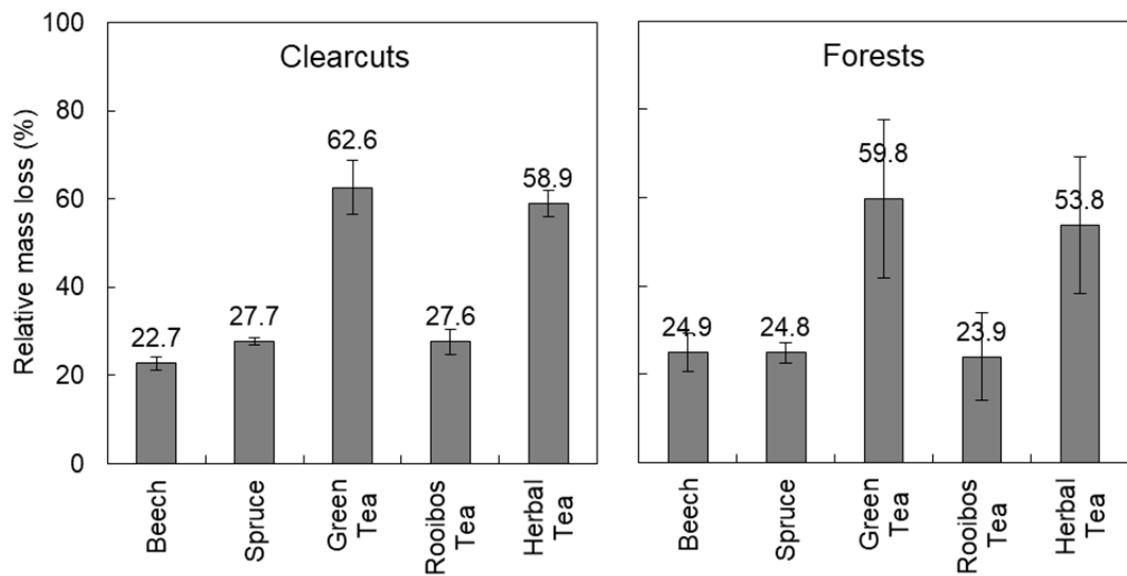
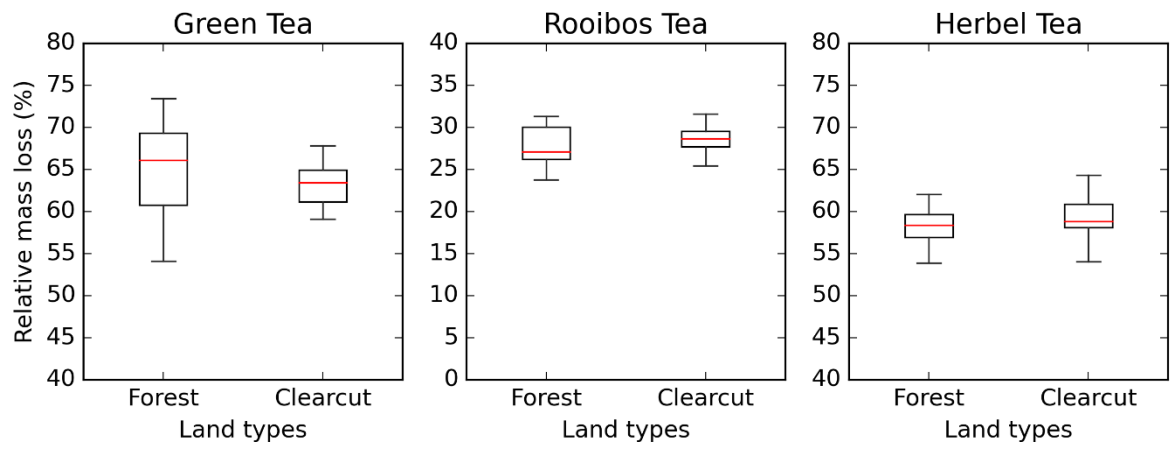


Figure E-2. relative mass loss of local litter (Norway spruce and European beech) and standardized litter (green tea, rooibos tea and herbal tea).

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