Regulation of litter decomposition in bamboo stands

マリー オレゴ モラレス

https://hdl.handle.net/2324/7157394

出版情報：Kyushu University, 2023, 博士（農学）, 課程博士
バージョン：
権利関係：

Regulation of litter decomposition in bamboo stands

A dissertation

submitted to the Graduate School of Bioresource and Bioenvironmental Sciences,

Kyushu University,

Japan,

for the degree of

Doctor of Philosophy

Marly Orrego Morales

July 2023

Abstract

Litter decomposition is an essential process that regulates the fate of carbon and nutrients in soils through the progressive breakdown of organic matter, and thus is crucial for the functioning of terrestrial ecosystems. In East Asia, bamboo invasion is a serious concern due to its ecological and socio-economic implications, and thus evaluating litter decomposition dynamics in bamboo stands is essential to better assess their impacts in forest ecosystems.

The aim of this thesis is to further our understanding of litter decomposition and nutrient dynamics in Moso bamboo (*Phyllostachys edulis*) stands and explore the controlling factors regulating litter decomposition processes. The first part of the thesis explored the influence of macroenvironmental, soil and stand structure factors on early-stage litter decomposition and stabilization in bamboo stands at a regional scale. The results showed that climatic factors are the main drivers of decomposition processes in Moso bamboo stands. Long-term climate influences litter stabilization, while the interaction between precipitation and temperature affects litter decomposition rates at early stages. Stand structure and soil properties have limited direct effects, but indirect effects from stand density impact litter stabilization through organic matter input and soil bulk density. These results further suggest that future environmental changes resulting from global climate change would greatly affect decomposition and soil carbon storage in this region.

The second part of the thesis evaluated the interactive effects litter traits and soil fauna on litter decomposition processes of above- and below-ground organs in Moso bamboo. After two years of litter decomposition, the mass loss followed the order of leaf > fine root > rhizome = branch > culm litter. The results showed that chemical and structural litter traits were predictors of mass and carbon loss but not nitrogen loss. The presence of soil fauna did not change the relationship between litter traits and decomposability, indicating that soil fauna effects were not dependent on litter quality. Soil fauna decreased litter mass and carbon loss of leaf and branch litter, but had limited effects on fine root, rhizome and culm litter decomposition. The large disparities in the contribution of soil fauna to litter decomposition and nutrient release suggest that considering the effects of

soil fauna in whole-plant litter decomposition is essential for understanding the role of soil decomposers in bamboo forest carbon cycling.

The third part of the thesis investigated the chemical and morphological controls on below-ground litter decomposition following a root functional order classification. The results highlight the morphological and chemical heterogeneity of fine roots in Hachiku (*Phyllostachys nigra*), Madake (*Phyllostachys bambusoides*) and Moso bamboo (*Phyllostachys edulis*). The analysis of root litter using ^{13}C-NMR spectroscopy revealed differences in the biochemical composition within the branching root system. Notably, slower decomposition rates were observed in lower order roots compared to higher order roots. The results also revealed the limited predictability of litter C/N and lignin/N ratios on fine root litter decomposition. Furthermore, the recalcitrance of lower roots was associated with the presence of aromatic compounds, while the rapid decomposition of higher order roots was linked with the presence of labile cellulosic compounds. Given that lower order roots are typically short-lived and represent a significant proportion of the total fine root biomass in bamboo stands, their slower decomposition may have significant effects in soil carbon cycling through the formation of stable soil organic matter.

The fourth part of the thesis explored the influence of fallen bamboos on the forest floor and soil fauna on litter decomposition dynamics and discussed whether the removal of these structural components as part of management practices could potentially affect litter decomposition and nutrient cycling. The results showed that dead culms in Moso bamboo stands play a crucial role in modifying the soil microenvironment, enhancing litter biotic activity and accelerating the loss of litter mass, carbon and nitrogen. The dead culms have a significant impact on mesofauna abundance, diversity and fauna assemblage during litter decomposition. However, the presence of dead culms does not alter the direct effect of soil fauna on litter decomposition, suggesting that their influence is mainly through changes in the soil environment and litter microbial activity. Dead bamboo culms are important structural components that affect decomposer organisms and the litter nutrient dynamics in bamboo stands. These results further show that the removal of dead culms from the forest floor could have substantial effects on soil biota and ecosystem processes in managed stands.

In conclusion, this thesis contributes to the understanding of the interplay among various factors that regulate litter decomposition, and illustrates how climate, litter quality and soil fauna impact decomposition processes in bamboo stands. Moreover, the findings on the indirect impacts of dead culms on nutrient cycling hold practical implications for the management of bamboo stands.

Contents

Chapter 1 General Introduction

Chapter 2 Climate, soil and plant controls on litter decomposition

Chapter 3 Litter quality and soil fauna effects on whole-plant litter decomposition

Chapter 4 Chemical and morphological controls on fine root litter decomposition

Chapter 5 Dead bamboo culms and soil fauna effects on leaf litter decomposition

List of Tables

Chapter 2

Chapter 3

Chapter 4

Chapter 5

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of abbreviations

Abbreviation	Unit	Definition
^{13}C-NMR		^{13}C nuclear magnetic resonance spectroscopy
3-D	cm^2 cm^{-3}	Litter three dimensionality
AIC		Akaike Information Criterion
BD	g cm^{-3}	Soil bulk density
C	%	Carbon concentration
CCA		Canonical correspondence analysis
CO_2		Carbon dioxide
corCAR1		Continuous autoregressive process (autocorrelation structure of order 1)
CWD		Coarse woody debris
DBH	cm	Diameter at breast height
DMC	g g^{-1}	Litter dry matter content
DW	g	Litter dry weight
GLM		Generalized linear models
GLMM		Generalized linear mixed effects model
H'		Shannon-Wiener diversity
IRGA		Infrared gas analyzer
LMM		Linear mixed effects models
MAP	mm	Mean annual precipitation
MAT	C	Mean annual temperature
N	%	Nitrogen concentration
NMDS		Non-metric multidimensional scaling
OLS		Ordinary least squares regression
PCA		Principal Component Analysis
PERMANOVA		Permutational multivariate analysis of variance
PLS-SEM		Partial least structural equation model
R^2c		R^2 conditional from linear mixed models
R^2m		R^2 marginal from linear mixed models
RTD	g cm^{-3}	Root tissue density

Abbreviation	Unit	Definition
SA	$cm^2 g^{-1}$	Litter specific area
SiO_2		Silicate
SMA		Standardized major axis regression
SOM		Soil Organic Matter
SRA	$cm^2 g^{-1}$	Specific Root Area
SRL	$m g^{-1}$	Specific Root Length
TGA		Thioglycolic Acid Method
VIF		Variance Inflation Factor
WC	%	Soil water content
WHC	$\%H_2O$ g	Litter water holding capacity

Chapter 1

General Introduction

1.1 Background

Litter decomposition is an essential process in terrestrial ecosystems, in which dead organic matter undergoes physical and chemical breakdown, releasing carbon to the atmosphere and nutrients into the soil (Berg and McClaugherty, 2014; Chapin et al. 2011). The decomposition process is responsible for a significant portion of the terrestrial global CO_2 flux, with approximately 60 Pg of carbon released annually into the atmosphere (Pan et al., 2011). The nutrients released from litter decomposition, which are byproducts of the feeding activity of soil animals and microbes such as fungi and bacteria, contribute to primary production and the recycling of nutrients (Chapin et al., 2011; Swift et al., 1979). Thus, the role of decomposition is crucial in regulating the carbon and nutrient cycles at various scales, from individual ecosystems to the global scale.

Plant litter decomposition is controlled by multiple factors, including the abiotic environment (climate, soil conditions), the quality of litter (chemical and structural properties) and soil decomposers (fungi, bacteria, soil fauna) (Swift et al., 1979; Berg and McClaugherty, 2014). These factors can interact with each other, and their importance may vary depending on the scale of analysis (Swift et al., 1979; Smith and Bradford, 2003; Powers et al., 2009). At large scales, climate and litter quality are generally the dominant factors controlling litter mass loss (Couteaux et al., 1995; Aerts, 1997). However, the relative importance of climate has been subject to debate in recent years (Bradford et al., 2014; 2017). Global litter decomposition experiments and metanalyses have shown that litter quality is more important than macroclimate (Djukic et al., 2018; Zhang et al., 2008; Joly et al. 2017). Nonetheless, other broad-scale studies reported that climate is a predominant factor, accounting for 50-87% of the variance in litter decomposition rates (Berg et al., 1993; Couteaux et al, 1995; Joly et al. 2023). Climate can be more important than litter quality and soil conditions when data is aggregated at the site or at the biome level (Berg et al., 1993; Bradford et al., 2017; Djukic et al., 2018), especially in regions where temperature or moisture are unfavorable to the decomposition process (Prescott, 2002; Djukic et al., 2018). The factors that exert the greatest control on decomposition reflects the scale of the analysis and the variation of the environmental and biotic factors of the sites being considered. Given the context-dependency and the complex inter-relationships among the factors that influence decomposition rates, a comprehensive understanding of the drivers of decomposition is crucial for predicting carbon and nutrient dynamics in different ecosystems.

Litter quality and soil fauna are the main drivers of litter decomposition, especially on a local scale (Aerts, 1997; Powers et al., 2009). The structural properties and chemical composition of litter affects the activity and composition of the decomposer community (Cornelissen, 1997; Freschet et al., 2012). For instance, high concentrations of lignin in litter can reduce the availability of labile carbon and nitrogen compounds, thereby limiting the growth and activity of decomposers (Aerts, 1997; Chapin et al., 2011; Swift et al., 1979). In contrast, cellulose and hemicellulose are more easily broken down by microorganisms and are an important source of carbon and energy for decomposers (Chapin et al., 2011). Litter physical traits, such as the shape and surface area, also affect the rates of litter decomposition. Litter with high surface area to volume ratios decompose faster due to increased accessibility and greater surface area for microbial and faunal decomposers. Litter structural and chemical traits that affect litter decomposability do not only vary across species but also between plant organs, such as leaves, stems and roots (Freschet et al. 2013). Differences in organ decomposability can potentially have contrasting impacts on ecosystems processes, and thus it is essential to quantify the relative roles of above and below-ground litter in organic matter dynamics.

The influence of litter traits on decomposition is not only important for aboveground litter, but also for belowground processes such as root litter decomposition (Hobbie et al., 2010; Silver and Miya, 2001). Fine roots are a critical component of plant carbon allocation (Jackson et al., 1997), and their decomposition contributes significantly to the carbon and nutrient cycling in soils. Fine root morphological and chemical traits have been shown to have important effects on decomposition rates (Silver and Miya, 2001). However, within the branching root system (absorptive and transportive fine roots) variations in common chemical litter traits affect root litter decomposition differently than expected. For instance, absorptive fine roots (or lower order roots) associated with higher nitrogen concentrations have slower decomposition rates, while transportive fine roots (or higher order roots) associated with higher lignin concentrations have faster decomposition rates

(Fan and Guo, 2010; Goebel et al., 2011). Furthermore, traits such as root diameter, specific root length, and root tissue density have also been shown to have significant influence on decomposition (Minerovic et al., 2018). Therefore, understanding the impact of these traits on root litter decomposition is crucial for predicting belowground carbon and nutrient cycling in forest ecosystems.

While the litter quality is often considered the primary factor controlling decomposition rates (Wall et al., 2008; Makkonen et al., 2013), the activity of decomposers such as soil fauna also plays a critical role in the carbon and nutrient dynamics, contributing around 30% to the overall effect (Chapin et al., 2011; Garcia-Palacios et al., 2013). However, despite their importance, the decomposer community is not commonly considered in biogeochemical models (Osler and Sommerkorn, 2007). Soil fauna can directly affect decomposition rates by physically fragmenting litter and excreting nutrient-rich feces, which can stimulate microbial activity (Perterson and Luxton, 1982). In addition, faunal decomposers (e.g., Acari and Collembola) can indirectly affect decomposition rates by grazing microbial communities and reducing the density of microbial predators (Wardle and Lavelle, 1997; Seastedt, 1984). More importantly, soil fauna contribution to litter decomposition can vary greatly depending on litter type (Smith and Bradford, 2003). Contrasting results have been reported on the interactions between soil fauna and litter quality (Fujii et al., 2016; Yang and Chen, 2009; Schadler and Brandl, 2005), and large uncertainties still exist regarding the direction and strength of soil fauna effects on litter decomposition. Therefore, a better understanding of the complex interplay between soil fauna and litter quality is crucial for predicting litter decomposition rates in different ecosystems.

In addition to clarifying the factors than directly affect litter decomposition, it is also essential to understand how important structural elements in forest ecosystems could potentially influence litter decomposition rates through changes in soil conditions and decomposer communities. Coarse woody debris (CWD), which refers to the dead and decaying wood often lying on the forest floor, plays an important role in nutrient cycling (Harmon et al., 2004; Magnusson et al., 2016) and can indirectly impact ecosystem processes by modifying the surrounding soil environment (Kappes et al., 2007; Gonzalez-Polo et al., 2013). Previous studies have shown that CWD promotes rapid leaf litter decomposition, implying that the impacts of removing these elements through management practices could have significant impacts on biogeochemical cycles (Gonzalez-Polo et al., 2013; Remsburg and Turner, 2006). Besides affecting soil microclimate and microbial communities, CWD also influences the abundance and richness of microarthropods in the soil and litter layer (Evans et al., 2004; Hanula et al., 2006; Johnston and Crossley, 1993). This modulation of faunal decomposer communities may particularly alter decomposition rates; however, it is remains unclear whether the effects of soil fauna in the presence of CWD would have synergistic effects on litter decomposition on the forest floor.

1.2 Litter decomposition studies in bamboo forests

Bamboo forests can play significant roles in biogeochemical cycles because of their predominance in many subtropical and temperate ecosystems. Despite being herbaceous plants, woody bamboos have a tree-like stature (up to 20 m in height) and relatively high biomass accumulation. In East Asia, the common woody bamboo species, Moso bamboo (*Phyllostachys edulis*), covers over 3 million ha (Chen et al., 2009; Yen and Lee, 2011) and can store considerable amounts of above-ground carbon (>100 Mg C ha^{-1}), being comparable or sometimes exceeding those of other forests in the same region (Yuen et al. 2017, Song et al. 2017).

Moso bamboo is widely cultivated for its economic value and has been introduced to various countries in East Asian. Unlike trees, bamboo spreads through underground rhizomes and grows rapidly after emergence. These invasive traits allow bamboo to exclude the surrounding vegetation, forming monospecific stands. The increasing dominance of bamboo forests has raised several social and ecological concerns. Bamboo invasion can have negative impacts on forest productivity (Isagi et al., 1997), biodiversity (Ouyang et al., 2016) and hydrological processes (Shinohara and Otsuki, 2015; Komatsu et al., 2010; Ichihashi et al., 2015). The replacement of forests by bamboo stands can result in changes in soil properties (Song et al., 2016), microbial communities (Liu et al., 2021; Liu et al., 2019), and composition of soil fauna decomposers (Liu et al., 2021; Long et al., 2023; Xiao et al., 2023). Furthermore, processes such as litter decomposition can be significantly affected by bamboo invasion, not only through the input of different litter qualities but also through changes and modulation of decomposer communities (Luan et al. 2021).

Previous studies have investigated the differences in litter decomposition and nutrient cycling between bamboo and invaded forests. While it is suggested that the recalcitrance of bamboo litter may slow down carbon cycling (Watanabe et al., 2013; Austin and Marchesini, 2012; Tripathi and Singh, 1992), other studies comparing decomposability of Moso bamboo litter with that of conifer or broadleaf tree species have reported rapid decomposition rates of bamboo litter (Lin et al., 2019; 2020; Luan et al., 2021), indicating that they could accelerate the carbon cycle. Understanding litter decomposition dynamics in bamboo stands is crucial for evaluating the impacts of bamboo invasion on organic matter cycling. However, there is still limited knowledge on the carbon and nutrient cycles in bamboo forests, and moreover, considerable uncertainties exist regarding the strength and direction of litter decomposition drivers in these forests.

In order to clarify the regulation of carbon cycle in bamboo forests, it is essential to identify the relative role of control factors over decomposition at the scale at which they matter. At local scales, the amount of above and below-ground litter productions and their decomposability play significant roles in soil carbon and nutrient dynamics. While previous studies have primarily focused on leaf litter decomposability in bamboo forests, far less is known about the decomposability of other plant organs. Considering the large differences in structural and chemical traits among litter types, it is expected that variations in litter quality have substantial effects in carbon and nutrient cycling. Furthermore, very little is known on the quantitative importance between bamboo litter traits and decomposer communities on whole-plant litter decomposition.

In addition, woody bamboo species have a very well-developed root system, which can account for up to 30% of total bamboo biomass (Isagi et al., 1997). Consequently, below-ground processes, including root litter decomposition, play a crucial role in predicting soil carbon cycling in bamboo forests. However, mechanisms that control root litter decomposition within the fine root system are still poorly understood in bamboo forests. Thus, clarifying how variations in litter quality affect root litter decomposition within the fine root branching system is essential to better understand how bamboo invasion impacts soil biogeochemical cycles.

Furthermore, the expansion of unmanaged Moso bamboo stands has rapidly increased in the last decades (Isagi and Torii, 1997; Okutomi et al., 1996). These abandoned stands are characterized by high culm densities (> 8000 ind. per ha) (Yin et al., 2019) and the accumulation of fallen dead culms on the forest floor (Shimono et al., 2021). Dead bamboo culms have the potential to store carbon and nutrients; however, it is unknown whether the fallen culms would play an indirect role in carbon and nutrient dynamics by altering the decomposition process in the litter layer in bamboo stands.

At large scales, bamboo forests are distributed across various geographical regions and are expanding rapidly, with an annual increase rate of 3% in recent years (Suzuki and Nakagoshi, 2008). Given the wide environmental gradient in which Moso bamboo stands occur, it is crucial to understand the influence of climate and abiotic factors on important processes such as litter decomposition. Understanding the relative importance of decomposition drivers in Moso bamboo stands at regional scales could facilitate predictions of the response of carbon and nutrient cycling to future environmental changes.

1.3 Objectives and outline

The aim of this thesis is to improve our understanding of litter decomposition dynamics in bamboo stands and elucidate the controlling factors regulating litter decomposition processes. To this end, the influence of environmental factors (climate and soil conditions) on litter decomposition were examined in several bamboo stands distributed at a regional scale. Furthermore, the influence of litter quality and soil fauna on above- and below-ground litter decomposition processes were evaluated at a stand-level. In addition, the influence of dead culms and soil fauna on litter decomposition were evaluated to better understand the potential consequences of management practices, such as the removal of coarse woody debris in managed stands.

Thus, the specific objectives of this study are:

(1) To examine the factors controlling litter decomposition and stabilization at a regional scale
(2) To elucidate the effects of litter quality and soil fauna on whole-plant litter decomposition
(3) To elucidate the effects of chemical and morphological traits on fine root litter decomposition
(4) To elucidate the effects of dead bamboo culms and soil fauna on leaf litter decomposition

Consequently, the present study consists of four main chapters (Figure 1.1).

Chapter 1 (this chapter), includes the General Introduction, describes the background, objectives, and the entire outline of this study.

Chapter 2 examines the effects of climate, soil and stand properties on standard litter decomposition (tea bags) in Moso bamboo stands distributed along Kyushu Island (southern Japan) and Taiwan. Consequently, variations in litter decomposition at a regional scale were presented and the dominant factors affecting litter decomposition rates and potential soil carbon sequestration were discussed.

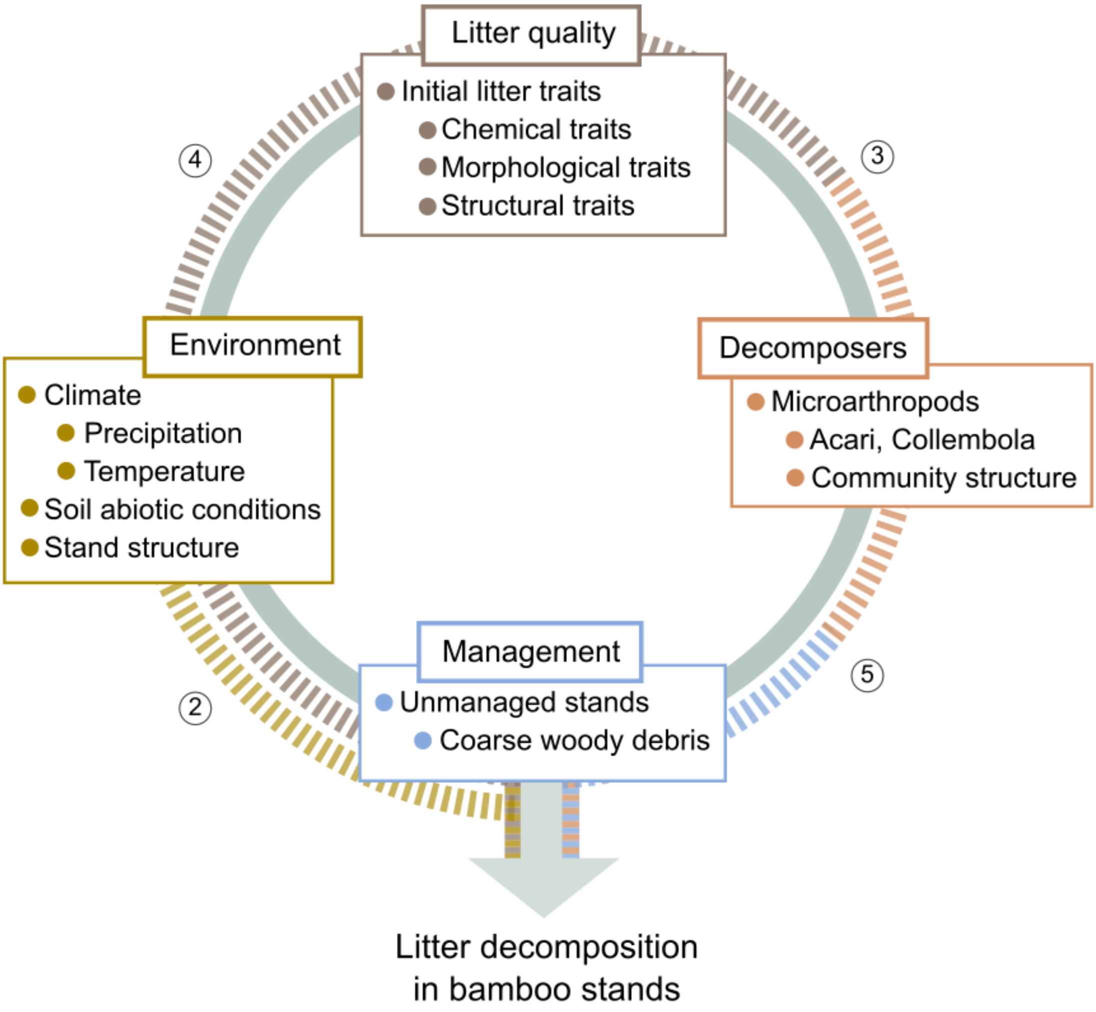

Figure 1.1 Conceptual diagram of the factors controlling litter decomposition (boxes) and specific factors and relationships assessed in this study (colored broken lines). Numbers above the broken lines indicate the specific chapters of this study.

Chapter 3 investigates the effects of litter quality and soil fauna effects on whole-plant litter decomposition in a Moso bamboo stand. This study involves a two-year decomposition experiment that controlled the access of soil mesofauna during the decomposition of branch, culm, fine root, leaves and rhizome litter. Consequently, the contribution of litter traits and its potential interactions with soil mesofauna in whole-plant litter decomposition were elucidated.

Chapter 4 investigates the influence of chemical and morphological controls in fine root litter decomposition in three woody bamboo species (Hachiku [*Phyllostachys nigra*], Madake [*Phyllostachys bambusoides*] and Moso [*Phyllostachys edulis*]). The effects of chemical (chemical proximal analyses and biochemical quality) and morphological traits among three root functional orders were considered to elucidate their effects in fine root litter decomposition.

Chapter 5 evaluates the effects of dead bamboo culms and soil fauna effects on leaf litter decomposition in an unmanaged Moso bamboo stand. This study involves a two-year decomposition experiment of leaf litter under dead culms and on the forest floor with access and restriction of soil mesofauna to the litter. The effects of dead bamboo culms on soil abiotic factors (moisture and temperature) and on soil fauna assemblage in leaf litter were evaluated to elucidate the indirect effects of dead culms on leaf litter decomposition.

Chapter 6 includes the General Discussion and integrates the results of Chapter 3, 4, and 5 and their implications for organic matter cycling in bamboo stands.

Chapter 7 includes the General Conclusion of this study.

Chapter 2

Climate, soil and plant controls on litter decomposition

2.1 Introduction

Moso bamboo [*Phyllostachys edulis* (Carrière) J. Houz, Poaceae] is one of the largest and most common bamboo species in East Asia. It was originally introduced from subtropical China to other regions, such as Japan, Korea, and Taiwan, for shoot and timber production (Canavan et al., 2017). Owing to their rapid growth and underground rhizome expansion, bamboo stands can rapidly displace the surrounding vegetation and progressively replace them with monospecific stands (Okutomi et al., 1996; Isagi and Torii, 1997). This species' invasive characteristics and the abandonment of previously managed stands have contributed to the continuous expansion of unmanaged areas over the last 30 years (Shinohara et al., 2014; Suzuki, 2015). Bamboo-dominated areas are currently distributed over many geographical regions, and their expansion rates are expected to increase in the future (Shinohara et al., 2014; Takano et al., 2017). As Moso bamboo stands occur along a wide environmental gradient, there is a need to understand how environmental factors, namely climate and edaphic conditions, control key ecosystem processes, such as litter decomposition, at large scales. Understanding the relative importance of decomposition drivers at regional scales could facilitate predictions of how carbon and nutrient cycling in Moso bamboo stands will respond to future environmental changes.

Litter decomposition is an essential process regulating nutrient cycling and carbon storage in terrestrial ecosystems. The decomposition of organic matter is mainly controlled by climatic, biotic (litter quality and soil decomposers), and edaphic factors (Coûteaux et al., 1995; Aerts, 1997; Berg and McClaugherty, 2014). At larger scales, the interplay of environmental and biotic factors affects the decomposition rate and stabilized material, which later forms part of the soil organic matter (Prescott, 2010). Climate is regarded as one of the most important environmental controls on litter decomposition at regional scales (Meentemeyer, 1978; Berg et al., 1993; Epstein et al., 2002). The influence of climatic drivers on litter decomposition has often been evaluated independently; however, previous studies have shown that precipitation and temperature (or soil moisture and temperature) can interactively affect the decomposition process (Taylor et al., 2017; Althuizen et al., 2018; Petraglia et al., 2019). Determining the thresholds at which the effect of one climatic factor is conditioned by the other is key to understanding the environmental controls of litter decomposition and soil carbon sequestration at broad scales (Prescott, 2010).

In addition to directly affecting litter quality, plant communities can indirectly influence the decomposition process through changes in litter input, soil microclimate, and chemical conditions (Wardle et al., 2004; Fang et al., 2015; Joly et al., 2017). In plant communities dominated by a single species, stand density and canopy structure variations can affect litter accumulation on the forest floor and the input of belowground organic matter (Penne et al., 2010; Na et al., 2021). Differences in litter accumulation may alter the water-holding capacity of the surface layer and provide a different microclimate for decomposer communities (Facelli and Pickett, 1991; Fekete et al., 2016). Variations in below-and above-ground litter input can alter soil pH or nutrient status (Xu et al., 2013; Liu et al., 2019b) and may indirectly affect belowground processes. In addition, canopy coverage can affect soil moisture conditions through rainfall interception or by decreasing the rate of evaporation from the soil through decreased sunlight (Prescott, 2002). Previous studies have shown that canopy structure is an important indirect driver of decomposition in regional and large-scale analyses (Joly et al., 2017; Wallace et al., 2018; Zhang et al., 2019). However, the overall contribution of stand structure and organic matter input can be masked by considering only their direct effects on litter decomposition (Wallace et al., 2018). As several factors within the decomposition system often affect each other, evaluating their direct and indirect effects could help elucidate the underlying mechanisms that simultaneously control the decomposition process.

Variation in litter quality in plant communities is expected due to differences in climate and soil conditions at broad scales. Litter decomposes faster in its original environment, as decomposers are adapted to degrade native litter (Veen et al., 2015). This process is known as home-field advantage and can represent potential pitfalls when evaluating the effect of litter quality on the decomposition process. To avoid this potential bias, Keuskamp et al. (2013) developed the Tea Bag Index (TBI) protocol based on two types of tea substrate as standard litter material. The contrasting decomposability of the substrates allows the calculation of the initial decomposition rate (k) and stabilization factor (*S*) after a short incubation period. Similar to the decomposition of other standard materials (i.e., cellulose paper), the TBI approach cannot predict actual carbon dynamics of native litter. However, the decomposition of tea substrates represents well the decay patterns of plant materials (Didion et al., 2016; Blume-Werry et al., 2021) and has a similar response to variations in moisture and temperature as local litter (Didion et al., 2016; Mueller et al., 2018). Using substrates of known litter quality makes it possible to exclude litter bias and better evaluate how environmental factors affect the decomposition parameters *k* and *S* (Keuskamp et al., 2013; Didion et al., 2016). In several studies, the TBI protocol was a reliable method for estimating the initial decomposition rates and the later stabilization phase across different environmental conditions and ecosystem types (Althuizen et al., 2018; Mueller et al., 2018; Petraglia et al., 2019).

In this chapter, I aimed to determine the relative importance of environmental factors, namely, climate and soil, as drivers of litter decomposition in Moso bamboo stands. A total of 13 sites comprising managed and unmanaged stands distributed along a broad climatic and latitudinal gradient (spanning 23°N to 33°N) across southern Japan and Taiwan were considered. Because the culm density of Moso bamboo varies depending on the management conditions (managed stands maintain densities of less than 4,000 culm ha^{-1}, whereas abandoned stands exceed densities of 8,000 culm ha^{-1}) (Inoue et al., 2018; Yin et al., 2019), the variation in stand properties and input of organic matter as potential drivers of decomposition was also considered. To avoid variation in litter quality and the possible influence of home-field advantage from local litter, the TBI method (Keuskamp et al., 2013) was used to estimate the decomposition parameters *k* and *S* as proxies for the initial decomposition rate and long-term carbon accumulation, respectively. I first investigated which controlling factors (climate, soil properties, stand properties, or organic matter input) exert predominant control over *k* and *S*. Then, it was determined how particular indicators of stand properties, organic matter input, and soil parameters directly or indirectly affected the decomposition process. To understand the relative contribution of climate, two types of temporal scales were considered: temporal climate, which refers to the temperature and precipitation during the incubation period (90 days), and long-term climate. It was hypothesized that climate would be an important driver of *k* and *S*. However, it was expected that the temporal climate would mainly control *k*, while the long-term climate would be more important for *S*. In addition, it was expected that soil and organic matter input parameters would be relatively more important for *S* than for k. Finally, it was expected that the stand structure variability of Moso bamboo stands would indirectly affect the decomposition parameters through changes in organic matter input and edaphic properties.

2.2 Materials and methods

2.2.1 Study sites

In total, 13 sites with Moso bamboo stands distributed along a wide latitudinal gradient from 33° 60′ N to 23° 40′ N across Taiwan and southern Japan were selected. Most of these sites were located on Kyushu Island (southern Japan), and one site was located in central Taiwan (Table 2.1). All locations corresponded to the warm temperate and humid climate biome (Breckle, 2002). Moso bamboo was the dominant species in the surveyed stands and few understory vegetation was present.

2.2.2 Climate data

Precipitation and temperature records were obtained from the Japan Meteorological Agency (2019) and Taiwan Central Weather Bureau (2019) from the meteorological station closest to each site. The mean annual temperature (MAT) and mean annual precipitation (MAP) for 10 years (2008–2018) ranged from 12.6 to 19.3°C, and 1660–3190 mm (Table 2.1). These data represented the “long-term climate.” The average daily temperature and total precipitation during the incubation period (June–September 2018) were obtained at the site level and represented the “temporal climate.” Precipitation and temperature values were not correlated across sites ($r_s = -0.14$, $P = 0.34$), whereas long-term climate was positively correlated with temporal climate (temperature: $r_s = 0.49$, $P < 0.01$; precipitation: $r_s = 0.85$, $P < 0.001$).

Table 2.1 Location, environmental features, and mean values of stand structure characteristics (stand density and DBH) and decomposition parameters (*k* and *S*) for the 13 sites. Average values for each site ($N = 4$) are shown with S.D. in parenthesis. Average values of *k* and *S* in Taiwan were calculated from $N = 3$.

Site name	Lat (°N)	Lon (°E)	Altitude (m.a.s.l.)	MAT (°C)	MAP (mm)	Stand density (/ha)	DBH (cm)	*k*	*S*
Ito North	33.6	130.2	58	16.7	1722	6250 ± 883	11.8 ± 0.5	0.015 ± 0.002	0.19 ± 0.03
Kasuya	33.6	130.5	161	16.1	1656	5781 ± 2127	8.7 ± 1.6	0.022 ± 0.005	0.20 ± 0.02
Ito South	33.5	130.2	60	16.7	1722	7031 ± 1795	12.4 ± 1.2	0.013 ± 0.001	0.17 ± 0.02
Iizuka	33.5	130.6	92	15.9	1874	8437 ± 2576	8.6 ± 1.2	0.014 ± 0.001	0.12 ± 0.04
Kurume	33.3	130.6	48	16.9	1987	6562 ± 2576	12.7 ± 1.2	0.014 ± 0.001	0.11 ± 0.04
Taku	33.3	130.1	181	14.9	2248	8437 ± 806	12.4 ± 0.2	0.022 ± 0.003	0.12 ± 0.03
Kurogi	33.2	130.6	110	15.4	2080	7968 ± 312	12.8 ± 0.5	0.016 ± 0.004	0.17 ± 0.07
Kumamoto	32.6	130.7	30	16.3	2274	4843 ± 1721	14.4 ± 0.2	0.010 ± 0.001	0.09 ± 0.01
Shiiba	32.3	131.1	630	12.6	3193	7500 ± 1692	9.8 ± 0.3	0.017 ± 0.004	0.11 ± 0.03
Satsumasendai managed	31.8	130.3	52	17.0	2380	3125 ± 510	12.2 ± 0.6	0.018 ± 0.003	0.19 ± 0.05
Satsumasendai unmanaged	31.8	130.3	43	17.0	2380	5937 ± 1943	11.9 ± 0.2	0.016 ± 0.001	0.12 ± 0.03
Takakuma	31.5	130.7	522	14.6	3072	5781 ± 1795	11.6 ± 1.0	0.023 ± 0.005	0.16 ± 0.02
Taiwan	23.6	120.8	1120	19.32	2793	5958 ± 3437	8.4 *	0.023 ± 0.004	0.08 ± 0.02

MAT, mean annual temperature; MAP, mean annual precipitation; DBH, diameter at breast height.

*Lin et al. (2017)

2.2.3 Soil properties

Four 2 m × 2 m plots were randomly established at each site, and soil properties were surveyed at the plot level. Plots were carefully selected to minimize variations in other soil conditions (slope, aspect, and distance to stand edges). Three soil core samples were collected from a depth of 5 cm and oven-dried at 70°C to determine gravimetric water content. From the fine soil fraction (sieve < 2 mm diameter), total carbon and nitrogen concentrations were measured using a CN analyzer (Yanaco MT-700, Kyoto, Japan). Soil pH (H_2O) (2:5 dry soil:distilled water ratio) was measured using a pH meter (Horiba D54-S, Kyoto, Japan), and soil bulk density was determined from the soil core samples at depths of 0–10 cm. The measured soil properties (pH, water content, bulk density, and C/N ratio) showed high variation among sites and low within-site variability, indicating high regional variation (Table 2.2).

2.2.4 Stand properties and organic matter input

We considered stand structure variability and the amount of organic matter input to be potential drivers of litter decomposition. In each plot, we recorded the diameter at breast height (DBH ≥ 5 cm) and counted the number of individual living culms to estimate the stand density. Canopy coverage was measured by obtaining hemispherical images 2 m above the ground using a fish-eye lens. The photographs were then analyzed using the software Gap Light Analyzer (Frazer et al., 1999).

In addition, leaf litter samples on the forest floor were collected using a 20 cm × 20 cm frame to determine the amount of litter accumulated in the organic layer. Litter samples were collected in mid-June 2018; therefore, they reflect the litterfall season in Moso bamboo stands that occurs during April–May (Song et al., 2016). Fine roots were separated from the soil samples and weighed to estimate the fine root biomass. Fine root biomass and litter mass accumulated at the plot level were considered indicators of organic matter input in the stands.

Because some of the surveyed sites corresponded to managed stands (five sites, i.e., KMT, SBA, SSM, IZK, and TWN), high variability of stand density and organic matter input properties were captured among plots and sites (Table 2.2). Regardless of management status, there was no clear separation between managed and unmanaged sites in relation to stand structure and organic matter input variables. Moreover, the high within-site variability indicated large local variation in the studied region.

Table 2.2 Description of factors and measured variables used in the structural equation model and elsewhere. Mean values (N = 51*) ± S.D. and range values among plots are shown.

Factor	Variable	Average ± S.D.	Range
Stand structure	Stand density (ind ha^{-1})	6441 ± 2178	2500 - 11250
	Canopy coverage (%)	93.6 ± 0.8	91.8 - 95.3
Organic matter input	Litter mass (Mg ha^{-1})	5.2 ± 3.0	0.5 - 12.2
	Fine root biomass (Mg ha^{-1})	719.5 ± 413	56.0 - 1580.5
Soil	pH	5.7 ± 0.5	4.1 - 6.8
	Bulk density (g cm^{-3})	1.2 ± 0.3	0.7 - 2.1
	C (%)	6.5 ± 3.1	2.1 – 16.3
	N (%)	0.54 ± 0.25	0.17 – 1.18
	C/N ratio	12.1 ± 1.1	10.4 - 15.0
	Water content (%)	0.5 ± 0.2	0.1 - 1.1

* One plot was excluded from the Taiwan site. See section 2.2.5.

2.2.5 Litter decomposition measurements

The TBI method was used to evaluate the influence of environmental factors and stand properties on decomposition. This method uses two types of tea (rooibos and green tea) as standard materials. Owing to their contrasting litter qualities, green tea decomposes faster than rooibos tea (Keuskamp et al., 2013). After approximately 90 days of litter decomposition, the mass loss of labile materials in green tea is used to calculate the stabilization factor (S), whereas the more recalcitrant materials still actively decomposing in rooibos tea allows for the estimation of the short-term decomposition rate (k) (Keuskamp et al., 2013).

At the beginning of the summer season (June 2018), two green (Lipton, Unilever, EAN: 87 22700 05552 5) and rooibos tea bags (Lipton, Unilever, EAN: 87 22700 18843 8) were placed on the soil in each plot, totaling 208 buried tea bags (4 tea bags × 4 plots × 13 sites). Following the method of Keuskamp et al. (2013), tea bags were collected after approximately 90 days of incubation and oven-dried at 70°C for 48 h to calculate the mass loss of each substrate. Because the tea samples had soil particles adhered to the substrates after collection, the tea substrates were incinerated at 600°C for 6 h, and the ash mass was subtracted from the dry mass to eliminate soil contamination in the samples.

The stabilization factor (*S*), which represents the proportion of the stabilized fraction that becomes recalcitrant after the initial phase of decomposition, was calculated as follows:

$$S=1-a_g/H_g \qquad \textit{Equation 1.1}$$

where a_g is the decomposed fraction of green tea after incubation, and *Hg* is the hydrolysable fraction of green tea (0.842 g g–1). Assuming that *S* is the same for both tea substrates, the decomposable fraction of rooibos tea (a_r) was calculated as follows:

$$a_r=H_r(1-S) \qquad \textit{Equation 1.2}$$

where *Hr* is the hydrolysable fraction of rooibos tea (0.552 g g^{-1}). The initial decomposition rate constant (*k*) was estimated using the following decomposition curve:

$$X(t)=a_r e^{-kt}(1-a_r) \qquad \textit{Equation 1.3}$$

where *X*(*t*) represents the fraction of remaining rooibos tea at time *t*. The labile fraction (a_r) decomposes at rate *k*, whereas the recalcitrant fraction ($1 - a_r$) is assumed to have a negligible decomposition rate during the initial phase of decay (Keuskamp et al., 2013). The mean values of *k* and *S* were calculated per plot, except for one plot located at the Taiwan site, where teabags could not be recovered.

2.2.6 Data analysis

Multiple linear regression analysis was used to test whether the climatic conditions affected the decomposition parameters. The best temporal and long-term climate models that explain the variation of *k* and *S* were selected. For each model, interactions between precipitation and temperature were also included. When these interactions were significant, we further analyzed the interactions using the Johnson-Neyman intervals (Bauer and Curran, 2005). Temperature was considered as the conditional variable and then calculated the main temperature intervals at which there would be significant changes in the slope of precipitation to explain a decomposition parameter. The specified alpha level for significance was set at $P < 0.05$. An adjustment was used to account for inflating Type I errors to calculate intervals (Esarey and Sumner, 2018). Interaction analysis and correction of intervals were performed using the “sim_slopes” function of the interactions package (Long, 2021) in the R software v.4.0.2 (R Core Team, 2021).

Linear mixed-effects models were used to separately test the effects of stand structure (stand density and canopy cover), organic matter input (litter mass and root biomass), and soil parameters (pH, C/N, water content, and bulk density) on *k* and *S*. In these models, the explanatory variables were considered fixed factors and the sites were included as random factors. The lme4 package was used to fit the linear mixed-effect models (Bates et al., 2015). Collinearity among variables was evaluated using variance inflation factors (VIF). Model selection was performed based on the lowest AIC, and then the R^2 (marginal and conditional) of the most parsimonious model was extracted using the “R.SquareGLMM” function of the MuMIn package (Bartoń, 2022).

The partial least squares structural equation model (PLS-SEM) approach was used to explore the direct and indirect effects of stand structure, organic matter input, and soil variables on *k* and *S*. Climatic variables were not included in the model because they could affect the decomposition indices interactively, and SEM models cannot account for such interactions. For a specific a priori model, we hypothesized that stand structure properties would indirectly control decomposition. For instance, higher canopy coverage increases soil moisture by reducing soil surface evaporation, thereby affecting the decomposition parameters (Prescott, 2002; Joly et al., 2017). In addition, higher stand density increases litter mass and fine root biomass, indirectly affecting *k* and *S* (Na et al., 2021). It was expected that litter mass and root biomass would affect soil properties, such as pH, water content, bulk density, and C/N ratio (Facelli and Pickett, 1991; Xu et al., 2013; Liu et al., 2019b). Finally, it was expected that soil properties would directly control both decomposition parameters (Prescott, 2010; Berg and McClaugherty, 2014). All data were standardized prior to performing the structural equation model, and non-parametric bootstrapping (5000 resamples) was employed to obtain the PLS parameter estimates. A bootstrap confidence interval of 95% to determine the significance of the path coefficients, and only the significant pathways were retained in the final model (Hair et al., 2017). PLS-SEM analysis was performed using the SmartPLS software v3.3.6 (Ringle et al., 2015).

2.3 Results

2.3.1 Identifying the direct controls of *k* and *S*

Across sites, the mean values of *k* and *S* ranged from 0.010 to 0.023, and from 0.08 to 0.20, respectively (Table 2.1). Climate significantly affected both the decomposition parameters (*k* and *S*). The most parsimonious model of the temporal climate explained 42% of the variance in *k*, whereas the long-term climate model explained only 16% (Table 2.3). Conversely, the long-term climate explained 21% of the variance in *S*, whereas the temporal climate explained 14% (Table 2.3). In both climatic models, precipitation and temperature interactively affected the decomposition rates. In the temporal climate model, the effect of precipitation on *k* was dependent on specific temperature thresholds. When the temperature was lower than 23.7°C, *k* decreased with increasing precipitation; when the temperature was between 23.7 and 26.8°C, precipitation did not affect *k*; and when the temperature was higher than 26.8°C, *k* increased with precipitation (Figure 2.1A). In the long-term climate model, the interaction showed that when MAT was higher than 15.6°C, *k* increased with MAP, whereas when MAT was lower than that value, MAP had no significant effect on *k* (Figure 2.1B). There was a nonlinear decrease in *S* with temperature in both the temporal and long-term climate models, while *S* increased nonlinearly with precipitation in the latter model (Table 2.3).

Table 2.3 Results of regression models for the temporal and long-term climate models. R^2 and AIC for the best models are shown.

	k				*S*		
	Slope (± SE)	Adj. R^2	AIC		Slope (± SE)	Adj. R^2	AIC
a. Temporal climate				**a. Temporal climate**			
t × p	5.13×10^{-6} ($\pm 1.41 \times 10^{-6}$)	0.42	-418.78	t^2	-6.43×10^{-3} ($\pm 2.51 \times 10^{-3}$)	0.14	-160.03
b. Long-term climate				**b. Long-term climate**			
MAT × MAP	3.16×10^{-6} ($\pm 1.29 \times 10^{-6}$)	0.16	-400.12	MAT^2	-7.23×10^{-3} ($\pm 2.85 \times 10^{-3}$)	0.21	-166.03
				MAP^2	9.65×10^{-8} ($\pm 3.68 \times 10^{-8}$)		

Climatic variables included in the models represent: t = mean temperature during the incubation period, p = total precipitation during the incubation period, MAT = mean annual temperature, MAP = mean annual precipitation.

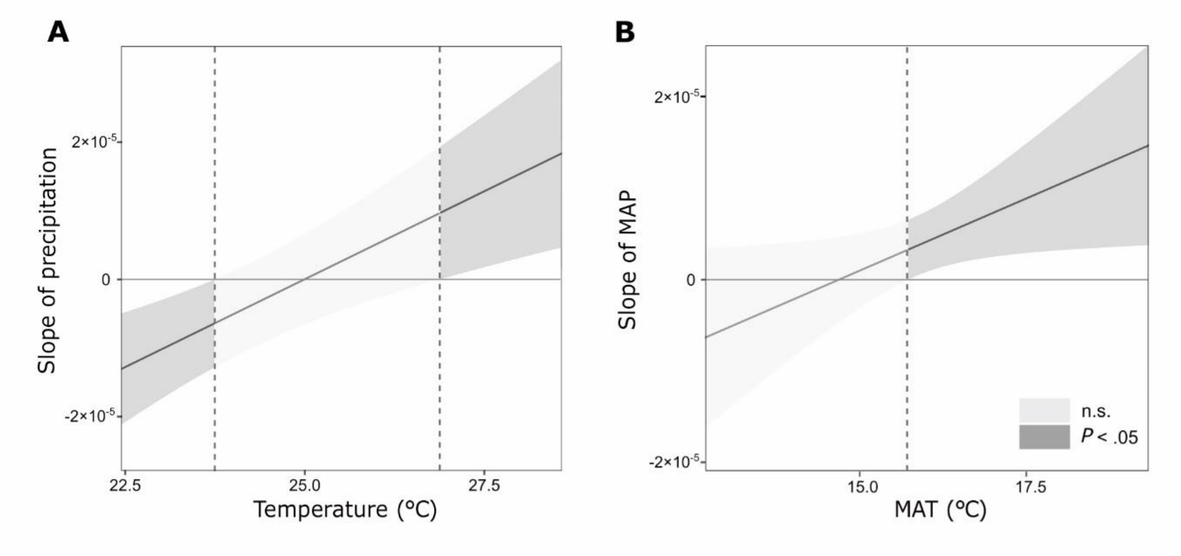

Figure 2.1 Johnson-Neyman plots showing the interactions between temperature and precipitation on the initial decomposition rate (*k*) in the (**A**) temporal climate and (**B**) long-term climate model. Dash lines show the temperature thresholds at which there are significant changes in the effect of precipitation on *k*.

The linear mixed-effects models showed that stand structure, organic matter input, and soil parameters had no significant influence on the initial decomposition rates across sites (Table 2.4). Fine root biomass had a marginal effect on S ($P < 0.1$) in the most parsimonious model of organic matter input and explained only 6% of the variance in S (Table 2.4).

Table 2.4 Results of multiple linear mixed models testing the effects of stand structure, organic matter input, and soil parameters on k and S. R^2m, R^2c, and AIC of the most parsimonious models are reported, and the retained variables are shown in bold.

	k			S		
	Slope (± SE)	R^2m/R^2c	AIC	Slope (± SE)	R^2m/R^2c	AIC
Stand Structure						
Stand density	-1.46×10^{-4} (6.06×10^{-4})	-	-	-9.29×10^{-3} (6.21×10^{-3})	-	-
Canopy cover	-5.92×10^{-4} (6.13×10^{-4})	-	-	1.01×10^{-2} (6.27×10^{-3})	-	-
Organic matter input						
Litter mass	6.17×10^{-4} (7.25×10^{-4})	-	-	-8.10×10^{-3} (7.52×10^{-3})	-	-
Fine root biomass	-4.99×10^{-4} (7.03×10^{-4})	-	-	**-1.21×10^{-2} (7.26×10^{-3})**	0.06/0.52	-154.57
Soil						
WC	-7.90×10^{-4} (7.96×10^{-4})	-	-	3.41×10^{-3} (8.73×10^{-3})	-	-
pH	4.13×10^{-6} (1.07×10^{-3})	-	-	1.32×10^{-2} (1.17×10^{-2})	-	-
BD	1.37×10^{-3} (1.28×10^{-3})	-	-	-9.81×10^{-3} (1.38×10^{-2})	-	-
C/N	-4.18×10^{-4} (7.50×10^{-4})	-	-	5.76×10^{-3} (8.22×10^{-3})	-	-

2.3.2 Identifying the indirect drivers of *k* and *S*

PLS-SEM models accounted for 23 and 27% of the variation in *k* and *S*, respectively (Figure 2.2). The model revealed interconnected relationships among the decomposition drivers, but none of the stand structure, organic matter input, or soil variables directly or indirectly affected *k* (Figure 2.2A). However, the model showed indirect cascading effects from stand density to *S*, mediated by changes in organic matter input and soil bulk density (Figure 2.2B). Stand density had a significant direct influence on litter mass (0.28) and fine root biomass (0.25). Both fine root biomass and litter mass negatively affected the soil bulk density (−0.22 and −0.31, respectively), while the latter negatively influenced litter stabilization (−0.31). Overall, this indicated that stand density and organic matter input had indirect positive effects on *S*, mediated by changes in soil bulk density. Although canopy cover did not affect soil conditions (Figure 2.2), these results demonstrate that stand structure variability can modify the soil environment and indirectly influence litter stabilization.

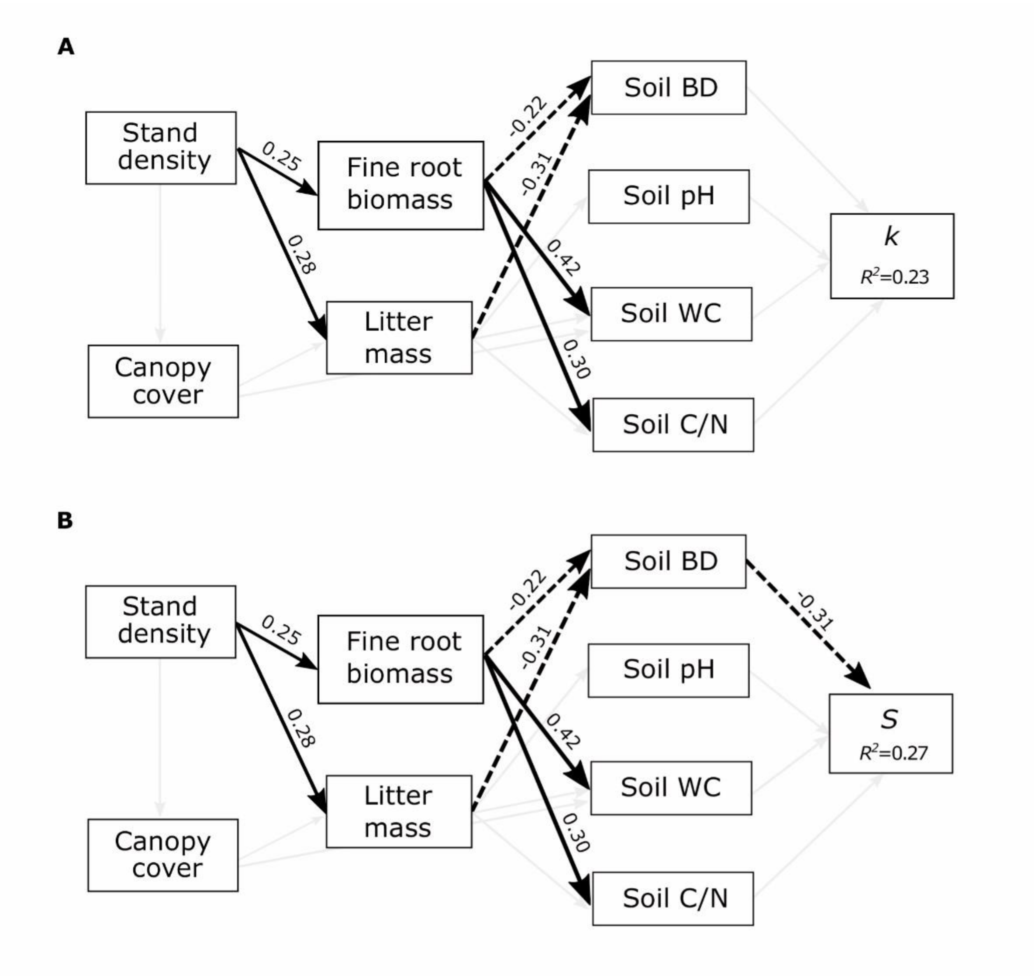

Figure 2.2 Structural equation models showing the effects of stand structure (stand density and canopy cover), organic matter input (fine root biomass and litter mass), and soil variables (bulk density, pH, C/N ratio, and water content) on (**A**) the initial decomposition rate (*k*) and (**B**) the stabilization factor (*S*). R^2 values represent the proportion of total variance explained by the model. Significant paths are shown in black arrows with solid and dashed arrows representing positive and negative effects, respectively.

2.4 Discussion

The climate variables were the most important drivers of the initial decomposition rate (*k*) and stabilization factor (*S*). However, the temporal scales of the climate affected the decomposition indices differently. The temporal climate was relatively more important, explaining 42% of the variation in *k*. This could be attributed to the variation in temperature and moisture conditions during the incubation period, which can directly influence microbial activity and leaching of soluble compounds, the latter of which is an important driver of mass loss in the early phases of litter decomposition (Cotrufo et al., 2010; Berg and McClaugherty, 2014). Conversely, the stabilization factor was primarily controlled by the long-term climate (21%) compared with the temporal climate (14%). Similar to these results, Althuizen et al. (2018) found that the long-term climate regime was more important for litter stabilization than variations in the short-term climate. The selected long-term climate model showed that temperature had a stronger effect on *S* despite low variability across the climatic gradient. The temperature sensitivity of carbon stabilization is a key factor in regulating soil carbon stocks (von Lützow and Kögel-Knabner, 2009). In warm temperate areas, soil carbon losses occur as microbial activity and heterotrophic respiration increase with temperature (Jackson et al., 2017). Although a negative nonlinear relationship between temperature and *S* was found, this contrasts with that of Xu et al. (2018), who reported that soil carbon stocks in Moso bamboo stands decreased linearly with mean annual temperature across a latitudinal gradient.

Compared to other vegetation types in the region (Suzuki et al., 2019), the decomposition parameters in Moso bamboo stands from this study were in the upper and lower range for *k* and *S*, respectively (Figure S2.1). The differences in the decomposition of standard litter could be attributed to the variation in environmental and site-specific conditions. Moso bamboo invasion into neighboring forests can lead to changes in the decomposition environment through the input of more recalcitrant litter (Song et al., 2016; Liu et al., 2019a). The slightly higher *S* (although not significantly different) in Moso bamboo stands than that of evergreen broadleaved forests could be related to the recalcitrance of bamboo litter and its lower decomposition rates, which may result in higher soil organic matter accumulation in the long-term (Liu et al., 2021). In addition, belowground biomass, which is significantly higher in Moso bamboo in comparison with evergreen broadleaved forests (Wang et al., 2013), may potentially contribute to increased carbon input and organic matter accumulation (Qin et al., 2017). The average *k* in Moso bamboo were comparable with that of evergreen broadleaf forests and higher than those of deciduous broadleaf, coniferous, mixed (broadleaf-conifer) forests and alpine shrubs. Similar initial decomposition rates in bamboo stands and evergreen broadleaf forests suggests that *k* was mainly influenced by climatic factors.

The interaction between precipitation and temperature was an important determinant of the variation in *k*. In this regional study, the effect of precipitation on *k* was mainly controlled by temperature thresholds. Increasing precipitation accelerated the initial litter decomposition at warmer sites, whereas decomposition was not determined and was negatively influenced by precipitation at the middle-range temperature and cooler sites, respectively. In this study, cooler sites were located at high altitudes and corresponded to locations with high mean annual precipitation (>3,000 mm). The negative effect of precipitation at these sites could be explained by the high amount of rainfall and oxygen depletion in soils, which can affect microbial communities and limit decomposition rates under such conditions (Schuur, 2001; Althuizen et al., 2018). Previous studies using the TBI method found that the effects of soil temperature on decomposition rates were dependent on soil moisture (Petraglia et al., 2019; Sarneel et al., 2020), indicating that complex interactions can affect decomposition rates during the early stages. Taylor et al. (2017) showed that, similar to our sites, warmer locations in tropical forests were associated with enhanced decomposition only under conditions of higher precipitation.

In this study, neither stand characteristics nor site conditions affected the initial decomposition rate (*k*). Specifically, soil properties had no direct effect on *k*, despite being important modulators of the abundance and activity of soil microbial communities and microarthropods (Prescott, 2010; Berg and McClaugherty, 2014). The limited contribution of soil parameters to *k* may be related to the greater importance of the leaching process during the early phases of litter decomposition (Cotrufo et al., 2010). However, as this study only focused on the controls of initial decomposition rates, the relative importance of soil parameters might change during the later stages of decomposition (García-Palacios et al., 2016). It is also important to note that climate data aggregated at the site level could lead to a larger contribution by climate on decomposition rates at large scales of analysis (Bradford et al., 2016). This could mask the contribution of other decomposition drivers at the local scale, such as variations in the microbial communities (Bradford et al., 2017). In addition, because water availability is an important driver of mass loss in tea bags (Djukic et al., 2018; Blume-Werry et al., 2021; Mori et al., 2021), the local-scale conditions of soil moisture measured continuously throughout the incubation period may better explain the variation in initial decomposition rates.

Contrary to expectations, the linear mixed-effect model showed no influence of soil properties on *S*, despite being highly variable across the studied region. However, SEM analysis, which tests the causal relationships among variables, showed that soil bulk density was negatively related to the stabilization factor. Organic matter can be stabilized in the soil through the physical protection of soil microaggregates. This mechanism protects organic matter from decomposition and, consequently, favors its accumulation in the soil (Six et al., 2002). Generally, increasing soil bulk density reflects a high degree of compaction and low porosity in the soil (Soane, 1990). As such, high bulk densities could lead to decreased micro-aggregation in soils and reduce the stabilization of organic matter (Six et al., 2002). In a previous study, Zhang et al. (2015) showed that soil bulk density was negatively associated with the topsoil organic carbon and was a good predictor of its spatial variation in Moso bamboo stands. The negative association between soil bulk density and litter stabilization found in this study further suggests that variations in soil structure could be important determinants of organic matter stabilization and potential soil carbon sequestration.

Stand structure did not directly explain the variability of the decomposition parameters; however, the SEM model showed indirect cascading effects from stand density to *S*. In the present study, bamboo stands with higher densities had increased amounts of litter mass accumulated on the forest floor and higher fine root biomass. Increasing litter mass and fine root biomass indirectly and positively affected the stabilization factor (*S*) through their effects on soil bulk density and not through soil microclimatic conditions, as initially expected. Above- and below-ground organic matter inputs can substantially influence the soil structure and carbon accumulation (De Deyn et al., 2008). For instance, rhizodeposition from roots is a source of labile carbon in the soil that can increase the presence of soil aggregates and binding structures and enhance the soil structure (Jobbágy and Jackson, 2000; Traoré et al., 2000). By altering soil structure and pores in the soil, roots can modify soil aggregation and short-term stabilization (Morel et al., 1991; Six et al., 2004). Additionally, litter decomposition and root turnover allow the progressive accumulation of organic matter in the soil (Jastrow and Miller, 1998), which has the potential to improve soil structure and promote organic matter stabilization (Kay, 1998; Abiven et al., 2009). Yang et al. (2021) showed that increased input of organic matter in extensively managed Moso bamboo stands were positively associated with soil aggregate stability and soil organic carbon. Altogether, these results suggest that variations in stand density and organic matter input in bamboo stands can modulate changes in soil structure and represent important indirect biotic controls of litter stabilization.

Variations in stand density and organic matter input in bamboo stands can represent important plant controls affecting below-ground processes and may be particularly relevant in bamboo-dominated communities that form dense monospecific stands and underground root networks (Fukuzawa et al., 2007; Yin et al., 2019). Unmanaged stands have higher densities than managed stands (Chen et al., 2016; Yin et al., 2019). However, the managed stands considered in this study had great variation in stand densities and did not differ in stand structure and organic matter input variables compared to unmanaged stands. Nevertheless, it is important to note that different management practices can affect soil conditions and may have further consequences for below-ground functions (Fu et al., 2014; Yuen et al., 2017; Yang et al., 2021). In addition, the time of management, or in the case of unmanaged stands, the time of abandonment, might also be factors to consider when evaluating below-ground processes and soil carbon storage (Yin et al., 2019; Yang et al., 2021). Although the effect of such factors may be inherent in the studied sites, our results still provide an understanding of the mechanisms by which stand structure controls organic matter stabilization and the potential soil carbon storage in bamboo stands. These results may provide further insights into how specific management practices (i.e., thinning) and the variability of stand density could influence the decomposition process in Moso bamboo stands.

2.5 Conclusion

This chapter suggests that climatic factors are the main drivers of decomposition processes in Moso bamboo stands on a regional scale. Long-term climate greatly influenced litter stabilization, whereas k was mostly affected by temporal climatic conditions. The analysis also revealed that k was strongly affected by the interaction between precipitation and temperature, suggesting that precipitation only accelerated the initial decomposition rates at warmer sites. Overall, stand structure and soil properties had limited direct effects on both the decomposition parameters. However, indirect cascading effects from stand density affected litter stabilization through variations in the amount of organic matter input and their consequent modifications to soil bulk density. These results demonstrate the importance of identifying direct and indirect pathways to disentangle the different mechanisms controlling litter decomposition and stabilization. Finally, the particular relevance of climate in this region suggests that changes in precipitation regimes or temperature would greatly affect the early phases of decomposition and potential soil carbon storage in Moso bamboo stands.

Chapter 3

Litter quality and soil fauna effects on whole-plant litter decomposition

3.1 Introduction

Plant litter decomposition is an essential process in the biogeochemical cycles of terrestrial ecosystems, influencing soil fertility and the carbon cycle (Chapin et al., 2011). At local scales, litter quality and the decomposer communities are the primary drivers of organic matter decay (Couteaux et al., 1995; Bradford et al., 2016). Chemical traits such as nitrogen and lignin concentration influence the metabolism of microbial decomposers and strongly regulates litter decomposability (Cornwell et al., 2008, Cornelissen and Thompson, 1997). For instance, higher litter nitrogen concentrations are associated with rapid decomposition, while higher lignin concentrations are associated with slower decomposition (Freschet et al., 2012; Cornwell et al., 2008). Litter structural and morphological traits can also affect litter decomposability by affecting the quality of habitat for decomposer communities. Differences in microenvironmental conditions and available surface area for colonization can be determined by the shape and form of litter, while litter physical resistance may prevent fragmentation by decomposers. In general, decomposition rates show a negative relationship with density and dry mass content (Zukswert and Prescott, 2017; Kazakou et al., 2019), and a positive relationship with litter water retention capacity (Makkonen et al., 2013). Chemical and structural traits that affect decomposition vary between plant organs (i.e., leaves, branches, stems, roots) and are essential in predicting whole-plant litter decomposability (Freschet et al., 2013). However, much less is known about how the afterlife effects of above and below-ground organs affect the role of soil faunal decomposers in whole-plant litter decomposition and nutrient mineralization.

Soil fauna play a significant role in litter decomposition by directly breaking down and consuming litter and indirectly interacting with microbial communities (Chapin et al., 2011; Garcia-Palacios et al., 2013). While the role of litter quality in decomposition is generally well known, the contribution of soil fauna to decomposition in relation to different litter qualities still remains poorly understood. Previous studies showed that soil fauna enhanced the decomposition of chemically labile leaf litter across several species (Coq et al., 2010; Fujii et al., 2018; Schadler and Brandl, 2005), while others showed that soil fauna played a greater role in the breakdown of recalcitrant litter (Filser, 2002; Yang and Chen, 2009). In contrast, Lin et al. (2019) found that soil fauna enhanced leaf litter decomposition in subtropical tree species, but their contribution to litter mass loss or nutrient release was not modulated by litter quality. Among plant organs, soil fauna had a higher contribution to the decomposition of leaf litter compared to root litter in tree species (Fujii et al., 2018; 2016), while faunal effects on root litter decay were greater than on leaf litter in grassland species (Song et al., 2020). These contrasting results suggest that soil fauna effects on litter decomposition and nutrient mineralization cannot be generalized and that their interactions with litter quality may depend on several factors (i.e., litter type, climate, soil conditions, incubation period) (Kampichler and Bruckner 2009). Moreover, the involvement of soil fauna in litter decomposition may differ between organs in response to litter palatability and their contrasting structural and morphological characteristics. Substrate differences can attract different faunal communities during litter decomposition (Fujii and Takeda, 2012; Fujii and Takeda, 2017). However, there is still large uncertainties about the community composition of soil mesofauna involved in above- and below-ground litter decomposition, and how it affects litter mass and nutrient loss, particularly for organs other than leaves and roots.

The aim of this chapter is to elucidate the contribution of soil mesofauna to whole-plant litter decomposition in a Moso bamboo (*Phyllostachys edulis*) stand. To evaluate the effects of litter type, soil fauna and their interaction on litter mass, carbon and nitrogen loss, and respirations rates, a litterbag experiment was performed with two litter mesh sizes to allow or restrict soil mesofauna presence on leaf, fine root, rhizome, branch and culm litter. As litter quality influences the decomposability of substrates and the activity of microbial decomposers, it was hypothesized that: (i) variations in the initial chemical and physical litter traits will influence the mass, carbon and nitrogen loss in Moso bamboo organs during decomposition. Given the potential interaction between soil fauna with litter quality (Yang and Chen, 2009; Coq et al., 2010; Fujii et al., 2018), the hypothesis that: (ii) soil fauna contributes more to the decomposition of high-quality organs than low-quality organs was further tested. In addition, the changes in soil fauna community during the decomposition of Moso bamboo organs were also evaluated.

3.2 Materials and methods

3.2.1 Site description

The decomposition experiment was conducted in an unmanaged Moso bamboo forest (*Phyllostachys edulis*) in Kasuya Research Forest, Kyushu University, located in Fukuoka prefecture, Japan (33°37'53.25"N, 130°30'31.83"E). The mean annual precipitation is 1650 mm, 50% of which falls during the rainy season from July to September. The mean annual temperature is 15.6°C, with minimum and maximum temperatures in January (3°C) and August (32°C), respectively (Japan Meteorological Agency, 2019). The bamboo stand is located near to an invaded broadleaf forest and extends into approximately 0.43 ha. The decomposition experimental plots were established in a bamboo dominated area with an average stand density and DBH (diameter at breast height) of 7500 culms ha^{-1} and 10.83 cm, respectively.

3.2.2 Experimental design and setup

All bamboo organs were collected between April and May 2019. Leaf litter was collected from litter traps and directly from the forest floor. Culm and branch litter samples were obtained from standing dead individuals. Culms were first cut into disk sections of 10 cm, and then into 3 cm-width pieces, with the longest dimension corresponding to the vertical orientation of the fibers. Branches (1-4 mm diameter) belonging to the second order branching were selected and cut into 7 cm long pieces. Below-ground organs were collected by digging out the soil up to 15 cm-depth. Rhizome samples were cut into pieces of 3 cm long. Rhizome and fine roots (< 2 mm diameter) were washed and cleaned from soil particles. All litter samples were oven-dried at 70°C for two days to a constant weight to determine the initial dry mass.

The litterbag method was used to measure the decomposition of bamboo organs. The effects of soil fauna on litter decomposition were evaluated using 42 µm and 1 mm mesh-size litterbags, which restricted and allowed the entrance of soil mesofauna, respectively. All litterbags (10 × 10 cm) were filled with approximately 3 g of litter dry weight (DW). Five replicate plots (2 × 2 m) were established in the bamboo stand. Each plot was divided into two subplots, where five bamboo organs of 1 mm mesh size litterbags were placed in one subplot and the ones of 42 µm mesh size litterbags were placed in the other. A total of 300 litterbags (five organs × two mesh sizes × six collection times × five plots) were placed on the forest floor in June 2019. Litterbags were retrieved after 90 d (September 2019), 180 d (December 2019), 270 d (March 2020), 360 d (June 2020), 540 d (December 2020), and 720 d (June 2021).

3.2.3 Initial litter traits measurement

An additional set of organ samples were prepared to quantify the initial chemical, physical and morphological traits potentially related to litter decomposition. Chemical properties included carbon, nitrogen and ash concentration. Oven-dried litter samples were ground to powder. Initial carbon and nitrogen concentrations were measured by dry combustion using a CN analyzer (Yanaco MT-700, Kyoto, Japan). Ash concentration was determined by ignition combustion in a muffle furnace at 600°C after 6 hours. Lignin content was determined by the gravimetric method of the thioglycolic acid (TGA) as described by Shimada et al. (2019). The recovery of lignin obtained by this method was confirmed by using standard lignin [lignin (alkaline) Nacalai Tesque, Kyoto, Japan] with different sample amounts, which were completely recovered after TGA ($R^2 = 0.99$). Note that the lignin obtained by TGA is not entirely lignin and thus contains some undissolved proteins. Silica content was determined by the gravimetric method with wet digestion. Briefly, 500 mg ground samples were digested with 3 ml nitric acid and 0.5 ml hydrogen peroxide in a block heater (110°C). The residue was filtered using a filter paper, burned at 550 °C for 2 hours and weighted as silicate (SiO_2).

Physical traits included water holding capacity (WHC), density and dry matter content (DMC); and morphological traits included specific area (SA) and three-dimensionality (3-D). Water saturation or WHC represents the amount of water that can be preserved in an organ. For this, bamboo litter was sprayed with 3 ml of water every three hours for 48 h, then the wet weight was compared to the dry weight and expressed as %H_2O g (Makkonen et al., 2013). Organ DMC was calculated as the oven dry mass (g) divided by the water saturated fresh mass (g). Three-dimensionality was expressed as the litter total surface area per volume ($cm^2\ cm^{-3}$), and specific area was calculated as the total surface area of the organ (cm^2) divided by the oven dry mass (g). Litter area was measured using ImageJ (Abramoff et al., 2004) and litter volume was measured using the displacement method (Chave et al., 2006). Organ density was calculated by dividing the oven dry mass (g) by the fresh volume (cm^3).

3.2.4 Litter mass loss and C and N dynamics

After each collection, litter samples were oven-dried to a constant weight at 70 °C for 48 h to determine their final dry mass. Litter mass loss (%) was calculated as: $(M_o - M_t)/M_o \times 100$, where M_o and M_t are the initial dry mass before incubation and at each collection time, respectively. Carbon and nitrogen loss (%) were determined using the formula: $[(M_o \times C_o) – (M_t \times C_t)]/(M_o \times C_o) \times 100$, where C_o is the initial concentration of carbon or nitrogen (% of the litter dry mass) and C_t is the concentration of carbon or nitrogen in the decomposing litter at time t.

The amount of N release, N immobilization and net N release were calculated as:

$\mathrm{N_{release}} = 100 – \mathrm{N_{min}}$ *Equation 3.1*

$\mathrm{N_{immobilization}} = \mathrm{N_{720}} – \mathrm{N_{min}}$ *Equation 3.2*

$\text{Net N release} = \mathrm{N_{release}} – \mathrm{N_{immobilization}}$ *Equation 3.3*

where $N_{release}$ is the maximum amount (%) of N release, $N_{immobilization}$ is the amount (%) of N immobilized, N_{min} is the minimum N remaining (%) during decomposition, and N_{720} is the N remaining (%) after 720 days of decomposition.

3.2.5 Litter respiration rates

After each retrieval, litter samples were cleaned from soil particles and brought to the laboratory to measure litter respiration rates in a closed dynamic chamber fitted with an infrared gas analyzer (IRGA; GMP343; Vaisala Group, Vantaa, Finland). CO_2 efflux was measured inside a room at constant air temperature (25°C) within the first 6 h after collection. The sample temperatures were measured with an infrared thermometer. Each litter sample was enclosed in the chamber for ~3 min. The litter respiration rates were calculated from the slope of the linear increase in CO_2 concentration inside the chamber and expressed as nmol CO_2 per unit litter dry mass (g) per unit time (s).

3.2.6 Soil fauna community

Immediately after the litter respiration measurements, litter samples from the 1-mm mesh litterbags were placed in a Tullgren extractor for 5-7 d to collect any soil mesofauna (Coleman et al., 1992). Invertebrates were identified to order level, except for Acari, which were classified to the suborder level (Krantz and Walter, 2009). The relative densities of the individuals and the soil fauna orders were expressed as number of individuals and orders per gram dried litter, respectively. The Shannon-Wiener diversity index was calculated as: $H' = -\sum_{i=1}^{S} p_i \, ln \, p_i$, where pi = (number of individuals per order / total number of individuals), and S = order richness.

3.2.7 Data analysis

Litter decomposition rates (k) were calculated using a negative exponential model: $M_t = M_0 e^{-kt}$, where M_0 is the initial litter mass, M_t, is the mass remaining after time t, and k is decay rate constant (Olson 1963). The contribution of soil fauna to litter mass was calculated as: fauna effect (%) = (mass loss in 1mm mesh size litterbags - mass loss in 42 μm mesh size litterbags)/(mass loss in 1mm mesh size litterbags) × 100.

Linear mixed effects models (LMMs) were used to determine the effects of litter type, soil fauna, decomposition time and their interactions on mass, carbon and nitrogen loss, and litter respiration rates, respectively. Soil fauna (mesh size) and litter type (organ) identity nested within plots were included as random effects to account for the spatial autocorrelation. The corAR1 function was used to account for the temporal pseudo-correlation associated with multiple litterbag collections over time, with ‘decomposition time’ (days) defining the correlation structure. The normal distribution and homogeneity of variance of the model residuals were checked, and the model with the lowest AIC was chosen as the best model.

A principal component analysis (PCA) was used to visualize the overall variation in morphological, physical and chemical traits of bamboo organs. The axis that explained the greatest variation of the organ traits was chosen for evaluating the relationship between litter traits and litter decomposability (mass, carbon and nitrogen loss). To test whether the effect of soil fauna altered the relationship between litter traits and decomposition, slope and intercepts were tested for significance with standardized major axis regressions (SMA). In addition, correlations between each individual trait with mass, carbon and nitrogen loss for the 42 μm and 1 mm mesh bags were tested using ordinary least squares regression (OLS).

To evaluate the effects of litter type and decomposition time on soil fauna density, order richness and diversity, generalized linear models (GLMs) were used. Order richness followed a Poisson distribution, Shannon diversity followed a Gaussian distribution and for individual density a quasipoisson link function was used due to the high number of zeros. *P*-values for comparing least square means in the GLMs were adjusted for multiple comparison using LSD Fisher. All statistical analyses were performed in R version 4.0.2 and the following packages: stats (R Core Team 2022), vegan (Oksanen et al., 2020) and smatr (Warton et al., 2012).

3.3 Results

3.3.1 Litter type and soil fauna effects on litter decomposition, C and N dynamics and respiration rates

There were significant differences in the decomposability of the five litter types. In the presence of soil mesofauna, litter decomposition rates (*k*) followed the ranking of leaves (0.37) > fine root (0.22) > rhizome (0.15) = branch (0.15) > culm (0.08) litter. Overall, soil fauna decreased the litter decomposition rates of branch and leaf litter, reducing their mass losses by 31% and 12%, respectively (Table 3.1).

Litter mass loss and carbon loss were affected by the interactions between litter type, soil fauna and decomposition time (Table 3.2). After 720 days of decomposition, litter mass loss was the highest in leaves, followed by fine root, rhizome, branch and culm litter (Figure 3.1). Similarly, carbon loss was greater for leaf litter (59.6 %) and lower for culm litter (10.8%) (Figure 3.1, Table 3.3). Soil mesofauna decreased the mass and carbon loss of branch and leaf litter only at later stages of decomposition (after 520 d) (Figure 3.1).

Similar to mass and carbon loss, litter nitrogen loss was also affected by the interactions between litter type, soil fauna and decomposition time (Table 3.2). Branch, culm, rhizome and fine root litter showed similar nitrogen loss patterns, with periods of high N immobilization at early stages of decomposition (Table 3.3, Figure 3.1). Leaf litter showed the lowest N immobilization among litter types and had consistent N loss during the decomposition period (Table 3.3, Figure 3.1). However, given the higher N release in culm and rhizome litter (60.9% and 56.7% in the presence of fauna, respectively), their net N release (35.7% and 24.5% with fauna, respectively) was higher than that of leaf litter (12.8% with fauna) (Table 3.3). Soil mesofauna decreased leaf litter nitrogen immobilization and nitrogen loss at 720 d, whereas they increased culm litter nitrogen loss at 360 d and 520 d (Table 3.3, Figure 3.1). Overall, the presence of soil mesofauna did not affect the net N release of bamboo litter during decomposition (Table 3.3).

Litter respiration rates were affected by the interaction between litter type and decomposition time (Table 3.1, $P < 0.001$). On average, litter respiration rates followed the ranking of leaves > fine root > rhizome > branch > culm litter (Figure 3.2). Soil fauna had no effect on litter respiration rates, however, the presence of soil mesofauna decreased litter respiration rates in branch litter only at 720 d (Figure 3.2).

Table 3.1 Decomposition rates (*k*) of bamboo litter in the presence (1mm) and absence of soil mesofauna (42 µm). Capital letters indicate significant differences in the decomposition rates among litter types ($P < 0.05$), while lower-case letters indicate differences in decomposition rates (*k*) between the mesofaunal treatments ($P < 0.05$). Faunal effects (%) are only shown for litter types where *k* with fauna vs. without fauna were significantly different.

Litter type	1 mm (with fauna) *k*	42 µm (without fauna) *k*	Fauna effect (%)
Branch	0.15 ± 0.01 aB	0.23 ± 0.03 bB	-30.9 ± 7.8 B
Culm	0.08 ± 0.01 aA	0.11 ± 0.02 aA	
Fine root	0.22 ± 0.02 aC	0.23 ± 0.01 aB	
Leaves	0.37 ± 0.01 aD	0.44 ± 0.02 bC	-11.9 ± 3.7 A
Rhizome	0.15 ± 0.02 aB	0.19 ± 0.02 aB	

Table 3.2 Results of general linear models evaluating the effects of litter type, soil fauna, decomposition time and their interactions on litter mass, carbon and nitrogen losses, and respiration rates. Significant effects ($P < 0.05$) are shown in bold.

Variable	Source of variance	*df*	*F*	*P*
Mass loss (%)	Litter type	4	1772.31	< **0.001 *** **
	Soil fauna	1	2.13	0.15
	Time	5	275.88	< **0.001 *** **
	Litter type × Soil fauna	4	9.80	**< 0.001 *** **
	Litter type × Time	20	9.84	**< 0.001 *** **
	Soil fauna × Time	5	3.90	**< 0.01 ** **
	Litter type × Soil fauna × Time	20	1.35	0.15
Carbon loss (%)	Litter type	4	1695.35	< **0.001 *** **
	Soil fauna	1	6.32	**0.01 * **
	Time	5	264.38	< **0.001 *** **
	Litter type × Soil fauna	4	12.95	**< 0.001 *** **
	Litter type × Time	20	10.86	**< 0.001 *** **
	Soil fauna × Time	5	3.48	**< 0.01 ** **
	Litter type × Soil fauna × Time	20	1.72	**0.03**
Nitrogen loss (%)	Litter type	4	83.19	< **0.001 *** **
	Soil fauna	1	0.59	0.44
	Time	5	115.44	< **0.001 *** **
	Litter type × Soil fauna	4	2.91	**0.02 * **
	Litter type × Time	20	32.56	**< 0.001 *** **
	Soil fauna × Time	5	0.67	0.64
	Litter type × Soil fauna × Time	20	1.80	**0.02 * **
Respiration rate (nmol CO_2 g^{-1} s^{-1})	Litter type	4	10.85	< **0.001 *** **
	Soil fauna	1	1.76	0.18
	Time	5	238.86	< **0.001 *** **
	Litter type × Soil fauna	4	0.74	0.57
	Litter type × Time	20	29.12	**< 0.001 *** **
	Soil fauna × Time	5	0.48	0.79
	Litter type × Soil fauna × Time	20	0.72	0.80

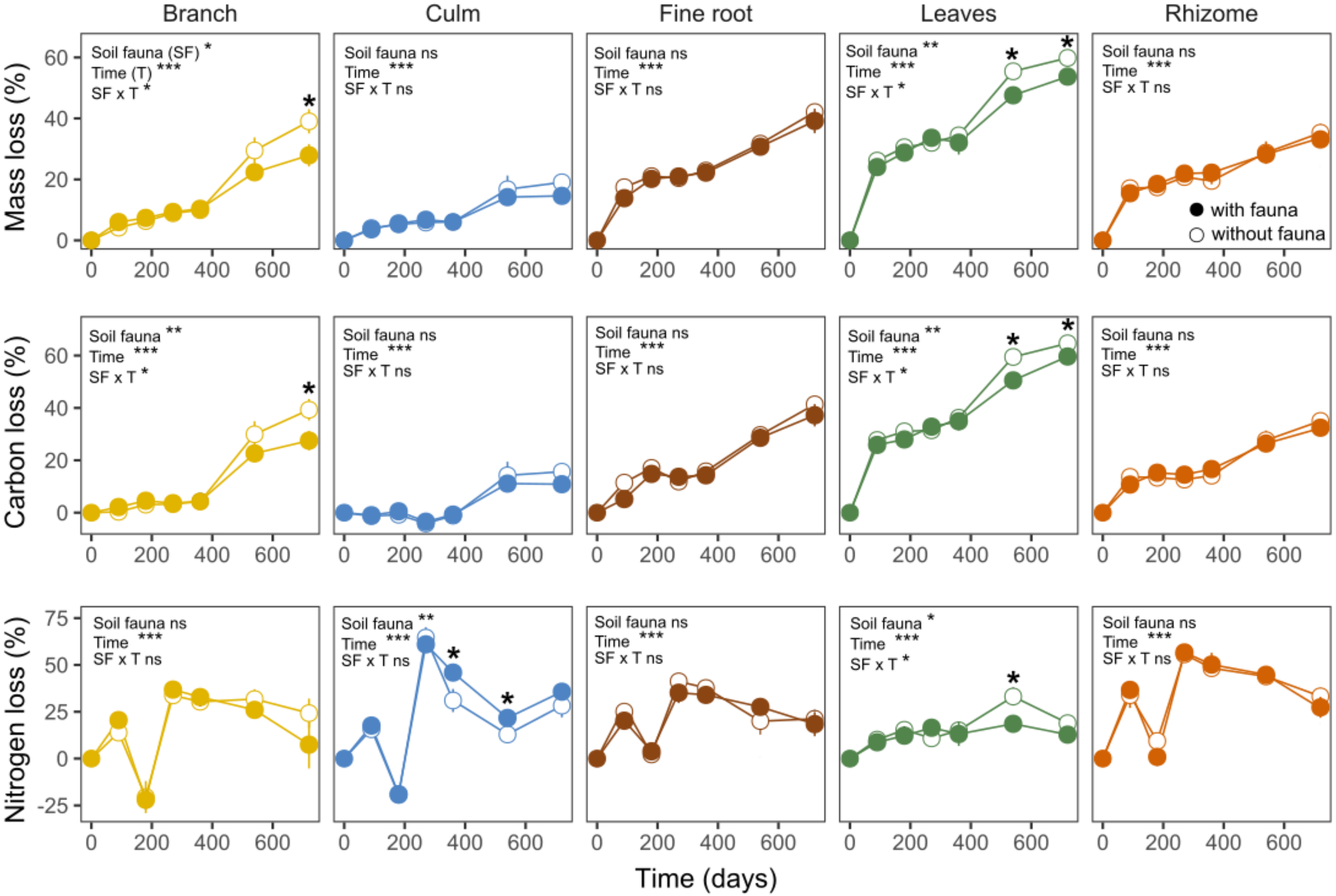

Figure 3.1 Effects of soil fauna and decomposition time on the mass, carbon and nitrogen loss in branch, culm, fine root, leaves, and rhizome litters. Significant effects are shown as: $P < 0.05$ *, $P < 0.01$ **, $P < 0.001$ ***, and ns: not significant.

Table 3.3 Mean (± S.E.) carbon loss (%, after 720 days), nitrogen release (%), nitrogen immobilization (%) and net nitrogen release (%) of bamboo litter in the presence (1 mm) and absence of soil mesofauna (42 μm). Different capital letters indicate significant differences in the decomposition rates among litter types ($P < 0.05$), while different lower-case letters indicate differences in decomposition rates between the mesofaunal treatments ($P < 0.05$).

Litter type	C loss (%)		N release (%)		N immobilization (%)		Net N release (%)	
	1 mm	42 μm	1 mm	42 μm	1 mm	42 μm	1 mm	42 μm
Branch	27.5 ± 3.7 aBC	39.3 ± 4.0 bB	35.7 ± 4.1 aB	33.7 ± 3.8 aA	28.3 ± 7.5 aB	19.5 ± 4.0 aA	18.4 ± 6.6 aAB	24.2 ± 7.7 aA
Culm	10.8 ± 2.4 aA	15.6 ± 2.3 aA	60.9 ± 4.0 aC	64.5 ± 5.4 aB	25.2 ± 5.0 aB	36.3 ± 9.0 aB	35.7 ± 4.1 aC	28.2 ± 6.2 aA
Fine root	37.2 ± 4.3 aC	41.4 ± 2.3 aB	35.2 ± 5.5 aB	41.2 ± 3.8 aA	16.8 ± 7.2 aB	20.0 ± 4.0 aB	18.4 ± 3.4 aB	21.2 ± 4.8 aA
Leaves	59.6 ± 2.1 aD	64.7 ± 1.4 bC	18.6 ± 1.6 aA	33.1 ± 4.8 bA	5.8 ± 3.1 aA	14.2 ± 4.9 bA	12.8 ± 2.8 aA	18.9 ± 4.2 aA
Rhizome	26.3 ± 2.6 aB	35.0 ± 2.7 bB	56.7 ± 3.6 aC	55.7 ± 4.0 aB	32.2 ± 7.3 aB	22.4 ± 6.6 aB	24.5 ± 5.6 aBC	33.2 ± 4.5 aB

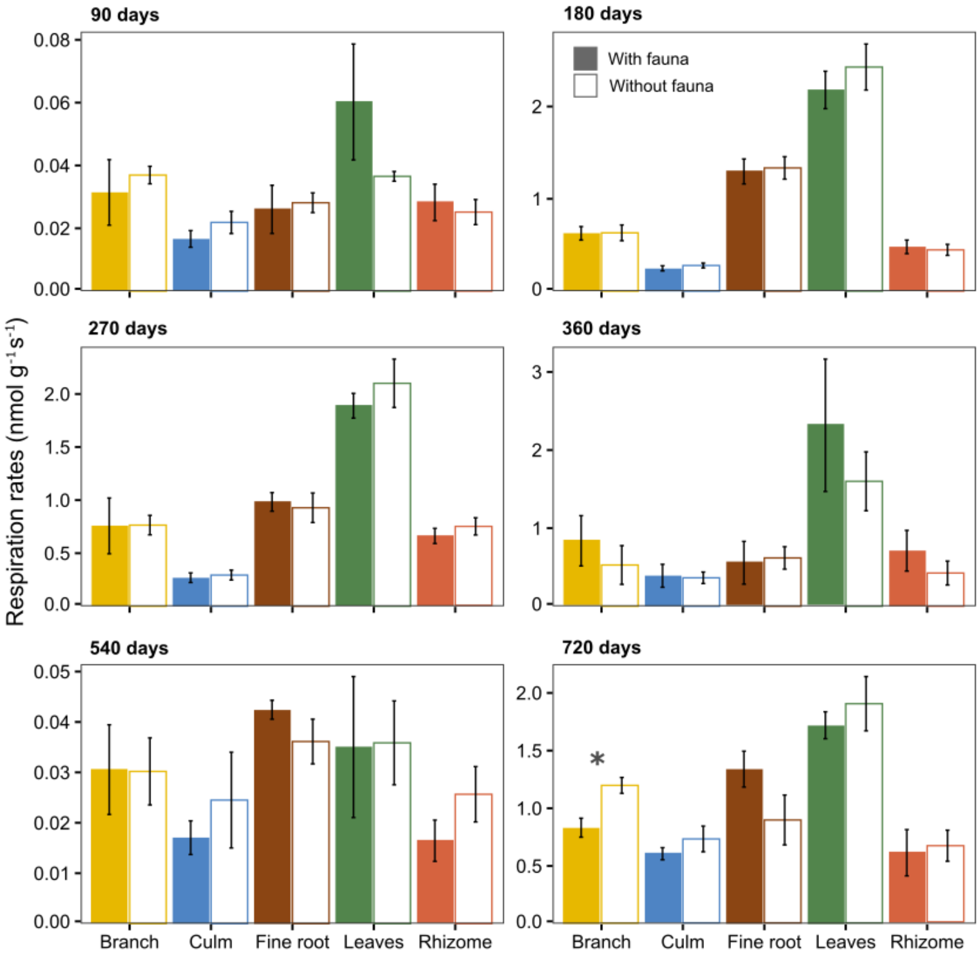

Figure 3.2 Soil fauna effects on litter respiration rates in five litter types (organs) at different retrieval times. Significant effects are shown as: *P* < 0.05 *, *P* < 0.01 **, *P* < 0.001 ***.

3.3.2 Initial litter traits of bamboo organs

Initial litter traits were different across litter types (Table 3.4, $P < 0.05$). Variations in chemical, physical and morphological traits of bamboo organs were well represented by the first two axes of the PCA analysis (97.1%) (Figure 3.3). The first axis accounted for 74.6% of the overall variation. Chemical traits such as C, N, ash, lignin, silica concentrations, C/N and lignin/N ratios, and morphological and physical traits such as 3-D and WHC contributed significantly to this variation. The second axis explained 12.5% of the variation, with density and DMC contributing substantially to the second PCA axis.

3.3.3 Soil fauna effects on trait-decomposability relationships

Litter mass loss and carbon loss correlated well with chemical, structural and morphological-related traits of bamboo organs ($P < 0.05$; Table 3.2). In particular, litter mass loss was negatively correlated with C/N ratio, C, lignin concentration and lignin/N ratios, and positively correlated with N concentration, ash content, silica, SA and 3-D. Similar relationships were found for carbon loss and the initial litter traits. Nitrogen loss tended to be positively correlated with C/N ratios and negatively correlated with N concentration ($P < 0.10$). The presence of mesofauna altered the relationships between nitrogen loss and initial traits (specifically initial N and C/N ratio), but not those of mass loss or carbon loss and litter traits.

Regardless of soil mesofauna presence, litter trait scores of the first PCA axis were correlated with litter mass loss ($P < 0.05$; Figure 3.4a) and carbon loss ($P < 0.05$; Figure 3.4b), but not nitrogen loss ($P > 0.19$; Figure 3.4c). For these relationships, the regression lines of the treatment with mesofauna showed no differences in slopes ($P = 0.98$, Figure 4a; $P = 0.93$, Figure 3.4b) nor intercepts ($P = 0.12$, Figure 3.4a; $P = 0.14$, Figure 3.4b) compared with the treatment without mesofauna. In contrast, there was no correlation between organ litter scores of the second PCA axis and litter mass, carbon nor nitrogen loss.

Table 3.4 Initial litter traits (mean ± S.E.) of bamboo organs. Different letters represent significant differences in a given litter trait within a row (*P* < 0.05). DMC: dry matter content; 3-D: three dimensionality; SA: specific area; WHC: water holding capacity, N: nitrogen concentration, C: carbon concentration; C/N: carbon to nitrogen ratio; Lignin/N: lignin to nitrogen ratio.

Litter trait	Branch	Culm	Fine root	Leaves	Rhizome
C/N	83.02 (3.09) b	132.94 (4.97) c	81.11 (2.55) b	47.48 (1.09) a	79.97 (4.84) b
N (%)	0.53 (0.02) b	0.33 (0.01) a	0.51 (0.01) b	0.82 (0.02) c	0.56 (0.04) b
C (%)	43.74 (0.16) c	43.88 (0.18) c	41.38 (0.19) b	38.96 (0.24) a	43.73 (0.31) c
Ash (%)	3.48 (0.11) c	1.71 (0.02) a	4.97 (0.37) d	16.3 (0.26) e	2.54 (0.32) b
Lignin (%)	47 (0.31) c	40.38 (0.68) b	37.27 (1.62) b	17.82 (1.66) a	45.97 (0.81) c
Lignin/N	89.25 (3.63) c	122.49 (5.66) d	73.04 (3.65) b	21.75 (2.19) a	84.51 (6.88) bc
Silica (mg g^{-1})	23.37 (0.72) c	5.85 (0.21) a	22.43 (2.04) c	139.22 (2.9) d	12.01 (0.44) b
WHC (%)	25.18 (0.96) a	23.21 (0.90) a	96.09 (4.1) d	76.51 (3.49) c	40.36 (6.83) b
SA (cm^2 g^{-1})	9.53 (1.0) a	1.87 (0.06) a	32.06 (1.76) a	442.49 (31.98) b	7.48 (1.44) a
Density (g cm^{-3})	0.85 (0.05) d	0.64 (0.00) bc	0.73 (0.06) c	0.34 (0.02) a	0.55 (0.01) b
DMC (g g^{-1})	0.67 (0.01) c	0.54 (0.00) b	0.57 (0.04) b	0.55 (0.01) b	0.48 (0.01) a
3-D (cm^2 cm^{-3})	22.32 (0.85) a	3.79 (0.05) a	119.59 (19.21) b	171.55 (6.2) c	2.97 (0.24) a

Table 3.5 Coefficients of ordinary least squares regression (*r*) between initial litter traits and mass, carbon, and nitrogen loss (%) after 720 days of litter decomposition in the presence (1 mm) and absence (42 μm) of soil mesofauna. DMC: dry matter content; 3-D: three dimensionality; SA: specific area; WHC: water holding capacity, N: nitrogen concentration, C: carbon concentration; C/N: carbon to nitrogen ratio; Lignin/N: lignin to nitrogen ratio.

Initial litter traits	Mass loss (%)		Carbon loss (%)		Nitrogen loss (%)	
	1 mm	42 μm	1 mm	42 μm	1 mm	42 μm
C/N	**-0.91***	**-0.96****	**-0.92***	**-0.96****	**0.84+**	0.5
N (%)	**0.92***	**0.95****	**0.95***	**0.97****	**-0.80+**	-0.54
C (%)	**-0.94***	**-0.86+**	**-0.93***	**-0.86+**	0.41	0.79
Ash (%)	**0.91***	**0.88***	**0.93***	**0.89***	-0.47	-0.73
Lignin (%)	**-0.81 +**	-0.72	-0.82	-0.73	0.2	0.71
Lignin/N	**-0.98****	**-0.98****	**-0.99*****	**-0.98****	0.62	0.66
Silica (%)	**0.86 +**	**0.86 +**	**0.90***	**0.87+**	-0.47	-0.69
WHC (%)	0.79	0.66	0.73	0.63	-0.28	-0.65
SA (cm^2 g^{-1})	**0.84 +**	**0.82 +**	**0.88 +**	**0.84 +**	-0.37	-0.65
Density (g cm^{-3})	-0.53	-0.49	-0.58	-0.51	-0.14	0.14
DMC (g g^{-1})	0.03	0.14	0.02	0.1	-0.66	-0.49
3-D (cm^2 cm^{-3})	**0.93***	**0.85+**	**0.92***	**0.83+**	-0.46	-0.47

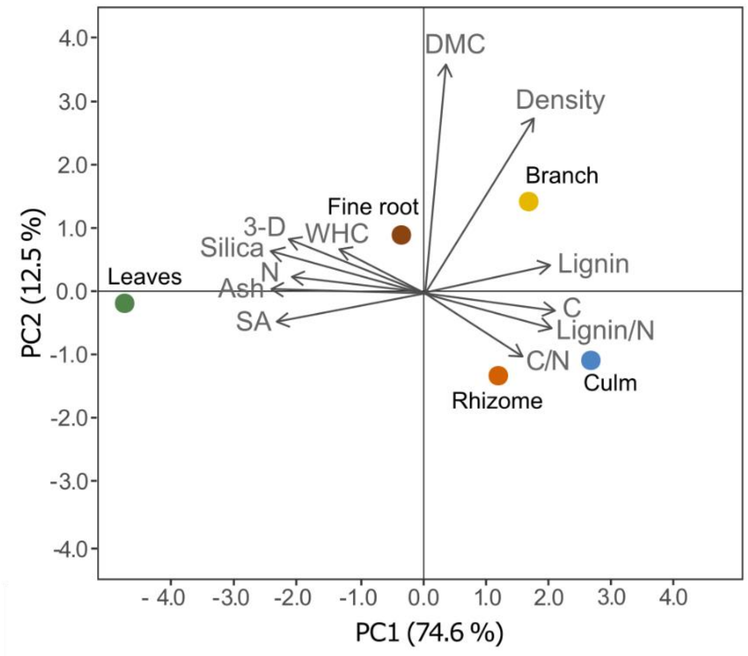

Figure 3.3 Biplot of PCA analysis of 12 initial litter traits for five litter types (bamboo organs). DMC: dry matter content; 3-D: three dimensionality; SA: specific area; WHC: water holding capacity, N: nitrogen concentration, C: carbon concentration; C/N: carbon to nitrogen ratio; Lignin/N: lignin to nitrogen ratio.

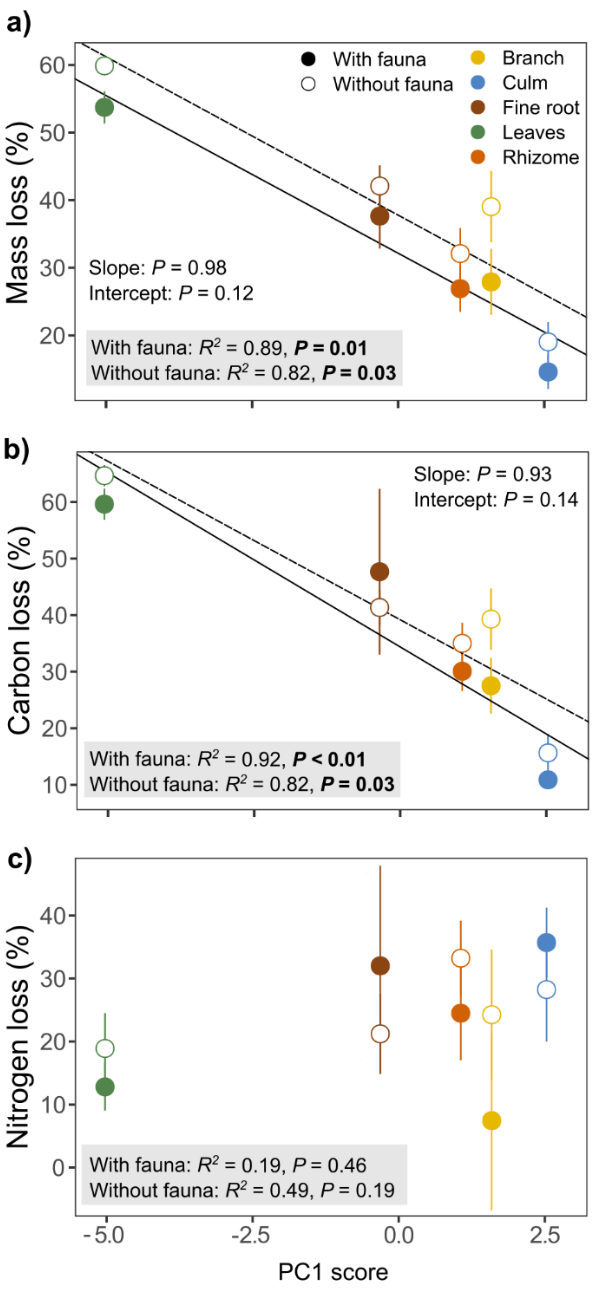

Figure 3.4 Relationships between litter type scores from the first PCA axis and litter mass loss (**a**), carbon loss (**b**), and nitrogen loss (**c**) after 720 days of litter decomposition. Regressions lines represent standardized major axis (SMA) regressions when relationships are significant ($P < 0.05$). Dashed lines indicate relationships in the absence of soil fauna while solid lines represent relationships in the presence of soil fauna. When these relationships are significant, differences in intercepts and slopes between these two lines are shown.

3.3.4 Soil fauna assemblage in bamboo organs during litter decomposition

A total of 2137 individuals were collected from the 1 mm litterbags and 23 groups of soil fauna were identified in this study. Five dominant fauna groups (Prostigmata mycophagous, Prostigmata predator, Collembola, Mesostigmata and Oribatida) contributed over 96% of total soil fauna abundance. There was a significant interactive effect between litter type and decomposition time on soil mesofauna abundance and richness (Figure 3.5; $P < 0.001$). The multiple comparisons showed that total mesofauna abundance and order richness were the highest in leaf litter, followed by rhizome and fine root litter, and were the lowest in branch and culm litter. The Shannon index varied significantly among litter types ($P < 0.001$) and decomposition time ($P < 0.001$), and similar to mesofauna abundance and order richness, diversity was the highest in leaf litter and the lowest in branch and culm litter (Figure 3.5).

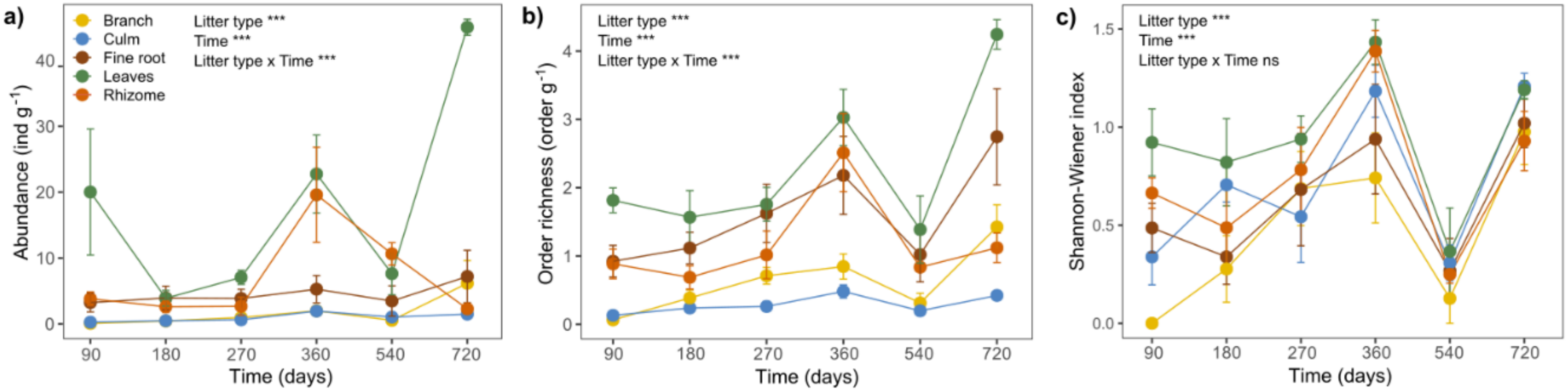

Figure 3.5 Effects of litter type and decomposition time on soil mesofauna a) abundance, b) order richness, and c) Shannon-Wiener diversity index. Significant effects are shown as: *P* < 0.05 *, *P* < 0.01 **, *P* < 0.001 ***, and ns: not significant.

3.4 Discussion

3.4.1 Litter quality effects on organ decomposability and litter C and N dynamics

Regardless of soil mesofauna presence, organ litter mass and carbon loss were well correlated with the variation in litter quality among organs. In this study, the PC1 scores derived from chemical and structural traits showed that litter quality was the highest in leaf litter and decreased for fine roots, rhizome, branch and culm litter. Specifically, litter mass and carbon loss of bamboo organs were positively correlated with initial nitrogen concentration, specific area, three dimensionality, and water holding capacity, and were negatively correlated with initial C/N ratio and lignin content. Litter nutrient concentration greatly affects decomposers' metabolism and influence the decomposability among organs (Cornwell et al., 2008; Manzoni et al. 2008). Furthermore, the significant correlation between litter specific area and three dimensionality with litter decomposition highlights the important role of morphological and structural traits in controlling whole-plant litter decomposability (Hobbie, 1996; Silver and Miya, 2001). In addition, litter microbial activity varied greatly among organs at all retrieval times. This is likely due to their contrasting litter qualities and also to differences in litter water holding capacity. Differences in the capacity of litter to retain moisture might be important for favoring the leaching of soluble compounds during early stages of decomposition, and for providing suitable conditions for microbial communities in later stages, especially during dry conditions.

In contrast to mass and carbon loss, nitrogen loss was not predicted by the overall variation of structural and chemical traits, instead it was negatively correlated with the initial nitrogen concentration only in the presence of soil fauna. Litter decomposition is generally limited by insufficient N and thus this element is a strong predictor of nitrogen immobilization and release during decomposition (Parton et al., 2007; Manzoni et al. 2008). In this study, all organs except for leaf litter had periods of higher N immobilization during decomposition. Given that culm, branch, rhizome and fine root litter had lower N concentrations (and higher C/N ratios) than leaf litter, it is likely that microbial decomposers translocated N from the soil environment to meet their nutrient requirements and thus immobilized N in the litter (Parton et al. 2007). Our results coincide with Lin et al., (2019), who found that N loss was not predicted by the interspecific variation in chemical and structural traits in leaf litter, but instead it was better explained by their initial N.

There were significant differences in C loss and net N release among bamboo organs. By the end of the decomposition period, leaf and fine root litter contributed to 60% of total carbon released by all organs, while culm litter only contributed to 7%. This further emphasized the role of culm litter in C storage in the long-term given the slow release of C during decomposition, similar to other CWD from tree logs (Harmon et al., 2004). As stated before, litter N dynamics were largely affected the initial litter N and C/N ratios. Litter with lower C/N ratios (47) such as leaf litter tended to have low or negligible N immobilization, while litter with higher C/N ratios (> 80) such as culm, rhizome, branch and fine root litter showed periods of high N immobilization. Interestingly, N immobilization occurred at different critical C/N ratios for each litter type. In culm litter, N was immobilized at C/N > 160, in branch and fine root litter at C/N > 97, and in rhizome litter at C/N > 109 (Figure S3.1). The critical C/N ratio for N immobilization might be determined by the C use efficiency and C/N of microbial decomposers. Thus, N immobilization at different critical C/N ratios indicates that different microbial communities were involved in the decomposition of bamboo organs (Manzoni et al., 2008). N immobilization was higher in rhizome and culm litter; however, their N net releases were the highest among the organs given that they had periods of higher N loss than the other litter types. Although the contribution of bamboo organs to N cycling might be better estimated by integrating both their N net release and rates of litter input, these results suggests that culm litter might be an important source of soil available N.

3.4.2 Soil fauna effects on trait-decomposability relationships

Although litter traits were well correlated with organ decomposability, this relationship was not significantly altered by the presence of soil fauna. It was initially expected that soil fauna effects on decomposition would be greater for high-quality organs (i.e., leaf litter) compared to low-quality organs (i.e., branch and culm litter). Instead, the contribution of soil fauna to litter decomposition and nutrient release did not interact with litter quality, but it was dependent on litter type and decomposition time. During the decomposition period, soil mesofauna did not affect the decomposability of root (medium quality), culm and rhizome litter (low-quality), but they decreased the decomposition rates and carbon loss of leaf (high-quality) and branch litter (low-quality) only at later stages. Previous studies have reported that differences in the contribution of soil fauna to above- and below-ground organs (leaves vs. root) may be related to their litter quality (i.e., nutrient content, palatability) (Fujii et al., 2018; Song et al. 2020). The results of this study showed that intraspecific litter quality was not a primary factor in determining the differences in the contribution of soil fauna to the decomposition of above- and below-ground bamboo litter. The importance of the decomposition stage in the soil fauna effects suggests that changes in litter quality during decomposition may have driven this late response. As microbial community composition changes during the decomposition process of plant litter (Liao et al., 2022), it is likely that such changes in litter quality along with the microbial communities over time can directly and indirectly modulate the decomposition process through changes in soil fauna communities.

Soil fauna is known to enhance and accelerate litter decomposition by promoting litter fragmentation or indirectly by interacting with microbial communities (Chapin et al., 2011; Garcia-Palacios et al., 2013). However, previous studies have also reported that the direction (positive or negative) and the magnitude of soil mesofaunal effects on decomposition can vary greatly depending on several factors (Kampichler and Bruckner, 2009). In this study, soil fauna had limited effects on the decomposition of culm, fine root and rhizome litter, while their presence decreased on average litter mass and carbon loss in leaf by 12% and 9%, respectively; and those in branch litter by 31% and 43%, respectively. This is partly in accordance with Lin et al. (2019), who found that soil meso- and macrofauna significantly decreased leaf litter mass loss in a Moso bamboo forest. One possible explanation for the negative faunal effects on decomposition in bamboo litter might be related to the dominance and abundance of mycophagous Prostigmata during the decomposition process. Prostigmata mites, many of which are microbe-consuming species can indirectly influence litter decomposition. Negative effects of soil mesofauna are usually attributed to a higher selective grazing that might lead to reducing microbial communities in the litter (Hättenschwiler and Gasser, 2005; Lussenhop, 1992). Although there were no significant effects of soil fauna on the litter respiration rates of leaf litter, there was a negative effect of soil fauna on the litter respiration of branch litter at the last retrieval time, which could indicate that the negative effects of soil mesofauna on litter mass and carbon losses might be related to the selective feeding on microbial decomposers by soil fauna.

3.5 Conclusion

This chapter evaluated the contribution of soil mesofauna to whole-plant litter decomposition in Moso bamboo. The results showed that decomposability of bamboo organs was highly correlated with their initial litter quality. In particular, chemical and structural traits predicted well litter mass and carbon loss but not nitrogen loss. Soil fauna did not alter the relationships between litter traits and decomposability, indicating that intraspecific variation in litter traits does not modulate the contribution of soil fauna to decomposition. Instead, the effects of soil mesofauna on litter mass and carbon loss depended on decomposition time and litter type. The presence of soil fauna decreased the mass and carbon loss in leaf and branch litter, with a larger negative impact on the latter. In contrast, soil mesofauna had no effects on bamboo litter net N release. The variations in the contribution of soil fauna to litter decomposition and C turnover among different organs highlights that considering soil fauna effects in whole-plant litter decomposition is essential to understand the role of soil decomposers in nutrient cycling in bamboo stands.

Chapter 4

Chemical and morphological controls on fine root litter decomposition

4.1 Introduction

Fine roots represent 14-30% of net primary production in terrestrial ecosystems (Jackson et al., 1997). The annual root litter input contributes largely to the carbon sequestered in the soil, and consequently root litter decomposition is an essential process for below-ground carbon and nutrient fluxes (Gill and Jackson, 2000; Silver and Miya, 2001).

Bamboo forests occupy large areas and are predominant in several ecosystems. In East Asia, bamboo forest expansion can impact ecosystem functions and biogeochemical cycles. Woody bamboos expand through underground rhizomes and have a very well-developed root system (Isagi et al., 1997). In bamboo stands, roots represent a major source of litter and can represent up to 30% of the total biomass (Shimono et al., 2022; Kobayashi et al., 2023). Below-ground processes such as root litter decomposition are crucial to predict soil carbon cycling. However, the mechanisms that control root litter decay within the fine root system are still poorly understood in bamboo forests.

Fine roots vary greatly in function and form: thin and more distal roots (low order) are involved in nutrient and water absorption, while thick and branched roots (high order) are primarily involved in transport and storage (McComarck et al., 2015). The functional and order-based approach determines important variations in root morphology and chemistry that are associated with litter decomposition (Beidler and Pritchard, 2017; Hishi, 2007). However, traits commonly associated with decomposability (greater concentrations of N, decreased diameter and lignin concentration) do not seem to predict decomposition across root orders. In fact, in several tree species, root litter decay tends to increase with branching order (Beidler and Pritchard, 2017; Goebel et al., 2011). One prevailing hypothesis suggests that low-order root recalcitrance might be related to their poor C quality and N inhibition during decomposition (Fan and Guo, 2010). Yet the specific components related to carbon quality and their relationship with root litter decay are not well understood.

Traditional litter quality indices such as C/N and lignin/N ratios can have limitations in predicting root litter decomposition because they represent the total amount of carbon and only a small fraction of recalcitrant compounds, respectively. In contrast, litter quality assessed by ^{13}C NMR spectroscopy can define different classes of organic C compounds, which can range from simple sugars and labile carbohydrates to more complex recalcitrant organic forms such as aliphatic and aromatic compounds (Kogel-Knabner, 2017). Moreover, previous studies showed that relative abundances of organic C compounds assessed by ^{13}C-NMR analyses are good predictors of litter decomposition (Bonanomi et al., 2013; Mathers et al., 2007; Ono et al., 2013).

The purpose of this chapter is to clarify the controlling factors affecting root litter decomposition within the root branching system in bamboo species. To better understand the effects of root morphology and chemistry in root litter decomposition, three common woody bamboo species in Japan were selected [Hachiku (*Phyllostachys nigra* var. *henonis*), Madake (*Phyllostachys bambusoides*) and Moso bamboo (*Phyllostachys edulis*)]. The specific objectives are: 1) clarify the morphological and chemical controls on root decomposition within root orders and species, 2) test whether organic C components (C functional groups and indexes using C-NMR) are good indicators of litter quality and correlate well with decomposition across different functional root orders. It was hypothesized that higher order roots will decompose faster than lower order roots and that this will be correlated to the higher concentration of O-alkyl C in higher order roots and higher content of aryl-C in lower order roots. In addition, differences in decomposition observed within the same root order could respond to potential chemical and morphological differences across bamboo species.

4.2 Materials and methods

4.2.1 Study sites and root collection

The study was conducted at the Hachiku, Madake and Moso bamboo stands located in Kasuya Research Forest of Kyushu University (Fukuoka, Japan). The average temperature and mean annual precipitation in these sites are 15.6 °C and 1650 mm, respectively. The Madake and Moso bamboo stands corresponded to completely bamboo dominated stands but with presence of some trees and understory vegetation. In the case of the Hachiku stand, the area selected was characterized by a mixed presence of trees and bamboo culms, and thus the culm density was lower compared to the other bamboo stands.

Several intact soil blocks (20 × 20 × 20 cm) were collected from each bamboo site in June 2021 and transported to the lab within 2 h of collection and frozen (-20°C) until later processing. Intact root branches were carefully washed and separated from the soil and classified into order classes following the method of Pregitzer et al. (2002). Given than the first two orders were very small and difficult to separate individually they were considered altogether as the 1 + 2 order. Thus, fine roots were separated into three functional classes: R1+2 (1st + 2nd), R3 (3rd), and R4 (4th order roots).

4.2.2 Root litterbag preparations and incubation

Oven-dried roots (0.500 – 0.900 g) were placed inside nylon litterbags (0.5 mm mesh). Root litter segments of each order were placed intactly in the litterbags, and thus the size of litterbags varied with the length of each order root class. Five replication plots were established at each site. All 180 litterbags (3 species × 3 root orders × 4 collection times × 5 replications) were vertically buried in the soil at a depth of 8 cm in August 2021. The litterbags were sequentially collected after 90 (November 2021), 210 (March 2022), 390 (September 2022) and 540 (February 2023) days.

4.2.3 Initial morphological and chemical traits

Morphological trait measurements were performed from an initial subset of root litter samples. Roots were scanned with an Epson GT-X980 scanner, then dried and weighed to a constant dry weight. Scanned images were analyzed using the RizhoVision Explorer software v.2.0.3 (Seethepalli et al., 2021) to generate measurements of average diameter (mm), specific root length (SRL, m g^{-1}), root tissue density (RTD, g cm^{-3}) and specific root area (SRA, cm^2 g^{-1}) for three replicates per root order and species.

Chemical analyses were performed from a separate set of initial root samples after these subsamples were oven dried and ground by mortar and pestle. Total C and N of initial root samples were measured using a CN Analyzer (Yanaco MT-700; Kyoto, Japan). Lignin content was determined by the gravimetric method of the thioglycolic acid (TGA) as described by Shimada et al. (2019). The recovery of lignin obtained by this method was confirmed by using standard lignin [lignin (alkaline) Nacalai Tesque, Kyoto, Japan]. Litter ash concentration was determined by ignition combustion in a muffle furnace at 600°C after 6 hours. All chemical concentrations were expressed in an ash-free dry mass basis.

4.2.4 Litter ^{13}C-NMR characterization

Fine powdered subsamples from initial root litter (not decomposed) were used for litter ^{13}C-NMR characterization in solid state. A composite root litter sample of 150-200 mg was obtained by mixing the subsamples of all replications (for each root order and species). A spectrometer (ECA-400, JEOL, Tokyo) was used, set up with a magic angle spinning of 16kHz, a recycle time of 1 s, contact time of 1 ms, acquisition time of 33.9 ms, and 30 000 – 45 000 scans. A broadening factor of 20 Hz was used in the Fourier transformation procedure.

Spectral regions and C types were selected based on previous NMR studies of leaf, root and wood litter (Bonanomi et al. 2013, Mathers et al. 2017). Thus, the following seven regions and C types were considered: 0-45 ppm (alkyl C), 45-60 ppm (methoxyl C), 60-90 ppm (O-alkyl C), 90-110 ppm (di-O-alkyl C), 110-140 ppm (H-C- substituted aromatic C), 140-160 ppm (O-substituted aromatic C) and 160-190 ppm (carboxyl C) (Table 4.1). The relative abundance of each region was determined based on the integration of peak areas in the NMR spectral regions. The calculated relative abundances were used to calculate the ratios of different decomposition indices based on previous literature (Bonanomi et al., 2013; Mathers et al., 2007): alkyl C (0-45 ppm)/O-alkyl C (60-90 ppm), O-alkyl C (60-90 ppm)/methoxyl C (45-60 ppm), aryl C (110-160 ppm)/O-alkyl C (60-90 ppm) and aryl C (110-160 ppm)/alkyl C (0-45 ppm).

Table 4.1 ^{13}C-NMR spectral assignment of C functional groups.

Chemical shift (ppm)	Assignment	Compounds included
0-45	Alkyl C	Terminal methyl (CH_3), long-chain aliphatics, fatty acids, waxes, cutins, suberins, lipids, hemicelluloses, acetate CH_3, polymethylene
45-60	Methoxyl C	-OCH_3, N-alkyl, amino acids
60-90	O-alkyl C	Carbohydrates, cellulose, hemicelluloses, polysaccharides, alcohols, amino sugars
90-110	di-O-alkyl C	Anomeric C1 of celluloses, tannin and lignin components
110-140	H-C-substituted aromatic C	Polyphenols, lignin and tannin components, C- and H-substituted aromatic C, olefinic C
140-160	O-substituted aromatic C	Phenols, lignin and tannin components, suberin O- and N- substituted aromatic C, olefinic C
160-190	Carboxyl C	Carboxylic acid (-COOH), amide and ester C, organic acids

4.2.5 Data analysis

Root litter morphological and chemical traits were evaluated by generalized linear models (GLM) to evaluate the effects of species, root orders and their interaction. Dynamics of litter mass remaining was evaluated by GLM, considering the effects of species, root order and decomposition time, as well as their interaction. For all GLM models, significant differences between groups were tested using Tukey's HSD post hoc test.

Litter decomposition rates (k) were calculated using a negative exponential model: $M_t = M_0e^{-kt}$, where M_0 is the initial litter mass, M_t, is the mass remaining after time t, and k is decay rate constant (Olson 1963). Univariate relationships were used to evaluate the relationships between litter decay rates (k) and litter morphological and chemical parameters (C and N concentrations, C/N and lignin/N ratios and data from C-NMR spectra). A principal component analysis (PCA) was performed for litter morphological, chemical and ^{13}C-NMR spectra regions independently. Then, multiple linear regression analyses were performed including the principal components derived by the PCA as independent linear combinations of the litter traits. All statistical analyses were performed with R version 4.0.2.

4.3 Results

4.3.1 Initial root litter morphological and chemical traits

Most morphological and chemical root traits depended on the interaction between root order and species. In general, with increasing order, root diameter and root tissue density increased (Figure 4.1a, d), while SRL and SRA decreased (Figure 4.1b, c). Among species, root diameter of R4 was lower in Moso bamboo roots, while SRL of R1+2 was significantly higher in Madake roots. Root tissue density of Hachiku roots was significantly higher across all root order classes.

Carbon content did not differ among root orders, but rather differed across species (Figure 4.2a). Nitrogen content decreased with increasing root order (Figure 4.2b), while C/N and lignin/N ratios increased with increasing root order (Figure 4.2c, d). Differences in N content, lignin/N and C/N ratios across species were observed in R3 and R4. For these particular root orders, the differences in chemical traits indicate that Madake root are more chemically labile, while Moso bamboo roots are more chemically recalcitrant.

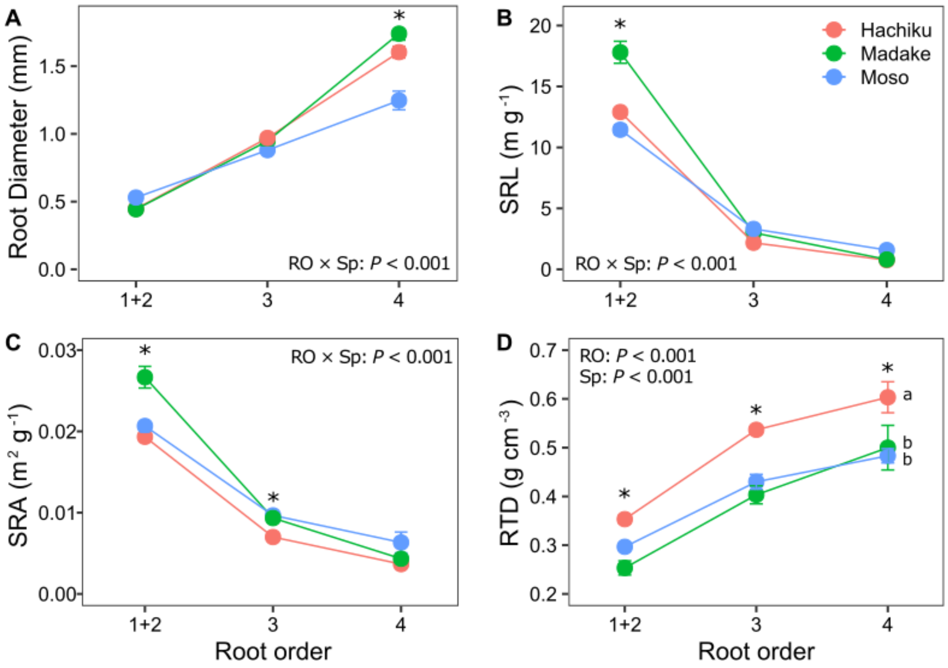

Figure 4.1 Morphological characteristics of Hachiku, Madake and Moso bamboo fine root systems (average ± SE, *N* = 3). Asterisk (*) indicates significant differences across species for each root order when interaction Root Order (RO) × Species (Sp) is significant ($P < 0.05$). Letters indicate differences across species when Species effect is significant ($P < 0.05$).

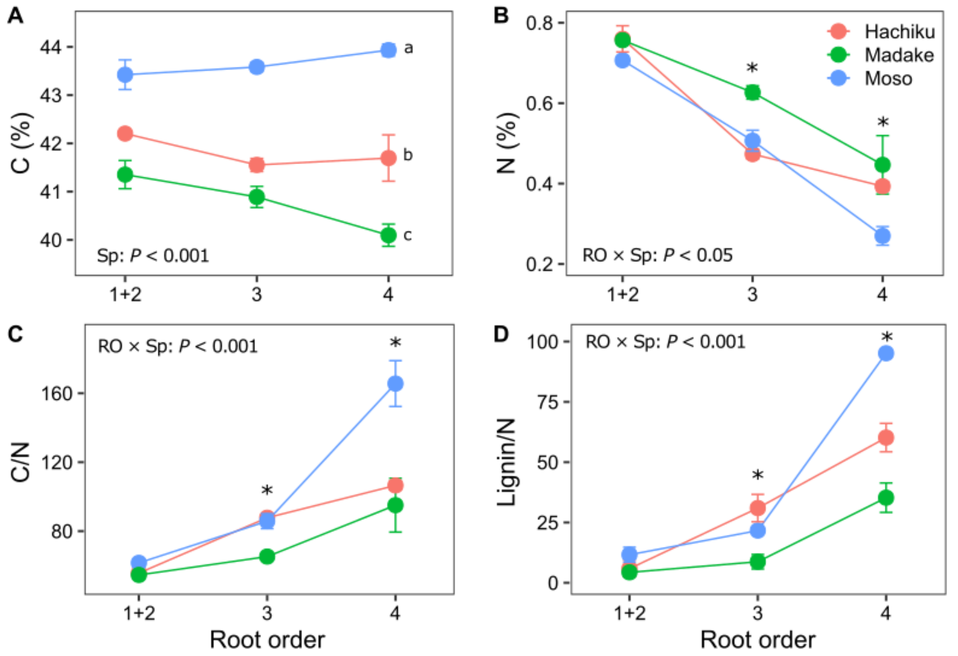

Figure 4.2 Chemical characteristics of Hachiku, Madake and Moso bamboo fine root systems (average ± SE, *N* = 3). Asterisk (*) indicates significant differences across species for each root order when interaction Root Order (RO) × Species (Sp) is significant ($P < 0.05$). Letters indicate differences across species when Species effect is significant ($P < 0.05$).

4.3.2 Litter ^{13}C-NMR characterization

Peak positions of the solid-state ^{13}C-NMR spectra for the initial root litter were similar among species (Fig. 4.3). These major peaks were observed at 22, 30, 56, 65, 73, 84, 105, 116, 130, 148, 153, 159 and 172 ppm. Differences in major peaks among roots orders were observed in the Alkyl C region (0-45 ppm) and the O-alkyl C region (60-90 ppm). The peak at 73 ppm in R4 were higher than those of R1+2 and R3, while peaks at 30/31 ppm were higher in R1+2 and R3 (Fig. 4.3). In addition, in Moso bamboo roots, the peaks at 83 and 105 ppm in the R4 were higher than those of R1+2 and R3 (Fig. 4.3c).

In general, O-alkyl C was the predominant component of root litter, accounting for 43.8-48.5% of the NMR spectra, followed by H-C- substituted aromatic C (11.7-14.2%), di-O-alkyl C (12.0-12.9%), alkyl C (8.0-9.2%), O-substituted aromatic C (6.1-7.3%), carboxyl C (5.9-7.2%) and methoxyl C (5.7-6.7%) (Table 4.2).

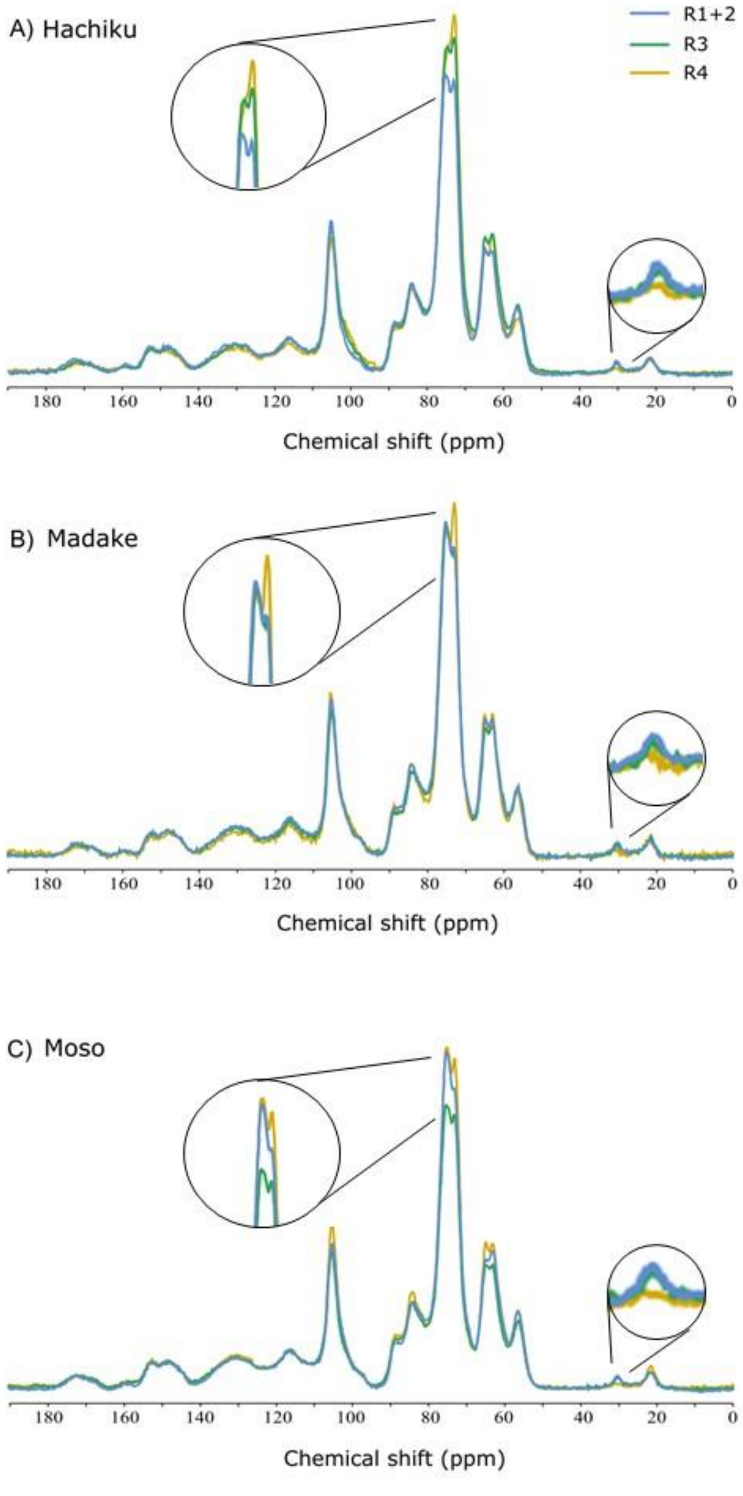

Figure 4.3 ^{13}C-NMR spectra of three root order classes (R1+2, R3 and R4) from initial samples of: **A**) Hachiku, **B**) Madake and **C**) Moso bamboo roots.

Table 4.2 Relative abundance (%) of main classes of organic C assessed by ^{13}C-NMR spectroscopy and NMR indices of initial root litter.

		Relative abundance (%)							NMR Index			
Species	Root order	Alkyl C (0-45 ppm)	Methoxyl C (45-60 ppm)	O-alkyl C (60-90 ppm)	di-O-alkyl C (90-110 ppm)	H-C-aromatic C (110-140 ppm)	O-aromatic C (140-160 ppm)	Carboxyl C (160-190 ppm)	Alkyl C/O-alkyl C ratio	O-alkyl C/methoxyl C ratio	Aryl C/O-alkyl C ratio	Aryl C/Alkyl C ratio
Hachiku	R1+2	8.85	5.94	44.47	12.37	13.78	7.34	7.24	0.199	7.49	0.372	2.39
	R3	8.81	6.51	46.46	12.26	12.93	6.61	6.42	0.190	7.13	0.333	2.22
	R4	8.53	5.75	47.32	12.70	12.30	6.65	6.75	0.180	8.22	0.316	2.22
Madake	R1+2	8.07	6.05	47.65	12.56	13.23	6.50	5.94	0.169	7.87	0.328	2.44
	R3	8.49	6.19	47.25	12.39	12.96	6.54	6.19	0.180	7.63	0.327	2.30
	R4	8.54	5.77	48.56	12.92	11.76	6.11	6.34	0.176	8.42	0.291	2.09
Moso	R1+2	8.58	6.69	46.38	12.04	13.60	6.69	6.02	0.185	6.93	0.347	2.36
	R3	9.29	6.31	43.81	12.16	14.22	7.22	7.00	0.212	6.95	0.383	2.31
	R4	8.64	6.40	45.68	12.27	13.55	6.94	6.51	0.189	7.13	0.354	2.37

Alkyl C/O-alkyl C: [0-45 ppm]/[60-90 ppm], O-alkyl C/Methoxyl C: [60-90 ppm]/[45-60 ppm], Aryl C/O-alkyl C: [110-160 ppm]/[60-110 ppm], Aryl C/Alkyl C: [110-160 ppm]/[0-45 ppm]

4.3.3 Litter decomposition dynamics

Root litter mass loss varied among root orders ($P < 0.01$) and species ($P < 0.001$) (Table 4.3). Root litter mass loss was rapid for R4 and slower for R3 and R1+2 order roots. Differences in decomposition among root orders were large especially at initial stages. During the first 90 days, mass loss was 13 ± 1.4% in order R1+2, 13 ± 1.2% in R3, and 20 ± 1.2% in R4. After 540 days, mass loss was 63 ± 1.8% in order R1+2, 60 ± 1.9% for R3, and 61 ± 1.6% for R4. Root order explained a larger proportion of the variation in root litter mass loss in Hachiku and Madake compared to Moso bamboo (Table 4.3).

On average, litter mass loss was greater for Madake roots, followed by Hachiku roots, and lower for Moso bamboo roots. Species effects were significant across all root orders; however, greater differences in decomposition rates among species were observed in the R4 (Figure 4.4). Hachiku, Madake and Moso bamboo root litter decay rates (yr^{-1}) were 0.29, 0.34 and 0.22 respectively for R1+2; 0.30, 0.43, and 0.24, respectively for R3; and 0.40, 0.48, and 0.23, respectively for R4.

Table 4.3 Results of GLM evaluating the effects of species, root orders, time and their interactions on root litter mass remaining after 540 days of decomposition.

Variables	*d.f.*	*F-value*	*P-value*
All litter			
Species (Sp)	2	36.3	**<0.0001**
Root order (RO)	2	8.3	**<0.001**
Time (T)	3	85.0	**<0.0001**
Sp × RO	4	1.2	0.31
Sp × T	6	2.4	**0.03**
RO × T	6	1.4	0.20
Sp × RO × T	12	0.4	0.94
Hachiku			
Root order (RO)	2	7.9	**<0.001**
Time (T)	3	30.6	**<0.0001**
RO × T	6	0.5	0.77
Madake			
Root order (RO)	2	5.3	**<0.01**
Time (T)	3	34.2	**<0.0001**
RO × T	6	0.4	0.85
Moso			
Root order (RO)	2	4.1	**0.02**
Time (T)	3	46.4	**<0.0001**
RO × T	6	0.5	0.76

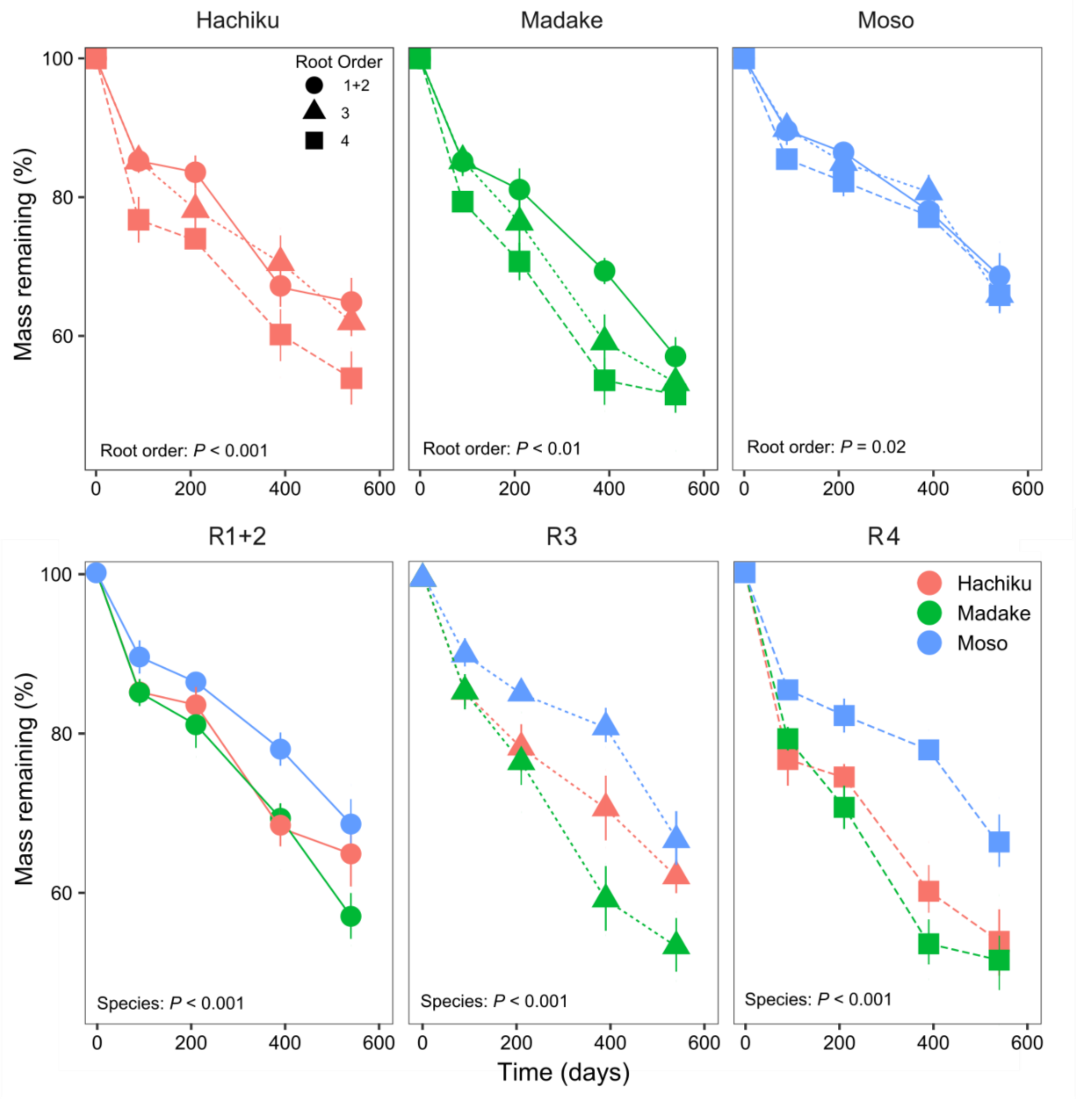

Figure 4.4 Dynamics of litter mass remaining in different root order classes (R1+2, R3 and R4) of Hachiku, Madake and Moso bamboo roots during 540 days of decomposition. (average ± SE, N = 5).

4.3.4 Relationships between root litter decay rate and litter quality

The principal component analysis provided a good characterization of root litter morphological and chemical traits across species and root orders, with the first three components accounting for 94% (70.4%, 16.9%, and 7.0%, respectively) of the total variance (Fig. 4.5a). The multiple regression analysis based on the scores from the first three components of both the litter chemical and the morphological and chemical traits provided good predictive models (Table 4.5). In particular, PC2 scores from both models were good predictors of litter decay rates, which suggests that k was negatively affected by increased C concentration in root litter.

Univariate relationships between individual litter morphological traits showed no significant correlations with root litter decay rates ($P > 0.05$). Among chemical traits, root litter decay was negatively correlated with initial C ($r = -0.82$, $P < 0.01$), while there was no correlation with initial N and lignin content ($P > 0.05$). The initial C/N and lignin/N ratios of root litter showed no correlation with litter decay rates (Figure 4.6).

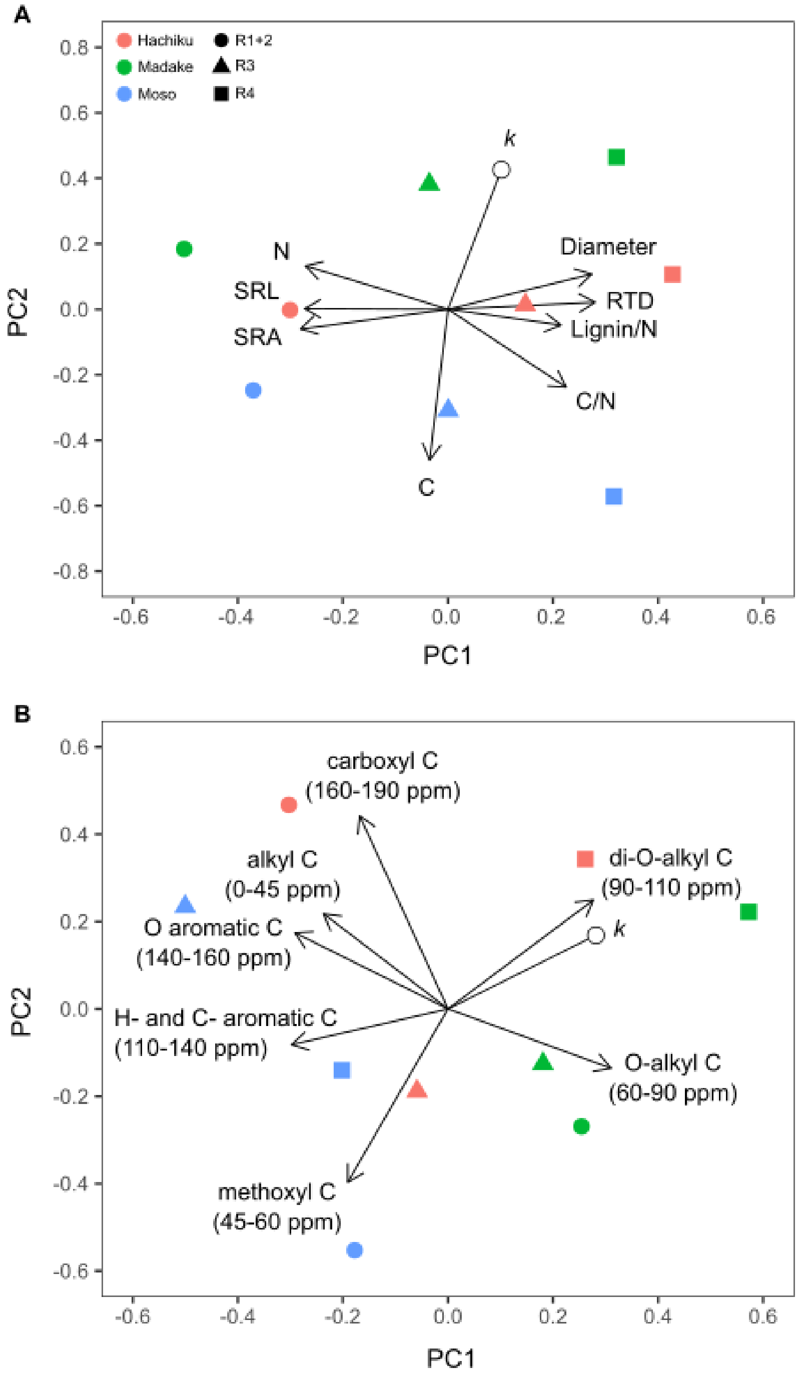

Figure 4.5 Principal component analysis of root litter morphological and traditional chemical traits (**A**), and ^{13}C-NMR spectral regions (**B**). Litter decomposition rates (*k*) is also plotted as a supplementary variable.

Table 4.4 Results of multiple regressions between root litter decomposition rates (*k*) and linear combinations of litter morphological, chemical and ^{13}C-NMR spectral regions. Independent predictive variables in the models correspond to the first three principal components (PC) in the ordination of chemical and morphological traits (multiple R^2 = 0.86 , F = 12.30, P = 0.03), morphological traits (multiple R^2 = 0.44, F = 1.30, P = 0.37), chemical traits (multiple R^2 = 0.80, F = 10.46, P = 0.04), and ^{13}C-NMR spectra regions (multiple R^2 = 0.84, F = 8.92, P = 0.01).

Independent variables	*B*	SE	*t*	*P*
Morphological and chemical traits model				
Intercept	0.33	0.03	23.89	**<0.001**
PC 1	-0.01	0.01	-1.79	0.13
PC 2	-0.07	0.01	-5.80	**<0.01**
PC 3	-0.00	0.04	-0.25	0.81
Morphological traits model				
Intercept	0.33	0.03	11.00	**<0.001**
PC 1	-0.02	0.02	-1.18	0.29
PC 2	0.11	0.07	1.56	0.18
PC 3	-0.02	0.09	-0.24	0.82
Chemical traits model				
Intercept	0.33	0.01	25.67	**<0.001**
PC 1	-0.01	0.01	-0.69	0.52
PC 2	-0.08	0.01	-6.36	**<0.01**
PC 3	-0.03	0.02	-1.56	0.17
^{13}C-NMR model				
Intercept	0.33	0.02	20.80	**<0.001**
PC 1	0.04	0.01	4.62	**<0.01**
PC 2	-0.03	0.01	-2.22	0.078
PC 3	0.02	0.02	0.71	0.511

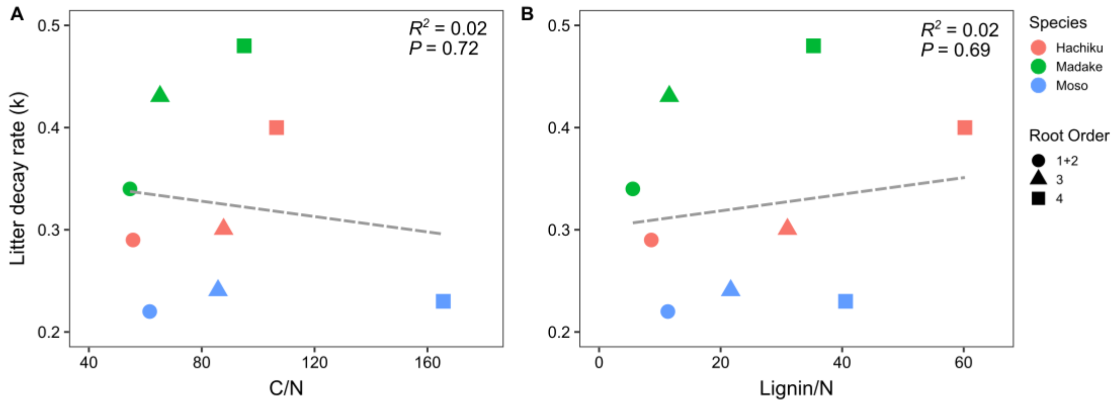

Figure 4.6 Relationships between litter decay rates (*k* [yr^{-1}]) and C/N (**A**) and lignin/N (**B**) ratios of three root order classes and species.

The principal component analysis showed a good ordination of the ^{13}C-NMR spectral regions of root litter across species and root orders (Fig. 4.5b). The first three components accounted for 99% (65%, 27%, and 7%, respectively) of the total variance. The multiple regression model based on the scores of these components provided a highly significant linear model, with a high predictive power of root litter decomposition rates from PC1 scores (Table 4.5), which indicates that *k* was positively affected by a higher relative abundance of di-O-alkyl C and O-alkyl C, and negatively influenced by a higher relative abundance of alkyl C, O aromatic C and H- and C- aromatic C.

Litter decay was not significantly related to two ^{13}C-NMR regions (alkyl C and carboxyl C). A significant positive correlation was found between root litter decomposition rates and O-alkyl C ($r = 0.76$, $P < 0.05$) and di-O-alkyl C regions ($r = 0.87$, $P < 0.01$), whereas a negative correlation was found with methoxyl C ($r = -0.74$, $P < 0.05$), H-C-substituted aromatic C ($r = -0.86$, $P < 0.01$) and O-substituted aromatic C ($r = -0.71$, $P < 0.05$). Regarding the decomposition indices based on the C-NMR spectra, root litter decay rate was positively correlated with the O-alkyl C/methoxyl C ratio ($r = 0.89$, $P < 0.01$) and negatively correlated with the aryl C/O-alkyl C ratio ($r = -0.77$, $P < 0.05$) (Figure 4.7)

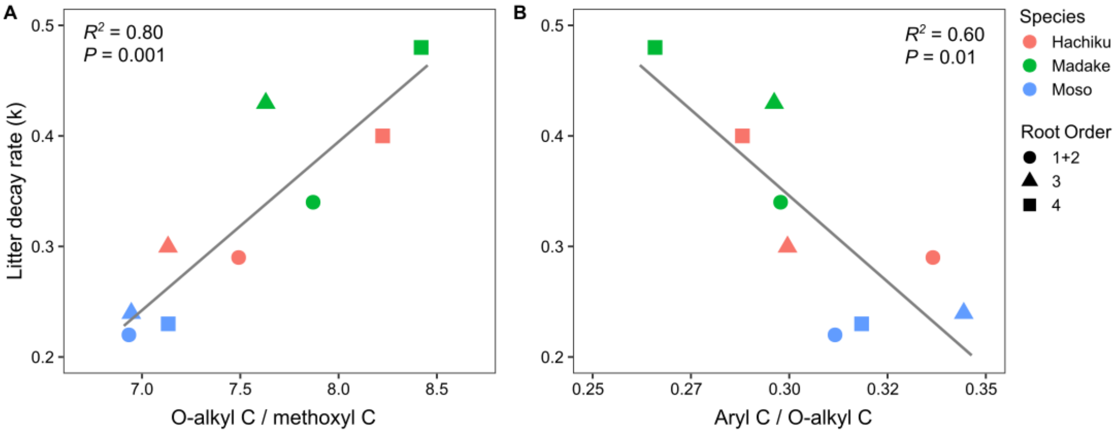

Figure 4.7 Relationships between litter decay rate (*k* [yr^{-1}]) and indices from ^{13}C-NMR spectra: O-alkyl C (60-90 ppm)/methoxyl C (45-60 ppm) (**A**) and Aryl C (110-160)/ O-alkyl C (60-110 ppm) (**B**) ratios of three root order classes and species.

4.4 Discussion

4.4.1 Morphological and chemical heterogeneity of bamboo fine roots

Significant variations were observed in both morphological and chemical traits among different root orders, although some of these differences depended on bamboo species. Generally, root diameter, tissue density, lignin content and C/N ratio increased with root order, while SRL, and N content decreased with root order, which is consistent with previous studies on morphological and chemical traits across branching orders in tree roots (Guo et al., 2004; Pregitzer et al., 2002; McComarck et al., 2015). These results further indicate that the fine root system in Hachiku, Madake and Moso bamboo can be classified into thin nutrient-rich absorptive roots and thick nutrient-poor transportive roots. Similar to other woody plant species, relying on a single diameter value for fine root classification in woody bamboos would oversimplify and overlook functional traits that account for substantial variability in root morphology or tissue chemistry within the fine root system. Therefore, taking into account the fine root heterogeneity might provide valuable insights into fine root C allocation and below-ground processes in bamboo stands.

4.4.2 Root litter characterization by ^{13}C-NMR spectra

Root litter characterization by ^{13}C-NMR spectra showed differences in peak values primarily in two C regions among root orders. In the O-alkyl C region (60-90 ppm), associated with sugars and polysaccharides, higher peaks at 73 ppm were observed in higher order roots (R4) across all species. The higher relative abundance of carbohydrates in higher order roots is likely related to their storage function. Consistent with previous studies, higher order roots of tree species have been characterized by increased concentrations of non-structural carbohydrates (NSC) and cellulose (Fan and Guo, 2010; Sun et al., 2018; Guo et al., 2004).

In the alkyl C region (0-45 ppm), characteristic of lipids, waxes and long chain aliphatic structures, the peaks at 30 ppm were higher for the lower root orders (both R1+2 and R3). The relative intensity of methylene carbon in this region indicates the presence of suberin (Angst et al., 2016), which forms lipid barriers in the distal and thinner roots to protect against biotic and abiotic stress (Chen et al., 2022). The higher presence of this compound in lower orders roots coincides with previous studies reporting high concentrations of acid unhydrolyzable fraction (AUF) in the first and second order roots, which includes aliphatic components and defensive compounds (Fan and Guo, 2010; Xiong et al., 2013).

The descriptive analysis using ^{13}C-NMR provided valuable insights into the biochemical differences among root orders. Interestingly, this study found no significant differences in total C concentration across root orders, emphasizing the limitations of only considering the total amount of organic carbon, which fails to take into important biochemical characteristics of fine roots (Bonanomi et al., 2013). Litter characterization by ^{13}C-NMR spectra allowed a more comprehensive (semi-quantitative) description of carbon quality among root orders and further highlights differences in specific organic compounds within the fine root branching system.

4.4.3 Controls of root litter decomposition across orders and species

The results showed that lower order roots decompose at a slower rate compared to higher order roots in woody bamboo species. This observation is consistent with previous studies in several temperate and subtropical tree species (Fan and Guo, 2010; Goebel et al., 2011, Xiong et al., 2013; Sun et al., 2016; Sun et al., 2018; Wang et al., 2019). The patterns of decomposition among root orders in this study are strongly in line with the C quality hypothesis, which suggests that lower order roots decompose more slowly due to their poor C quality (Beidler and Pritchard, 2017). In this study, root litter decay rate was positively correlated with the O-alkyl and di-O-alkyl C regions. For instance, higher order roots of Madake and Hachiku bamboo were characterized by a higher relative abundance of O-alkyl C compounds, represented by cellulose, hemicellulose and polysaccharides, which are easily degradable and lost rapidly during early stages of decomposition. In contrast, root litter decomposition rates were negatively correlated with the aryl C regions, and the methoxyl C region. The higher relative abundance of aromatic and methoxyl compounds in lower order roots suggests that the recalcitrance of the finest roots in woody bamboos is related to their higher content of lignin and tannins. Previous studies found that root litter decay rates in the branching root system were positively correlated with NSC (Fan and Guo, 2010) and negatively correlated with initial concentrations of AUF and condensed tannins (Sun et al., 2013).

In this study, Moso bamboo roots decomposed slower than Hachiku and Madake roots, which is consistent with the common paradigm of nitrogen-poor litter and the limitation of microbial growth and metabolism during decomposition (Berg and McClaugherty, 2008). Differences in decomposition rates across species were in accordance with litter chemical recalcitrance as shown by their C/N and lignin/N ratios. However, the correlations between decomposition rates and root N concentrations across species contrasted with the no significant relationships between decomposition rates and N content among root orders. This further reinforces the limits of traditional decomposition indices from proximate analysis in describing litter quality and predicting fine root decomposition (Beidler and Pritchard, 2017; Bonanomi et al., 2013).

Regarding the morphological control over litter decomposition rates, it would be expected that the large surface area (higher SRA), length (SRL) and small diameter of lower order roots would be associated with rapid decomposition rates (Goebel et al., 2011). Although significant differences in key morphological traits were found across species and orders, they were limited in predicting root litter decay rates in this study. In contrast, the chemical traits were the predominant controls of decomposition and specifically the statistical model from principal components of the spectral regions showed highly significant predictions of litter decay rates. In particular, the O-alkyl C/methoxyl C and aryl C/ O-alkyl C indices derived from the C-NMR spectra explained 60 to 80% of the variance in root litter decay rates. These indices represent the ratio between labile (carbohydrates)/recalcitrant (lignin) compounds and recalcitrant (lignin, tannins, phenols)/labile (carbohydrates) compounds, respectively. Therefore, litter organic C characterization has the potential to provide a more predictive descriptions of litter decomposition rates across species and root branching orders.

4.5 Conclusion

Using a functional order approach, the results of this chapter showed that lower order roots of woody bamboo species had slower decomposition rates compared to higher order roots. The branching orders in these species integrated well significant differences in morphological and traditional chemical traits; however, these traits did not fully explain the variability in decomposition rates within the branching root system. Root litter characterization by ^{13}C-NMR spectra had the highest predictive power over root litter decomposition across species and root orders. Specifically, the low decomposability of lower order roots was associated with their higher relative abundance in the aromatic C regions and their lower relative abundance in the O-alkyl and di-O-alkyl C regions. This study further highlights the importance of considering the fine root heterogeneity in woody bamboos and the variations in carbon quality among branching orders for accurate predictions of below-ground processes. Given that lower order roots are short-lived and constitute a significant proportion of the fine root biomass, their slower decomposition rates might have substantial implications for soil carbon cycling in bamboo stands.

Chapter 5

Dead bamboo culms and soil fauna effects on leaf litter decomposition

5.1 Introduction

Coarse woody debris (CWD) is an important element in forest ecosystems and directly contributes to biogeochemical processes as a long-term carbon reservoir (Harmon et al., 2004; Magnússon et al., 2016). CWD may indirectly impact ecosystem processes by modifying the surrounding soil environment and, by extension, releasing additional carbon and nutrients in the soil (Gonzalez-Polo et al., 2013; Kappes et al., 2007; Magnússon et al., 2016). CWD can influence soil microclimatic conditions such as temperature and moisture (Boggs et al., 2020; Perreault et al., 2021). In addition, soluble compounds leached from CWD into the soil may alter soil chemistry and benefit microbial decomposers (Peršoh and Borken, 2017; Spears et al., 2003). Previous studies reported that soils near CWD have relatively higher microbial biomass and enzymatic activity (Gonzalez-Polo et al., 2013; Minnich et al., 2021). The modifications in soil biota and physicochemistry mediated by CWD can accelerate carbon mineralization in the soil and the litter layer (Peršoh and Borken, 2017). In temperate forests, previous studies showed that CWD promotes a rapid leaf litter decomposition near their surroundings, suggesting that the removal of CWD components would have significant impacts on biogeochemical cycles through their indirect effects on litter decomposition (Gonzalez-Polo et al., 2013; Remsburg and Turner, 2006).

Soil fauna play important roles in litter decomposition mainly by interacting with soil microbial communities and contributing to litter fragmentation (Petersen and Luxton, 1982; Seastedt, 1984). Soil invertebrates in the litter layer may respond to the changes in habitat structure and moisture conditions caused by CWD (Hanula et al., 2006; Johnston and Crossley, 1993). For instance, some microathropod groups, such as Oribatida, Collembola, and Coleoptera, are relatively more abundant in the litter layer near decomposing logs (Evans et al., 2003; Ulyshen et al., 2011; Ulyshen and Hanula, 2009). Previous studies have reported high densities of predators and detritivores near CWD, likely related to the resource availability and litter accumulation around logs (Castro and

Wise, 2010; Jabin et al., 2004; Kappes et al., 2007; Ulyshen et al., 2011). CWD can influence the spatial distribution of microarthropods in the litter layer (Castro and Wise, 2010; Evans et al., 2003), and particularly may alter decomposition by modulating faunal decomposer communities (Kappes et al., 2007). Thus, in the presence of CWD, soil fauna might make a comparatively greater contribution to litter decomposition and nutrient mineralization than on areas of the forest floor where CWD is absent.

In many temperate and (sub)tropical ecosystems, woody bamboos form monospecific dense stands and can substantially affect ecosystem processes. Moso bamboo (*Phyllostachys edulis*) is a rapid-growing and tree-like stature bamboo commonly planted for the production of timber and edible shoots in East Asian countries (Canavan et al., 2017; Song et al., 2011). In certain regions, previously managed stands have been abandoned, and as a consequence, the coverage area of unmanaged bamboo stands has rapidly increased in recent years (Isagi and Torii, 1997; Suzuki, 2015). Managed stands are regularly thinned to maintain low densities and in addition, standing old culms (stems) and fallen dead culms on the forest floor are frequently removed (Song et al., 2011). By contrast, in unmanaged stands, culm senescence and self-thinning likely occur due to higher stand densities (> 8,000 ind. ha^{-1}) (Liu et al., 2016; Yin et al., 2019), resulting in large amounts of dead culms accumulated on the floor (Shimono et al., 2021). Isagi et al. (1997) reported that Moso bamboo stands can accumulate dead culms at a rate of ~7 t ha^{-1} yr^{-1}. Owing to their recalcitrant nature, dead bamboo culms decompose slowly and are important carbon and nutrient reservoirs (Liu et al., 2015; Shimono et al., 2021; Ugawa et al., 2011). However, it is not known to what extent dead bamboo culms on the forest floor could indirectly influence leaf litter decomposition and nutrient dynamics by altering soil conditions and decomposer communities in the litter layer. Given the long-term persistence of fallen culms on the forest floor, it is essential to understand the contribution of dead culms to carbon and nutrient cycling, particularly as abandoned Moso bamboo stands continue to expand.

The aim of this chapter is to assess the interactive contributions of dead culms and soil fauna on leaf litter decomposition in an unmanaged Moso bamboo stand. The presence of dead culms and soil mesofauna were controlled in order to evaluate their impact on leaf litter mass, carbon and nitrogen loss, and microbial activity (litter respiration rates). In addition, the influences of dead culms on soil environmental conditions and soil mesofauna assemblage in the decomposing litter were also explored. Soil fauna communities in leaf litter may be altered by the presence of coarse woody debris (CWD) on the forest floor. Thus, it was hypothesized that dead culms and soil fauna will synergistically affect leaf litter decomposition (Figure 5.1). Specifically, it was expected that litter mass, carbon and nitrogen loss, and litter respiration rates would be relatively higher under the dead culms, primarily owing to the favorable soil microclimate conditions and enhanced soil fauna abundance and diversity in the litter decomposing beneath the culms.

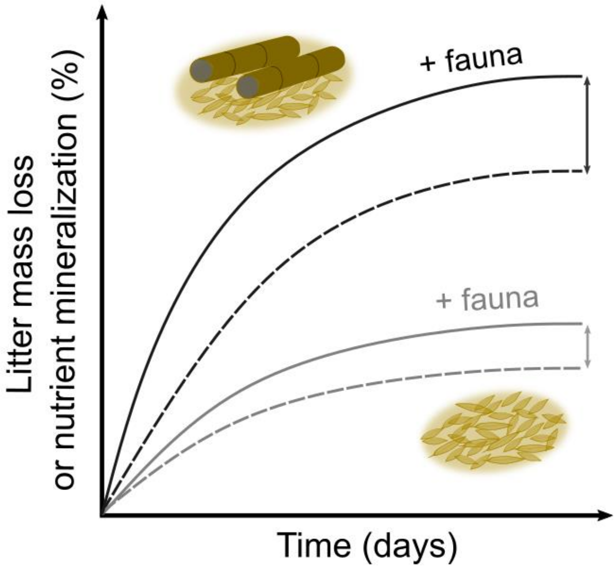

Figure 5.1 A conceptual framework of leaf litter mass loss and nutrient release beneath dead bamboo culms (black lines) and on the forest floor (gray lines) under two soil fauna treatments: with mesofauna (solid lines) and without mesofauna (dashed lines).

5.2 Materials and methods

5.2.1 Study site

A litter decomposition experiment was set up in an unmanaged Moso bamboo (*Phyllostachys edulis*) stand in Kasuya Research Forest, Kyushu University, Kyushu Island, Japan. In this location, the mean annual precipitation is 1650 mm, 50 % of which falls during the rainy season from July to September. The mean annual temperature is 15.6 °C, with minimum and maximum temperatures in January (3 °C) and August (32 °C), respectively (Japan Meteorological Agency, 2019). The bamboo stand is located near an invaded broadleaf forest. Nevertheless, we established the decomposition experimental plots in a bamboo-dominated area, where the average stand density and DBH (diameter at breast height) were 7500 culms ha^{-1} and 10.83 cm, respectively.

5.2.2 Experimental design

Standing dead culms of Moso bamboo (*Phyllostachys edulis*) were collected to measure their effects on leaf litter decomposition. The culms had an average diameter of 8.6 cm (± 1.46 S.D.) and were cut into segments 60–80 cm in length. The effects of soil mesofauna were evaluated using 1-mm and 42-µm mesh size litterbags. The former allowed soil mesofauna to enter while the latter restricted their entrance. The mesh sizes were selected based on the fact that mesofauna body sizes are in the range of 100 µm to 2 mm (Swift et al., 1979). Moso bamboo leaf litter was collected from litter traps and the forest floor after litterfall in April and May. About 3 g dry weight (DW) leaf litter was placed inside each 10 cm × 10 cm litterbag. Five replicate plots (2 m × 2 m) were established in the bamboo stand. At each plot, three or four dead culm segments were placed close to each other occupying approximately 2400 cm^2 (30 cm × 80 cm) on the forest floor. These areas represented the ‘dead culm’ treatment, whereas areas of the forest floor 1 m distant from the dead culms represented the ‘control’ treatment. Then, litterbags with and without soil mesofauna were placed beneath the dead culms and on the forest floor (control), respectively. In total, 120 leaf litterbags (two treatments × two mesh sizes × six collection times × five replicates) were prepared. The decomposition experiment was set up in June 2019 and the litterbags were collected after 90 d (September 2019), 180 d (December 2019), 270 d (March 2020), 360 d (June 2020), 540 d (December 2020), and 720 d (June 2021).

5.2.3 Soil microenvironmental conditions

Soil surface temperature and moisture content were measured from June 2019 to July 2020 to identify any differences in soil microenvironmental conditions between the dead culms and the forest floor. At each plot, soil moisture was measured using a 5-cm depth probe (ML3 Theta Probe; Delta-T Devices, Burwell, UK) placed under the dead culms and on the forest floor (control). Every hour, soil surface temperature was measured in a representative plot with a temperature logger (TR-71wb; T&D Co. Ltd., Matsumoto, Japan). Sensors were buried to 3–4 cm depth under the dead culms and the control area. As a consequence of battery malfunction, no data could be collected between March 3, 2020 and June 1, 2020.

5.2.4 Litter respiration measurements

After each collection, the litterbags were cleaned of soil particles, and brought to the laboratory where the litter respiration rates were measured in a closed dynamic chamber fitted with an infrared gas analyzer (IRGA; GMP343; Vaisala Group, Vantaa, Finland). CO_2 efflux was measured inside a room at constant air temperature (25 °C) within the first 6 h after collection. The sample temperatures were measured with an infrared thermometer. Each leaf litter sample was enclosed in the chamber for ~3 min. The litter respiration rates were calculated from the slope of the linear increase in CO_2 concentration inside the chamber and expressed as nmol CO_2 per unit litter dry mass (g) per unit time (s) (Katayama et al., 2021).

5.2.5 Soil fauna community in the leaf litter

Immediately after the litter respiration measurements, leaf litter from the 1-mm mesh litterbags was placed in a Tullgren extractor for 5-7 d to collect any soil mesofauna. The fine-mesh litterbags were not used for soil faunal extraction because a previous litter decomposition study showed no evidence of mesofauna presence in small mesh size litterbags (Homet et al., 2021). Invertebrates were identified to order level, except for Acari, which were classified to the suborder level (Krantz and Walter, 2009). The mesofauna orders and suborders were categorized into the following functional groups: detritivores, predators, omnivorous, fungivorous, and saprophagous (Adl, 2003). The relative densities of the individuals and the soil fauna orders were expressed as the number of individuals and orders per gram-dried litter, respectively. The Shannon-Wiener diversity index was calculated as: $H' = -\sum_{i=1}^{S} p_i \, ln \, p_i$, where p_i = (number of individuals per order / total number of individuals), and S = order richness.

5.2.6 Litter mass, carbon and nitrogen loss

Litter samples were oven-dried to a constant weight at 70 °C for 48 h to determine their initial dry mass before incubation (M_0) and their dry mass at each collection time (M_t). Litter mass loss (%) was calculated as: $(M_0 - M_t)/M_0 \times 100$. Dried leaf litter samples were ground and homogenized, and their carbon and nitrogen content were measured using a CN analyzer (Yanaco MT-700; Kyoto, Japan). Carbon and nitrogen loss (%) were determined using the formula: $[(M_0 \times C_0) - (M_t \times C_t)]/(M_0 \times C_0) \times 100$, where M_0 is the initial litter dry mass, M_t is the dry mass of decomposed litter at time t, C_0 is the initial concentration of carbon or nitrogen (% of the litter dry mass), and C_t is the concentration of carbon or nitrogen in the decomposing litter at time t. In addition, litter C/N ratios of initial representative samples ($N = 5$) and all litter samples were determined after each collection.

5.2.7 Data analysis

Linear mixed-effect models (LMMs) were performed to determine the effects of dead culms, soil fauna, decomposition time, and their interactions on the losses of litter mass, carbon and nitrogen, and C/N ratio. To account for the spatial structure of the experimental design, soil fauna nested into dead culm treatment, and the latter two nested into plots were included as the random effect. To account for the temporal correlation and the effect of consequent litterbag collections on litter mass, carbon and nitrogen loss and C/N ratio, decomposition time was considered as a continuous covariate in the LMMs. The effects of treatments on litter respiration rates were analyzed with a generalized linear mixed-effect model (GLMM) using a Gamma distribution with the log link function. Treatments and their interactions were considered fixed effects whereas the spatial correlation structure was included as the random effect. Then, a nested analysis was performed to evaluate the effects and the difference in the group means of the dead culms and soil fauna treatments at each collection time. In addition, soil mesofauna contributions to litter mass loss were calculated as: [(mass loss in 1-mm mesh bag – mass loss in 42-µm mesh bag)]/(mass loss in 1-mm mesh-bag). Positive and negative values indicate positive and negative contributions of the soil mesofauna to litter mass loss, respectively. Mesofaunal contributions affected by dead culms, soil fauna and their interactions were evaluated in a LMM including dead culm treatment nested into plots as the random effect.

The differences in soil surface moisture and temperature (daily minimum and maximum) between the dead culms and the control were evaluated with *t*-tests for the first year of evaluation. As the influences of the dead culms on soil temperature may vary with season (Goldin and Hutchinson, 2015), the mean daily minimum and maximum soil temperatures in summer (July and August 2019) and winter (January and February 2020) were compared between treatments using *t*-tests.

To test the effects of dead culms and decomposition time on soil fauna relative density and order richness and diversity, GLMMs were performed including dead culm treatment nested into plots as the random effect. A Gamma distribution was assumed for mesofauna density and order richness, whereas a Gaussian distribution was assumed for diversity.

Non-metric multidimensional scaling (NMDS) analysis was conducted using a matrix of the square root-transformed abundances of the soil fauna groups to visualize the differences in mesofauna community composition between the dead culm and control treatment at each retrieval time. Distances between groups were calculated using the Bray-Curtis distance index (range: 0–1). A stress level threshold of < 0.2 was used to validate the NMDS goodness of fit. A permutational multivariate analysis of variance (PERMANOVA) with 999 randomizations was performed to determine whether the soil mesofauna community composition significantly differed between treatments and among collection periods. A canonical correspondence analysis (CCA) was used to explore the relationships between soil fauna orders or suborders and potential explanatory variables (treatment, time, litter mass loss, litter C/N and litter water content). The significances of the CCA model, the first two axes, and the explanatory variables were calculated with permutation tests.

All statistical analyses were conducted in R v. 4.0.2 (R Core Team, 2021). NMDS, PERMANOVA, and CCA were performed using the ‘vegan’ package in R (Oksanen et al., 2020). LMMs and GLMMs analyses were performed with the ‘nlme’ (Pinheiro et al., 2019) and the ‘lme4’ (Bates et al., 2015) packages, respectively. The corCAR1 function in the ‘nlme’ package was used to define the temporal autocorrelation structure.

5.3 Results

5.3.1 Effects of dead culms and soil fauna on leaf litter decomposition

The dead culm and soil fauna treatments significantly affected litter mass loss but no interaction between these two factors was detected (Table 5.1 and Figure 5.2a). The litter mass loss under the dead culms was 30.4% higher on average than the control. Soil fauna decreased litter mass loss. However, no difference in mesofauna contribution between the dead culm treatment and the control was found throughout the decomposition period (Table 5.1, Figure S5.1).

As with mass loss, the carbon and nitrogen losses were strongly affected by dead culms and soil fauna but not by their interaction (Table 5.1 and Figure 5.2b, c). Relatively higher carbon and nitrogen losses occurred under the dead culms and in the absence of soil mesofauna (Table 5.1 and Figure 5.2b, c). A larger decrease in litter C/N ratio was observed in the litter under the dead culms than the control (Table 5.1 and Figure 5.2d). Soil mesofauna had no effect on litter C/N ratio (Table 5.1 and Figure 5.2d) whether or not dead culms were present.

The dead culm treatment and decomposition time significantly affected the litter respiration rates (Figure 5.3; $P < 0.001$). The litter respiration rates were higher under the dead culms compared to the control during the decomposition experiment except for the last sampling period at 720 d, at which no differences between the treatments were observed (Figure 5.3; $P > 0.05$). Notably, across all retrieval times, soil mesofauna had no significant influence on the litter respiration rates (Figure 5.3; $P > 0.05$).

Table 5.1 Results of LMMs evaluating the effects of treatment (dead culm and control), soil mesofauna (with and without fauna), decomposition time and their interactions on litter mass loss, carbon and nitrogen loss, and C/N ratio; and the effects of treatment and decomposition time on the mesofaunal contribution to litter mass loss.

Variable	Source of variance	df	*F*	*P*
Mass loss (%)	Treatment (Tr)	1	125.85	< **0.001** ***
	Soil fauna (SF)	1	9.95	**0.01** *
	Time (T)	5	165.81	< **0.001** ***
	T × SF	1	0.01	0.91
	Tr × T	5	3.69	< **0.01** **
	SF × T	5	1.69	0.14
	Tr × SF × T	5	0.79	0.55
Mesofaunal contribution to mass loss (%)	Treatment (Tr)	1	0.01	0.93
	Time (T)	5	1.57	0.19
	Tr × T	5	0.73	0.60
Carbon loss (%)	Treatment (Tr)	1	98.09	< **0.001** ***
	Soil fauna (SF)	1	7.27	**0.03** *
	Time (T)	5	207.03	< **0.001** ***
	Tr × SF	1	0.06	0.81
	Tr × T	5	3.67	< **0.01** **
	SF × T	5	1.77	0.12
	Tr × SF × T	5	0.83	0.53
Nitrogen loss (%)	Treatment (Tr)	1	27.91	< **0.01** **
	Soil fauna (SF)	1	11.97	< **0.01** **
	Time (T)	5	28.54	< **0.001** ***
	Tr × SF	1	1.59	0.24
	Tr × T	5	8.21	< **0.001** ***
	SF × T	5	1.51	0.19
	Tr × SF × T	5	0.99	0.42
C/N ratio	Treatment (Tr)	1	29.28	< **0.01** **
	Soil fauna (SF)	1	0.03	0.87
	Time (T)	5	132.61	< **0.001** ***
	Tr × SF	1	1.33	0.28
	Tr × T	5	5.03	< **0.01** **
	SF × T	5	0.57	0.72
	Tr × SF × T	5	0.58	0.71

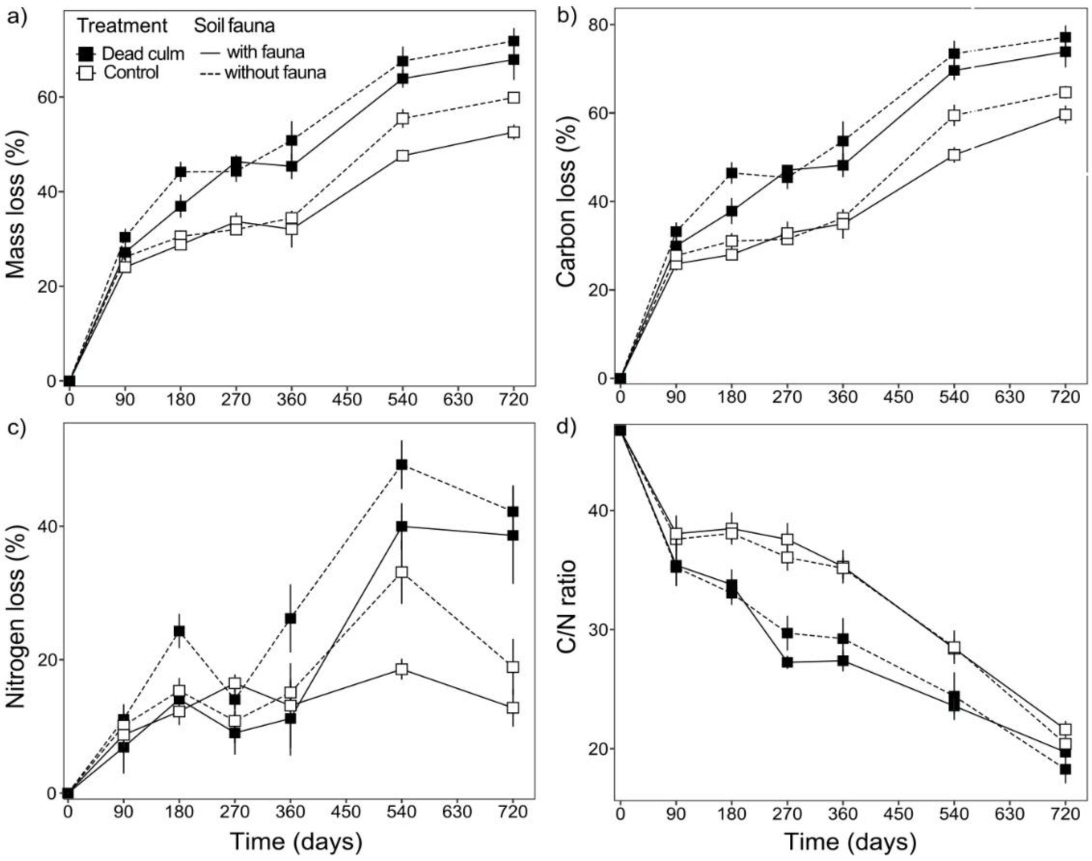

Figure 5.2 Changes in leaf litter a) mass loss, b) carbon loss, c) nitrogen loss, and d) C/N ratio showing the effects of dead culms and soil mesofauna over 720 days of litter decomposition. Error bars indicate standard errors (*N* = 5).

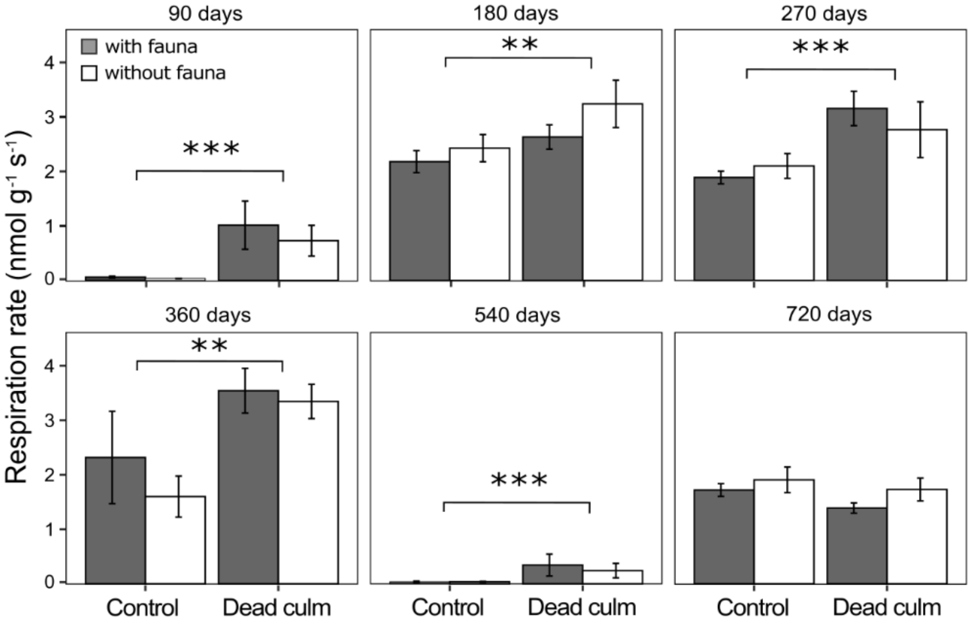

Figure 5.3 Effects of dead culms and soil fauna on litter respiration rates (nmol CO_2 g^{-1} s^{-1}) for each decomposition period. Error bars indicate standard errors (*N* = 5).

5.3.2 Effects of dead culms on soil microenvironmental conditions

There were large significant differences between treatments in terms of soil water content (Figure 5.4a; $P < 0.001$), specifically, the soils under the dead culms had higher moisture content than the control. There were no detectable significant differences between treatments in terms of mean daily minimum or maximum soil temperature throughout the year ($P > 0.05$). However, the mean daily minimum temperatures were significantly higher (~1.3 °C) under the dead culms than the control during the winter season (Figure 5.4b; $T = 3.4$; $P < 0.001$).

5.3.3 Effects of dead culms on litter fauna assemblage

Dead culms and decomposition time significantly influenced soil mesofauna abundance, order richness, and diversity (Figure 5.5; $P < 0.01$). At all sampling times, litter fauna density and order richness were always higher in the presence of dead culms (Figure 5.5a, b; $P < 0.05$). The litter under the dead culms had comparatively higher densities of predators, detritivores, and fungivorous mesofauna. Temporal changes in the composition of the soil fauna functional groups differed between the control and the dead culms treatments (Figure 5.6). For both treatments, the relative abundance of fungivorous fauna varied greatly with decomposition time and reached a minimum at 270 d. The proportions of detritivores and predators in the litter under the dead culms remained consistent throughout the decomposition period (Figure 5.6).

Dead culms significantly affected the soil fauna assemblages in the leaf litter (PERMANOVA; *Pseudo* $F = 6.97$; $P < 0.01$). However, the differences in soil fauna community between the control and dead culm treatments depended on the incubation period (PERMANOVA; *Pseudo* $F = 2.79$; $P < 0.01$). NMDS showed that the largest differences in soil fauna community occurred at 180 d (December 2019) and 540 d (December 2020) which corresponded to the winter season surveys (Figure S5.2). Along with the effects of treatment ($F = 3.59$; $P < 0.01$) and time ($F = 3.37$; $P < 0.01$), the CCA showed that the decomposition stage (litter mass loss) ($F = 3.69$; $P < 0.01$), litter moisture content ($F = 5.54$; $P < 0.01$) and litter C/N ratio ($F = 2.32$; $P < 0.01$) significantly influenced the soil faunal assemblage in the leaf litter (Figure 5.7).

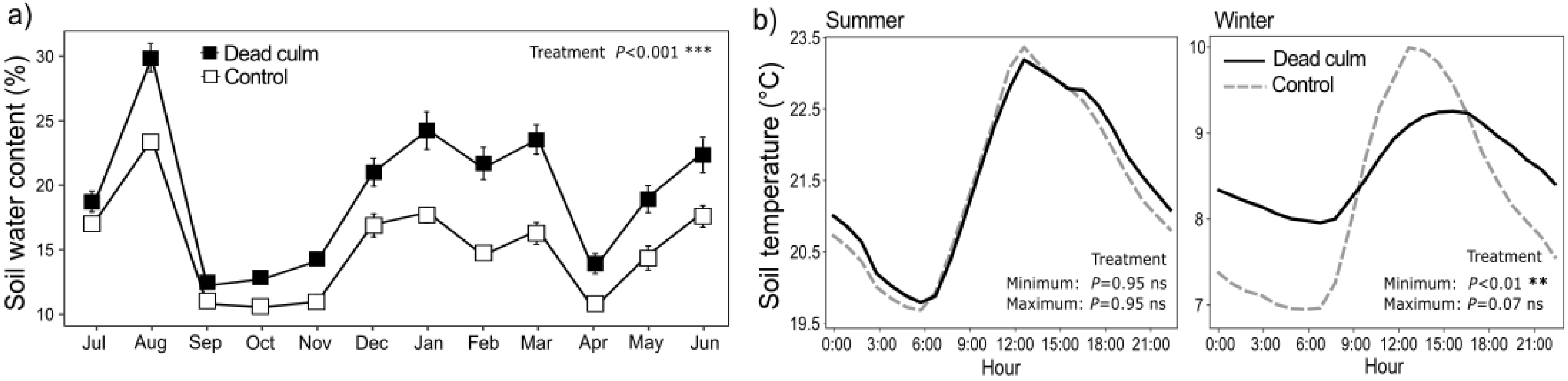

Figure 5.4 Effects of dead culms on soil surface microclimatic conditions. A) Monthly variation in soil water content (%) throughout a year (July 2019 to June 2020) and b) diurnal soil temperature in summer and winter showing comparisons of mean daily minimum and maximum temperatures between treatments (dead culm and control).

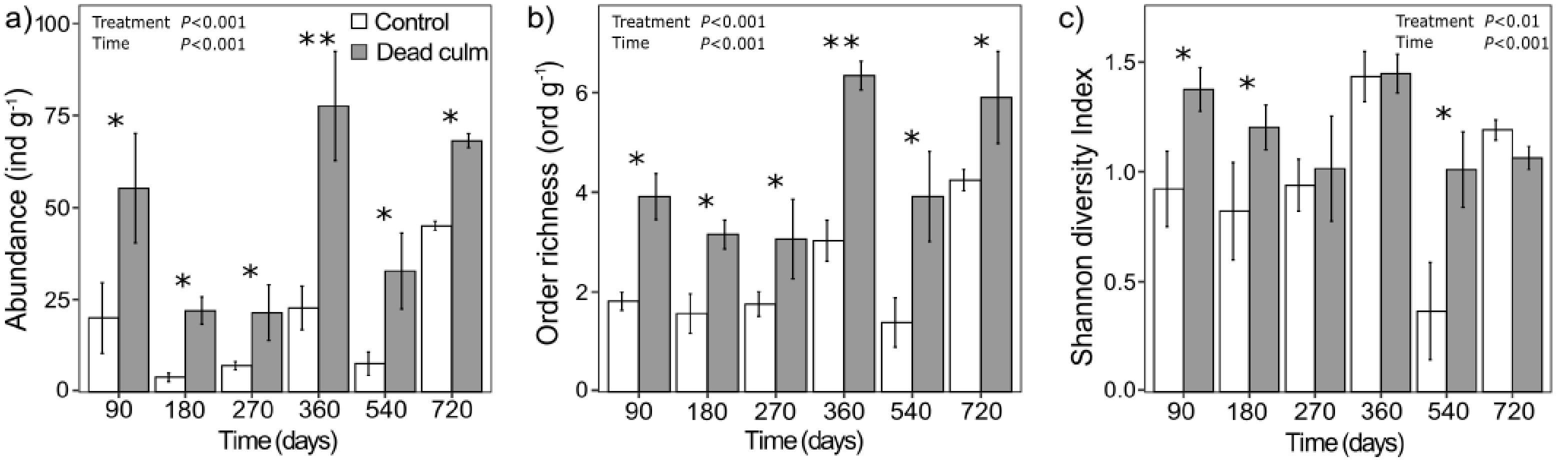

Figure 5.5 Effects of dead culms on a) abundance (ind. g^{-1} dry litter), b) richness (number of orders g^{-1} dry litter), and c) Shannon-Wiener diversity index of soil mesofauna in leaf litter from the 1-mm mesh litterbags. Error bars indicate standard errors (N = 5).

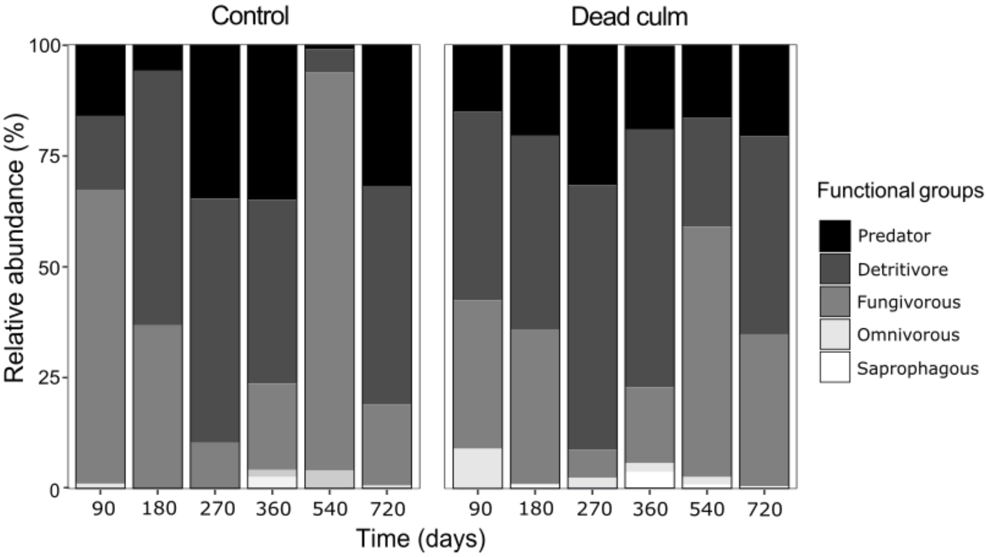

Figure 5.6 Dynamics of the relative abundance (%) of different functional groups of soil mesofauna in the 1-mm mesh litterbags showing the differences between dead culms and control.

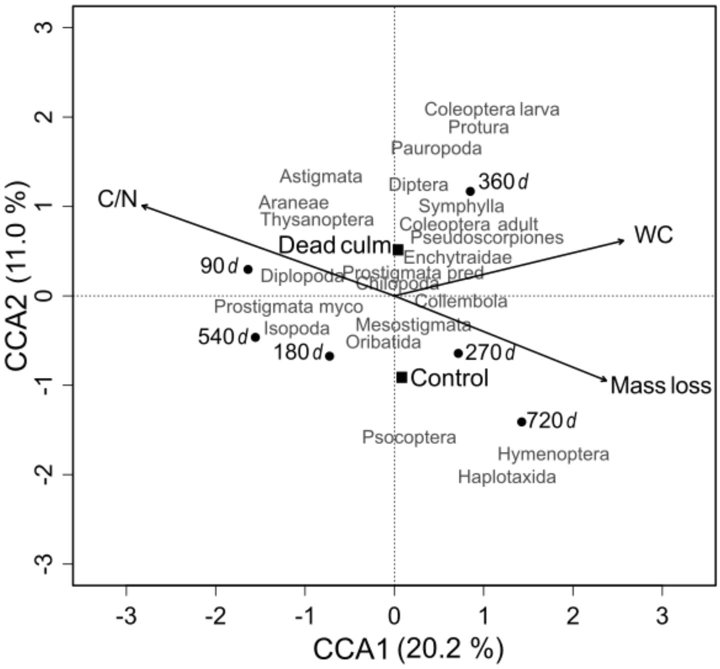

Figure 5.7 Ordination from Canonical Correspondence Analysis (CCA) showing the association of soil mesofauna orders from the 1-mm mesh litterbags to treatment (squares) and decomposition period (circles). Arrows show the association of soil mesofauna orders to litter variables (mass loss, water content, and C/N ratio). The overall model was significant (P = 0.001), and all the explanatory variables considered exerted significant effects on the composition of soil mesofauna ($P < 0.01$).

5.4 Discussion

5.4.1 Influences of dead culms and soil fauna on litter decomposition

Dead woody materials are important forest floor components. CWD can alter soil biotic and abiotic conditions and indirectly affect litter decomposition (Gonzalez-Polo et al., 2013; Remsburg and Turner, 2006). In this study, the dead bamboo culms indirectly promoted litter mass loss by modifying soil moisture availability and litter biotic activity. Moreover, in accordance with our hypothesis, the presence of dead culms increased the losses of litter carbon and nitrogen. The litter C/N ratio decreased with increasing decomposition time, but to an even greater extent in the litter under the dead culms than the control. In general, litter C/N ratio decreases due to greater carbon than nitrogen loss as decomposition progresses (Couteaûx et al., 1995). Here, the rapid decrease in the C/N ratio of the litter beneath the dead culms was the result of faster decomposition rates and greater carbon loss than the control. Taken together, these results suggest that the biotic and abiotic changes mediated by dead bamboo culms accelerated litter decomposition and nutrient mineralization and significantly modulated biogeochemical cycling.

Soil mesofauna decreased litter mass, carbon and nutrient loss but had no effect on litter respiration. It is generally assumed that soil fauna enhance litter decomposition (García-Palacios et al., 2013; Seastedt, 1984). Previous studies using similar mesh size litterbags as in this study (1 mm and ≤ 42 µm) found that mesofauna enhanced litter mass loss by 20% (Joo et al. 2006; Song et al. 2020; Wang et al. 2015), while another reported that they decreased litter decomposition (Fujii et al. 2016). The great variability in the magnitude and direction (positive or negative) of mesofaunal effects on decomposition suggests that their effects may depend on several factors (Frouz, 2018). For instance, confounding effects may occur because of the differences in moisture conditions as a consequence of using litterbags with small mesh sizes (Kampichler and Bruckner, 2009). Here, no significant differences were found in terms of litter or litterbag moisture content between the mesh sizes. Thus, it is unlikely that changes in moisture conditions and potential confounding effects on litter decomposition or the activity of soil mesofauna occurred in this study. Furthermore, these results are in line with Lin et al. (2019), who found that the presence of soil meso- and macrofauna significantly reduced leaf litter mass loss in a Moso bamboo forest. The inhibition of decomposition by soil fauna could be a result of indirect interactions and their impacts on microbial communities during decomposition (Kampichler and Bruckner, 2009; Lussenhop 1992).

Soil mesofauna can decrease litter decomposition rates by overgrazing and preying on litter microbial communities (Hättenschwiler and Gasser, 2005; Lussenhop, 1992). In this study, soil mesofauna had a slightly positive effect on litter mass loss after 270 days of decomposition. Notably, this effect was only observed when mycophagous Prostigmata and Collembola, which also includes many fungivorous species, had the lowest density and relative abundance. This could suggest that mainly fungivorous fauna preyed upon the microbial communities throughout most of the decomposition period, leading to a negative contribution of soil fauna to decomposition and reduced rates of litter mass and nutrient loss. Contrastingly, litter respiration rates were not influenced by the presence of soil mesofauna. This could be attributed to the activity of litter-feeding fauna and the conversion of litter into fecal pellets that may stimulate microbial activity (Briones, 2018; David, 2014). Thus, it is possible that the litter respiration rates in the presence of soil fauna were similar to those in the fine-mesh litterbags despite the negative effect of mesofauna on litter mass loss (Fujii et al., 2016).

It was initially hypothesized that the soil fauna under the dead bamboo culms would have a relatively greater impact on litter decomposition than on the forest floor (control). Nevertheless, the interaction between soil fauna and dead culm treatment was not significant. There were comparatively higher mesofauna density and richness in the litter under the dead culms than the control. However, the relative contributions of the soil fauna to litter decomposition did not differ between treatments. Earlier studies associated soil fauna diversity and richness with accelerated litter decomposition (Liu et al., 2019; Tresch et al., 2019). In contrast, other studies showed that microarthropod abundance and richness did not always correspond to an increased impact of soil fauna on litter mass loss (Irmler, 2000; Neher et al., 2012). Moreover, it seems that taxon diversity is less important than the presence of certain key species that facilitate and directly contribute to litter decomposition (Cragg and Bardgett, 2001; Setälä, 2002; Wardle, 2002). Besides the effect of dead culms on soil fauna abundance and diversity, their presence may simultaneously affect multitrophic interactions among decomposers (Castro and Wise, 2010; Jabin et al., 2004). The complex relationships within the soil food web may mask the influence of certain mesofaunal groups as they also interact with other microbial feeders that affect decomposition (Scheu et al., 2005). Further research is required to elucidate the roles of soil fauna mediated by CWD and their overall impact on litter mass loss and nutrient dynamics.

5.4.2 Influence of dead culms on soil environmental conditions

The higher soil moisture retention found under the bamboo culms is congruent with earlier research that reported higher moisture conditions near CWD. This trend is often attributed to reduced evaporation from soils beneath coarse woody materials (Boggs et al., 2020; Goldin and Hutchinson, 2014; Pettit and Naiman, 2005). Moreover, the soils under CWD are generally cooler in summer and warmer in winter than those that are away from logs (Boggs et al., 2020; Goldin and Hutchinson, 2015). In this study, the winter daily minimum temperatures were slightly moderated by the dead culms, indicating that the presence of this material can maintain warmer soil temperatures during the colder seasons. Unlike CWD from logs, dead culms have only a minor effect on the soil surface temperatures during the summer. This is likely because bamboo culms have comparatively smaller volumes and contact areas with the soil than the logs (Goldin and Hutchinson, 2015).

5.4.3 Influence of dead culms on litter soil fauna community

There are several possible explanations for the differences in the litter fauna assemblages between the control and dead culm treatments. CWD may provide a suitable habitat for the soil fauna communities by promoting favorable microsite conditions for them in the litter layer (Hanula et al., 2006; Jabin et al., 2004). In this study, relatively greater soil mesofauna abundance and diversity were found in the litter under the dead culms. Previous studies showed similar soil fauna patterns in the litter adjacent to CWD (Castro and Wise, 2010; Jabin et al., 2004). However, other studies reported taxon-dependent differences in microarthropod abundance and richness (Déchêne and Buddle, 2010; Evans et al., 2003; Ulyshen et al., 2011; Ulyshen and Hanula, 2009). The significant interaction between treatment and decomposition time on mesofauna community composition revealed relatively greater differences in soil fauna assemblage during the winter periods. This suggests that the slightly higher soil temperatures under the dead culms may benefit soil fauna that are sensitive to microenvironmental changes in the forest floor. In addition, the CCA biplot showed that soil fauna such as Pseudoscorpionida, Diptera, and Coleoptera associated with the dead culms were positively correlated with the litter water content. Hence, dead bamboo culms might favor the proliferation of soil fauna preferring high moisture content in the litter layer (Castro and Wise, 2010; Kappes et al., 2007).

The soil fauna assemblage may respond to the resources and food provided by CWD (Kappes, 2005). In our study, the increased litter respiration rates under the dead culms may have affected the densities of fungivorous fauna in this treatment likely because they prefer litter with high microbial activity (Harrop-Archibald et al., 2016; Zimmer et al., 2003). Moreover, as indicated by the constant relative abundance of predators, the dead culms may have provided both refuge and resources for predatory fauna throughout the decomposition period. Another study reported a similar association between the presence and abundance of predatory fauna and decomposing logs (Castro and Wise, 2010).

Changes in litter quality during decomposition may also influence soil fauna community composition (Evans et al., 2003; Hasegawa and Takeda, 1995; Wardle and Lavelle, 1997). We found that the soil fauna assemblage responded to litter quality and litter mass loss (or decomposition stage). Rapid changes in the C/N ratios of the litter under the dead culms may have affected the abundance of certain soil fauna groups such as detritivores that may prefer decomposed and more palatable litter (Dudgeon et al., 1990). This further highlight that one of the main effects of dead culms on litter fauna assemblage comes from the rapid changes in litter quality and fast decomposing litter under the culms.

5.4.4 Implications for management

Increasing expansion of Moso bamboo stands may result in large areas dominated by this plant in the near future (Shinohara et al., 2014; Suzuki, 2015). In unmanaged stands, dead culm accumulation may account for nearly 31% of the total aboveground biomass and substantially contribute to long-term carbon nutrient storage (Shimono et al., 2021; Ugawa et al., 2011). These findings indicate that the legacy of dead bamboo culms extends well beyond their direct role as a carbon reservoir. On the forest floor, dead culms play an indirect role in short-term carbon dynamics and nutrient cycling. They provide spatially heterogeneous biotic and abiotic conditions on the forest floor where litter decomposition and nutrient loss are actively enhanced. Moreover, dead culms affect litter fauna assemblage during decomposition and thus provide resources and refuge for mesofauna that are sensitive to microclimate variations in the litter layer. The ecological importance of dead culm accumulation and their contribution to nutrient cycling in bamboo stands should be further recognized and considered in management decisions. Common management practices that involve the removal of dead culms could adversely affect litter nutrient cycling and alter the spatial distribution of soil microarthropods on the forest floor.

5.5 Conclusion

This chapter demonstrated that dead culms modified the soil microenvironment, increased litter biotic activity, and accelerated litter mass, carbon and nitrogen loss. Dead culms significantly increased mesofaunal abundance and diversity and affected fauna assemblage during litter decomposition. However, the fauna effect on litter decomposition was not altered by the presence of dead culms, suggesting that indirect effects of dead bamboo culms on litter decomposition were mainly through changes in the soil environment and litter microbial activity. Taken together, these results show that dead bamboo culms are important structural components that influence decomposer organisms and litter nutrient dynamics in Moso bamboo stands. The persistence of dead culms on the forest floor might have long-lasting effects on nutrient turnover through indirect influence on litter decomposition.

Chapter 6

General Discussion

6.1 How do above- and below-ground litter decomposition, soil fauna and dead bamboo culms influence organic matter cycling in bamboo stands?

Litter traits have significant effects on plant organ decomposability and nutrient mineralization (Freschet et al., 2013; Wardle et al., 2004). In Moso bamboo, whole-plant litter decomposition was highly correlated with intraspecific litter quality (Chapter 3). Variations in chemical and structural traits predicted organ decomposability and litter carbon loss, while only initial N concentration predicted N release during decomposition. After two years of decomposition, carbon loss was the greatest in leaf, followed by root, rhizome, branch and culm litter, while net N release was highest in culm and rhizome litter, followed by branch, fine root and leaf litter.

To understand the influence of above- and below-ground litter on soil organic matter dynamics, it is necessary to consider both organ decomposability and their annual litter input (Freschet et al., 2013). In an unmanaged Moso stand, Isagi et al. (1997) reported that culm litter accounts for 55% (7.0 Mg ha^{-1} yr^{-1}) of the total annual above-ground litter input, while leaf litterfall contributes only 34% (4.4 Mg ha^{-1} yr^{-1}). Below ground, fine root litter input would represent a significant proportion due to the rapid turnover of fine roots. However, there is no reliable or published data on litter mass input of fine roots or rhizome in Moso bamboo stands. Building upon this understanding, Figure 6.1 quantitatively illustrates the contribution of bamboo organs to C and N release during litter decomposition in a Moso bamboo stand. The total C and N input was estimated using annual litter input data from Isagi et al. (1997), the initial C and N litter concentrations and the rates of C and net N release from bamboo litter in Chapter 3.

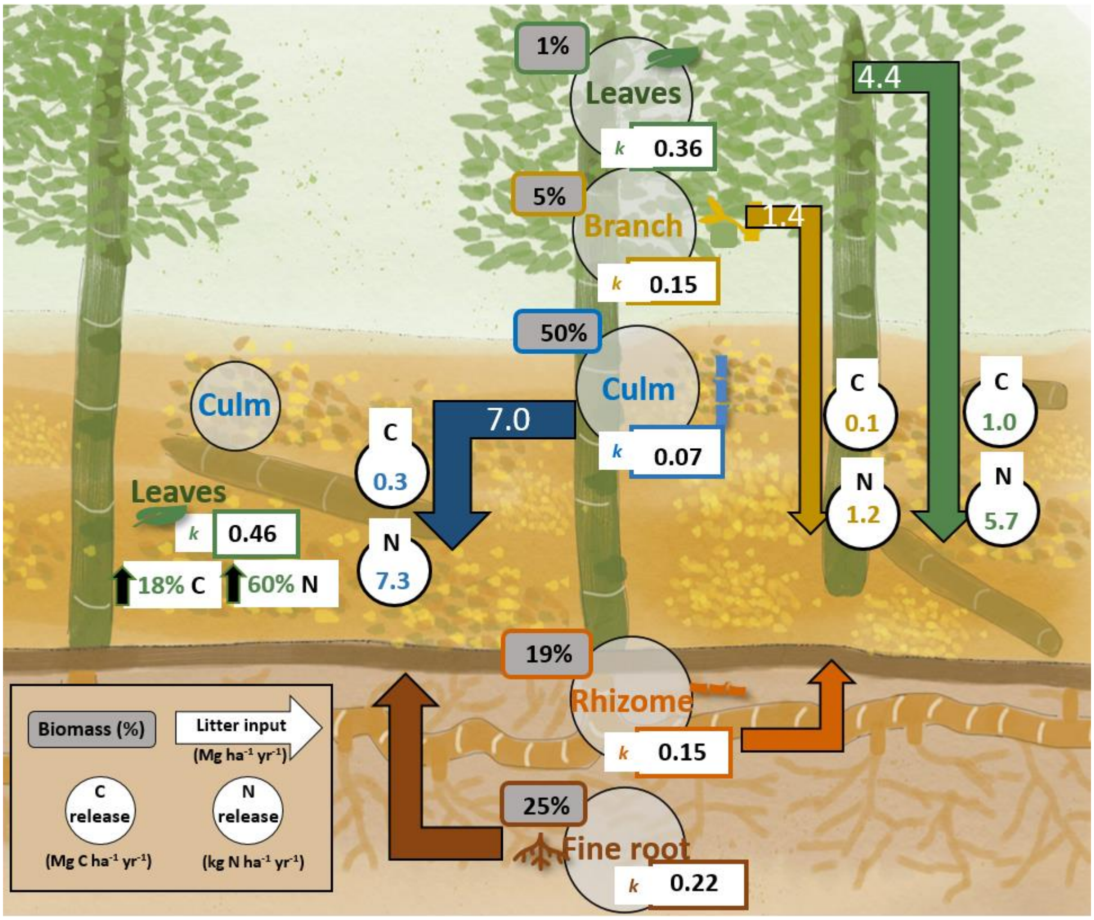

Figure 6.1 Quantitative illustration of the contribution of aboveground bamboo organs and dead bamboo culms to C and N release (in the presence of soil fauna) in an unmanaged Moso bamboo stand. Annual litter input is shown in arrows (Isagi et al., 1997), biomass allocation is shown in grey boxes (Kobayashi et al., 2023), litter decomposition rates are shown in square white boxes (Chapter 3 and Chapter 5), and estimated C (Mg C ha^{-1} yr^{-1}) and N (kg N ha^{-1} yr^{-1}) release are shown in white circles.

Despite constituting only 34% of above-ground litter input, leaf litter contributed to 71% of the total C released (1.0 Mg C ha^{-1} yr^{-1}) due to its rapid rates of decomposition and C loss. In contrast, culm and branch litter contributed only 21% (0.3 Mg C ha^{-1} yr^{-1}) and 8% (0.1 Mg C ha^{-1} yr^{-1}) of the C released annually, respectively (Figure 6.1). The contribution of bamboo organs to N release varies from their contribution to C release. Leaf litter, despite having higher initial N content and a consistent N release during decomposition, accounts for 40% (5.7 kg N ha^{-1} yr^{-1}) of the total N released among above-ground organs. Notably, culm litter, contributing 55% of total above-ground litter yet having the lowest initial N concentration, accounts for 52% (7.3 kg N ha^{-1} yr^{-1}) of the total annual N release (Figure 6.1).

Woody bamboos allocate less biomass to leaves compared to many tree species (Kobayashi et al., 2023), thus leaf litter represents a smaller proportion of the above-ground litter input, especially when compared to culm litter (Isagi et al., 1997). Nevertheless, leaf litter decomposition contributes significantly to C release and accelerates C cycling in bamboo stands. The role of leaf litter decomposition in N cycling is also significant given its high initial nutrient content and consistent N release; however, its contribution to stand-level N input may not be comparable to that of culm litter (Figure 6.1).

During a 2-year decomposition period, culm litter was characterized by alternating periods of N retention and N release, with an average net N release of 36% of its initial N content (Chapter 3). N accumulation in culm litter may be due to its translocation from external sources, which can then favor N mineralization by microbial communities. N immobilization during CWD decomposition has been well-documented (Yuan et al., 2017; Laiho and Prescott, 2004), with N accumulating for decades or being released only after long periods (>20 years) (Holub et al., 2001; Palvaiainen et al., 2010). In temperate and boreal forest ecosystems, CWD input ranges from 3-70% of aboveground litter input. However, due to the long-term N retention during decomposition, CWD contributes to <5% of N released (Laiho and Prescott, 2004; Palviainen et al. 2008; Laiho and Prescott, 2004). In contrast, bamboo culms serve as N pools and release N relatively rapidly during early stages of decomposition. Although the results of this study provide a limited understanding of long-term N dynamics during culm litter decomposition, they still suggest that culm litter plays a significant role in N cycling in bamboo stands. Furthermore, to better understand the external sources of N translocation and clarify N dynamics, future research should focus on using alternative analytical methods, such as $\delta^{15}N$, at different stages of culm litter decomposition (Rinne et al. 2017).

Similar to CWD from trees, dead bamboo culms serve as long-term C reservoirs due to their slow C release (Chapter 3). Moreover, they also play an indirect role in C cycling by promoting leaf litter decomposition (Chapter 5). The presence of dead bamboo culms enhances soil and litter moisture retention, providing favorable habitats for microarthropods on the forest floor. The ecological significance of dead culms and their contributions to carbon and nutrient cycling should be considered in management decisions.

In Moso bamboo stands subject to intensive and extensive management, practices often involve the removal of dead culms, leaving no standing dead bamboo culms or debris on the forest floor. As shown in Chapter 3 and 5, dead bamboo culms can directly accelerate N cycling through litter decomposition and indirectly increase C and N release (by 18% and 60%, respectively) in leaf litter decomposing beneath the culms (Figure 6.1). Thus, incorporating management decisions that include the retention of certain amounts of dead bamboo culms could improve nutrient availability in Moso bamboo stands.

Soil mesofauna plays an important role in litter decomposition processes through ingesting and fragmenting litter, and through their interactions with litter microbial communities (Chapin et al., 2011). Generally, it is assumed that soil fauna enhances litter decomposition by 20-45% (Garcia-Palacios et al., 2013; Song et al. 2020; Wang et al., 2015). However, there a few reports on the negative effects of soil fauna on litter mass loss (Fujii et al., 2016; Lin et al., 2019). Moreover, the contribution of soil fauna on decomposition to litter decomposition can depend on litter quality (Coleman et al., 2004), which further suggests that the effects of soil fauna cannot be generalized. In Chapter 3, the contribution of soil mesofauna to decomposition of bamboo litter was not dependent on litter quality. Instead, the effects of soil fauna were only observed in branch and leaf litter at later stages of decomposition. Soil fauna decreased litter decomposition in branch and leaf litter and reduced their C release by 43% and 9%, respectively. The results showed that soil mesofauna had no effects on N cycling but had a significant effect on C cycling by decreasing the decomposition of above-ground organs. The large disparities in the contribution of soil fauna to the decomposition of different organs highlights the importance of evaluating the effects of soil fauna on whole-plant litter decomposition for a comprehensive understanding of organic matter cycling in bamboo stands.

6.2 How does root litter quality and decomposition within the branching root system contribute to soil carbon cycling in bamboo stands?

Using a functional order approach to fine root decomposition in woody bamboo species, lower order roots decomposed more slowly than higher order roots (Chapter 4), consistent with previous studies on root decomposition in temperate and subtropical tree species (Fan and Guo, 2010; Goebel et al., 2011, Sun et al., 2018). Fine root litter decomposition rates were correlated with root carbon quality among bamboo species and root orders. Higher decomposability in higher order roots was associated with labile C compounds (i.e., carbohydrates, polysaccharides), while the reduced decomposability of lower order roots was associated with the higher relative abundances of recalcitrant C compounds (i.e., lignin, tannin, aromatic compounds). The correlation between root decay rates and C-NMR spectral regions aligns with the C-quality hypothesis, suggesting that the lower decomposability of lower root orders relates to their poor C quality (Fan and Guo, 2010). Despite relatively small differences in the relative abundances of organic C compounds among root orders, the significant differences in the decomposability of lower and high order roots could be also attributed to their contrasting N concentration. Higher nitrogen concentrations in the presence of acid insoluble compounds (as in lower order roots) can inhibit decomposition trough the formation of recalcitrant compounds (Berg, 2000).

Root decomposition showed no correlation with the alkyl C region in the C-NMR spectra, which is representative of aliphatic compounds and suberin (Chapter 4). Root suberin is a recalcitrant biomolecule and may contribute to the formation of stable SOM (Poirier et al., 2018). Additional research is needed to determine whether root suberin resists decay during litter decomposition and confers some degree of recalcitrance to lower order roots. Previous studies have shown that nonstructural carbohydrates are quickly lost during root decomposition, specially in higher order roots (Fan and Guo, 2010). However, the fate of recalcitrant compounds such as tannin, phenols, and lignin among different branching orders remains unknown. Further studies should also explore organic C changes during root litter decomposition and how these changes differ in lower order compared to higher order roots.

Root litter input and quality are major factors regulating SOC storage and stabilization in soils. Root decomposition strongly influences SOM stabilization through litter quality. Generally, root recalcitrant compounds, which are harder to decompose, contribute more to SOM stabilization than high quality litter. This is due to their resistance against enzymatic breakdown and stimulation of fungal growth rather than bacteria. In contrast, high quality or labile roots decompose rapidly, leading to increased accumulation of microbial products and the formation of stable SOM. In this context, variations in litter quality and decomposability across the branching root system would imply distinct roles of roots orders in soil C retention (Fan and Guo, 2010, Beidler and Pritchard, 2017). From a litter-centered approach, lower order roots would contribute to effective SOM stabilization through their slow decomposition and the presence of recalcitrant organic compounds (Poirier et al., 2018). Zhou and Fu (2008) classified Moso bamboo fine roots based on diameters and reported that the finest roots (< 0.5 mm), likely corresponding to first and second order roots, constitutes over 26% of the fine root volume. Consequently, given than lower order roots have rapid turnover rates and may represent a significant proportion of the fine root biomass in bamboo stands, their slower decomposition could make a large contribution to SOM stabilization and soil carbon storage.

The role of root decomposition in SOM stabilization is also crucial for predictions of how changes in vegetation composition due to bamboo invasion might impact soil carbon storage. Recalcitrant Moso bamboo roots decomposed slower, in contrast to the labile roots Madake and Hachiku which decomposed faster (Chapter 4). From a litter quality approach, fine root decomposition in Moso bamboo stands may contribute to higher SOM stabilization compared to Madake and Hachiku. This further implies that differences in root litter quality among Madake, Hachiku and Moso bamboo will result in distinct effects of bamboo invasion on SOM stabilization and storage. Root biomass can represent up to 30% of the total standing bamboo biomass and is an important source of litter input in bamboo stands. Notably, woody bamboos can allocate two times (or even more) fine root biomass compared to trees (Kobayashi et al., 2023; Shimono et al., 2022), thus root litter input and turnover can greatly affect below-ground processes during invasion. Further research should focus on how root litter input and quality of different invasive bamboo species would impact soil carbon storage and the carbon cycle at the ecosystem level.

Chapter 7

General Conclusion

This chapter presents an overview by summarizing the key research findings of the study and discussing the value and contribution thereof. The present study aimed to investigate litter decomposition dynamics and elucidate how different factors interact to regulate decomposition processes in bamboo stands. Specifically, environmental controls, litter quality, soil fauna and the presence of coarse woody debris were considered to evaluate their impacts on litter decomposition and nutrient cycling in bamboo stands. The results of this study are divided into four sections:

1) At large scales, climate plays a significant role in regulating decomposition processes in Moso bamboo (*Phyllostachys edulis*) stands. The findings emphasized that long-term climate played a crucial role in litter stabilization, while temporal climatic conditions predominantly affected decomposition rates. The interaction between precipitation and temperature was a strong determinant of decomposition rates, indicating that precipitation accelerated initial decomposition rates in warmer sites, and inhibited decomposition in cooler sites. Furthermore, the findings demonstrated the limited direct effects of stand structure and the accumulation of organic matter on decomposition processes but revealed their indirect effects through variations in soil conditions. The relevance of climate in this region indicates that future climatic changes in precipitation patterns or temperature could greatly affect early decomposition phases and soil carbon storage in Moso bamboo stands.

2) The effects of litter quality and soil mesofauna on whole-plant litter decomposition in Moso bamboo were investigated. The results revealed that the decomposability and carbon loss of bamboo organs correlated strongly with their initial chemical and structural traits. Leaf litter had the highest carbon release, while culm and rhizome litter had the highest net nitrogen release during a two-year decomposition period. At the stand level, leaf litter decomposition

accelerates C cycling, while the rapid N release and substantial culm litter input, relative to leaf litter input, suggests that culm litter decomposition play a significant role in N cycling. Soil fauna did not alter the relationships between litter traits and organ decomposability, suggesting that intraspecific variation in litter traits did not modulate the contribution of soil fauna to decomposition. The results revealed that soil fauna decreased mass and carbon loss in leaf and branch litter, while they had no effects on litter nitrogen release. This further suggests that soil mesofauna slow down C cycling by negatively affecting above-ground litter decomposition. Such differences in the contribution of soil fauna to the decomposition of above- and below-ground organs highlight the importance of considering soil fauna effects in whole-plant litter decomposition to understand the role of soil decomposers in carbon and nutrient cycling in bamboo stands.

3) A functional order approach was used to assess the effects of litter quality on root litter decomposition of Hachiku (*Phyllostachys nigra*), Madake (*Phyllostachys bambusoides*) and Moso bamboo (*Phyllostachys edulis*). The findings revealed that lower order roots exhibited slower decomposition rates compared to higher order roots. While morphological and traditional chemical traits varied significantly among branching orders, they did not entirely account for the variability in root litter decomposition rates. Root litter characterization using ^{13}C-NMR spectra exhibited the highest predictive power for root litter decomposition across species and root orders. The results clarified that the low decomposability of lower order roots was associated with their higher relative abundance in aromatic C compounds and lower relative abundance of labile C compounds. These findings highlight the importance of considering the fine root heterogeneity in woody bamboos and the variations in carbon quality among different branching orders for accurate predictions of below-ground processes.

4) The influence of dead culms and soil fauna on leaf litter decomposition dynamics was evaluated in Moso bamboo stands. The findings demonstrated that dead culms modified the soil microenvironment, leading to increased litter biotic activity and rapid litter mass and nutrient loss. The presence of dead culms had a substantial impact on the abundance and diversity of mesofauna and affected the composition of the fauna community during litter decomposition. Soil fauna

effects on leaf litter decomposition were not altered by the presence of dead culms, indicating that the indirect effects of dead bamboo culms on leaf litter decomposition primarily occurred through changes in the soil environment and litter microbial activity and not through changes in soil fauna communities. These results highlight the significance of dead bamboo culms as structural components and their influence on decomposer organisms and litter nutrient dynamics in Moso bamboo stands. The removal of dead culms from the forest floor as a consequence of common management practices may slow down litter C and N release in bamboo stands.

Overall, this thesis enhanced our understanding of litter decomposition dynamics and the factors regulating these processes in bamboo stands. This study provides insights into the contrasting roles of climate, litter quality and soil fauna in regulating above- and below-ground decomposition processes in bamboo stands and provides insights into their implications for soil carbon storage and nutrient cycling. In addition, the findings on the indirect impacts of dead culms on nutrient cycling hold practical implications for the management of bamboo stands.

Acknowledgments

I would like to express my deep gratitude to my advisor, Prof. Tsutomu Enoki, for his support, guidance, and invaluable insights throughout the course of this research. I extend my appreciation to the members of the doctoral committee, Prof. Tomonori Kume, Prof. Takuo Hishi, and Prof. Syuntaro Hiradate, for their constructive feedback and expert advice, which greatly contributed to this work.

I am happy to have collaborated with several professors and fellow researchers during this period. Their collaborative spirit and interesting discussions enriched this research. Special thanks to Prof. Ayumi Katayama (Kyushu University), Prof. Motohiro Hasegawa (Doshisha University), Prof. Akio Inoue (Kindai University), Prof. Shin Ugawa (Kagoshima University), Prof. Shinya Koga (Kyushu University), Prof. Ryunosuke Tateno (Kyoto University) and Sophie Laplace (National Taiwan University).

I am thankful to the following sources: JSPS KAKENHI (JP19H02996) and the Japan Science and Technology (JST) Agency, who provided financial support for this research. I also want to express my gratitude to the Ministry of Education, Culture, Sports, Science and Technology (MEXT) for the scholarship and financial support during my graduate studies.

I am grateful to all the professors of the Laboratory of Forest Resource Management, particularly Prof. Ryuji Ichihashi and Prof. Naoaki Tashiro for their constructive feedback on an early draft of this thesis. I also extend my appreciation to the students who helped in the setup of the decomposition experiments and participated in data collection: Masaki Akesaka, Tenshiro Matsuni, Haruka Sawae, Zin Naing Win, and Hiroto Harada. I also appreciate the support of the technical staff from the Kyushu University Forest, both in Kasuya Research Forest and Shiiba Research Forest.

Last but not least, I want to express my deepest gratitude to my family and friends for their encouragement and support throughout this academic journey. I am particularly grateful to Dr. Debbie Roberts, as well as my fellow PhD candidates, Fabienne Sandkühler and Elspeth Brooke, for the many hours writing together and talking about our research and plans. I also want to express my gratitude to many good friends who provided accountability and companionship in the last two years, including Carina, Rosa, Elia, Devi, Sue, Charlotte, Gianina, Rose and Yundi. This work would not have been possible without the encouragement and support from all those mentioned above.

I would also like to acknowledge the locations where this research took place: primarily the bamboo stands in Kasuya Research Forest. I spent countless hours immersed in these forests. They gave me valuable perspectives and joy in the research journey. Just as with people, I recognize and appreciate the energy they provided for this study.

References

Abiven, S., Menasseri, S., and Chenu, C. (2009). The effects of organic inputs over time on soil aggregate stability – a literature analysis. Soil Biol. Biochem. 41, 1–12. doi:10.1016/j.soilbio.2008.09.015

Abramoff, M. D., Magalhães, P. J., and Ram, S. J. (2004). Image processing with ImageJ. Biophotonics Int. 11, 36–42. Available at: http://localhost/handle/1874/204900 [Accessed August 14, 2020].

Adl, S. M. (2003). The Ecology of Soil Decomposition. Cambridge, MA: CABI Pub.

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439–449. doi:10.2307/3546886

Althuizen, I. H. J., Lee, H., Sarneel, J. M., and Vandvik, V. (2018). Long-term climate regime modulates the impact of short-term climate variability on decomposition in alpine grassland soils. Ecosystems 21, 1580–1592. doi:10.1007/s10021-018-0241-5

Angst, G., Heinrich, L., Kögel-Knabner, I., and Mueller, C. W. (2016). The fate of cutin and suberin of decaying leaves, needles and roots – Inferences from the initial decomposition of bound fatty acids. Org. Geochem. 95, 81–92. doi: 10.1016/j.orggeochem.2016.02.006.

Austin, A. T., and Marchesini, V. A. (2012). Gregarious flowering and death of understorey bamboo slow litter decomposition and nitrogen turnover in a southern temperate forest in Patagonia, Argentina. Funct. Ecol. 26, 265–273. doi: 10.1111/j.1365-2435.2011.01910.x.

Bartoń, K. (2022). MuMIn: Multi-Model Inference. Available at: https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. doi:10.18637/jss.v067.i01

Bauer, D. J., and Curran, P. J. (2005). Probing interactions in fixed and multilevel regression: inferential and graphical techniques. Multivar. Behav. Res. 40, 373–400. doi:10.1207/s15327906mbr4003_5

Beidler, K. V., and Pritchard, S. G. (2017). Maintaining connectivity: understanding the role of root order and mycelial networks in fine root decomposition of woody plants. Plant Soil 420, 19–36. doi: 10.1007/s11104-017-3393-8.

Berg, B. (2000). Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manag. 133, 13–22. doi: 10.1016/S0378-1127(99)00294-7.

Berg, B., and McClaugherty, C. (2014). Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. 3rd ed. Berlin: Springer.

Berg, B., Berg, M. P., Bottner, P., Box, E., Breymeyer, A., de Anta, R. C., et al. (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. Biogeochemistry 20, 127–159. doi:10.1007/BF00000785

Blume-Werry, G., Di Maurizio, V., Beil, I., Lett, S., Schwieger, S., and Kreyling, J. (2021). Don't drink it, bury it: comparing decomposition rates with the tea bag index is possible without prior leaching. Plant Soil 465, 613-621. doi:10.1007/s11104-021-04968-z

Boggs, A. D., Moorman, C. E., Hazel, D. W., Greenberg, C. H., Sorger, D. M., and Sorenson, C. E. (2020). Ground-dwelling invertebrate abundance positively related to volume of logging residues in the Southern Appalachians, USA. Forests 11, 1149. doi: 10.3390/f11111149.

Bonanomi, G., Incerti, G., Giannino, F., Mingo, A., Lanzotti, V., and Mazzoleni, S. (2013). Litter quality assessed by solid state 13C NMR spectroscopy predicts decay rate better than C/N and Lignin/N ratios. Soil Biol. Biochem. 56, 40–48. doi: 10.1016/j.soilbio.2012.03.003.

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., and Wood, S. A. (2016). Understanding the dominant controls on litter decomposition. J. Ecol. 104, 229–238. doi:10.1111/1365-2745.12507

Bradford, M. A., Veen, G. F. (Ciska), Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H. C., et al. (2017). A test of the hierarchical model of litter decomposition. Nat. Ecol. Evol. 1, 1836–1845. doi:10.1038/s41559-017-0367-4

Bradford, M. A., Warren Ii, R. J., Baldrian, P., Crowther, T. W., Maynard, D. S., Oldfield, E. E., et al. (2014). Climate fails to predict wood decomposition at regional scales. Nat. Clim. Change 4, 625–630. doi: 10.1038/nclimate2251.

Breckle, S.-W. (2002). Walter's vegetation of the Earth: the ecological systems of the geo-biosphere. 4th ed. Berlin: Springer.

Briones, M. J. I. (2018). The Serendipitous Value of Soil Fauna in Ecosystem Functioning: The Unexplained Explained. Front. Environ. Sci. 6, 149. doi: 10.3389/fenvs.2018.00149.

Canavan, S., Richardson, D. M., Visser, V., Le Roux, J. J., Vorontsova, M. S., and Wilson, J. R. U. (2017). The global distribution of bamboos: assessing correlates of introduction and invasion. AoB Plants 9, plw078. doi:10.1093/aobpla/plw078

Castro, A., and Wise, D. H. (2010). Influence of fallen coarse woody debris on the diversity and community structure of forest-floor spiders (Arachnida: Araneae). For. Ecol. Manag. 260, 2088–2101. doi: 10.1016/j.foreco.2010.08.051.

Chapin, F. S., Matson, P. A., and Vitousek, P. (2011). Principles of terrestrial ecosystem ecology. 2nd ed. New York: Springer-Verlag doi: 10.1007/978-1-4419-9504-9.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Steege, H. ter, and Webb, C. O. (2006). Regional and Phylogenetic Variation of Wood Density Across 2456 Neotropical Tree Species. Ecol. Appl. 16, 2356–2367. doi: 10.1890/1051-0761(2006)016[2356:RAPVOW]2.0.CO;2.

Chen, A., Liu, T., Wang, Z., and Chen, X. (2022). Plant root suberin: A layer of defence against biotic and abiotic stresses. Front. Plant Sci. 13. Available at: https://www.frontiersin.org/articles/10.3389/fpls.2022.1056008 [Accessed July 9, 2023].

Chen, T. H., Wang, D. H., and Wang, S. (2016). The trend of growth characteristics of Moso bamboo (Phyllostachys pubescens) forests under an unmanaged condition in central Taiwan. Taiwan J. For. Sci. 31, 75–87.

Chen, X., Zhang, X., Zhang, Y., Booth, T., and He, X. (2009). Changes of carbon stocks in bamboo stands in China during 100 years. For. Ecol. Manag. 258, 1489–1496. doi: 10.1016/j.foreco.2009.06.051.

Coq, S., Souquet, J.-M., Meudec, E., Cheynier, V., and Hättenschwiler, S. (2010). Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. Ecology 91, 2080–2091. doi: 10.1890/09-1076.1.

Cornelissen, J. H. C., and Thompson, K. (1997). Functional leaf attributes predict litter decomposition rate in herbaceous plants. New Phytol. 135, 109–114. doi: 10.1046/j.1469-8137.1997.00628.x.

Cornelissen, J. H. C., Pérez ‐ Harguindeguy, N., Díaz, S., Grime, J. P., Marzano, B., Cabido, M., et al. (1999). Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytol. 143, 191–200. doi: 10.1046/j.1469-8137.1999.00430.x.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., et al. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11, 1065–1071. doi: 10.1111/j.1461-0248.2008.01219.x.

Cotrufo, M. F., Galdo, I. D., and Piermatteo, D. (2010). “Litter decomposition: concepts, methods and future perspectives,” in Soil Carbon Dynamics: An Integrated Methodology, eds. A. Heinemeyer, M. Bahn, and W. L. Kutsch (Cambridge: Cambridge University Press), 76–90.

Couteaûx, M.-M., Bottner, P., and Berg, B. (1995). Litter decomposition, climate and liter quality. Trends Ecol. Evol. 10, 63–66. doi: 10.1016/S0169-5347(00)88978-8.

Cragg, R. G., and Bardgett, R. D. (2001). How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. Soil Biol. Biochem. 33, 2073–2081. doi: 10.1016/S0038-0717(01)00138-9.

David, J. F. (2014). The role of litter-feeding macroarthropods in decomposition processes: A reappraisal of common views. Soil Biol. Biochem. 76, 109–118. doi: 10.1016/j.soilbio.2014.05.009.

De Deyn, G. B., Cornelissen, J. H. C., and Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531. doi:10.1111/j.1461-0248.2008.01164.x

Déchêne, A. D., and Buddle, C. M. (2010). Decomposing logs increase oribatid mite assemblage diversity in mixedwood boreal forest. Biodivers. Conserv. 19, 237–256. doi: 10.1007/s10531-009-9719-y.

Didion, M., Repo, A., Liski, J., Forsius, M., Bierbaumer, M., and Djukic, I. (2016). Towards harmonizing leaf litter decomposition studies using standard tea bags—a field study and model application. Forests 7, 167. doi:10.3390/f7080167

Djukic, I., Kepfer-Rojas, S., Schmidt, I. K., Larsen, K. S., Beier, C., Berg, B., et al. (2018). Early stage litter decomposition across biomes. Sci. Total Environ. 628–629, 1369–1394. doi:10.1016/j.scitotenv.2018.01.012

Dudgeon, D., Ma, H. H. T., and Lam, P. K. S. (1990). Differential palatability of leaf litter to four sympatric isopods in a Hong Kong forest. Oecologia 84, 398–403. doi: 10.1007/BF00329766.

Epstein, H. E., Burke, I. C., and Lauenroth, W. K. (2002). Regional patterns of decomposition and primary production rates in the U.S. Great Plains. Ecology 83, 320–327. doi:https://doi.org/10.1890/0012-9658(2002)083[0320:RPODAP]2.0.CO;2

Esarey, J., and Sumner, J. L. (2018). Marginal effects in interaction models: determining and controlling the false positive rate. Comp. Polit. Stud. 51, 1144–1176. doi:10.1177/0010414017730080

Evans, A. M., Clinton, P. W., Allen, R. B., and Frampton, C. M. (2003). The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. For. Ecol. Manag. 184, 251–262. doi: 10.1016/S0378-1127(03)00158-0.

Facelli, J. M., and Pickett, S. T. A. (1991). Plant litter: its dynamics and effects on plant community structure. Bot. Rev. 57, 1–32. doi: 10.1007/BF02858763

Fan, P., and Guo, D. (2010). Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil. Oecologia 163, 509–515. doi: 10.1007/s00442-009-1541-4.

Fang, X., Zhao, L., Zhou, G., Huang, W., and Liu, J. (2015). Increased litter input increases litter decomposition and soil respiration but has minor effects on soil organic carbon in subtropical forests. Plant Soil 392, 139–153. doi:10.1007/s11104-015-2450-4

Fekete, I., Varga, C., Biró, B., Tóth, J. A., Várbíró, G., Lajtha, K., et al. (2016). The effects of litter production and litter depth on soil microclimate in a central European deciduous forest. Plant Soil 398, 291–300. doi:10.1007/s11104-015-2664-5

Filser, J. (2002). The role of Collembola in carbon and nitrogen cycling in soil: Proceedings of the Xth international Colloquium on Apterygota, České Budějovice 2000: Apterygota at the Beginning of the Third Millennium. Pedobiologia 46, 234–245. doi: 10.1078/0031-4056-00130.

Frazer, G. W., Canham, C. D., and Lertzman, K. P. (1999). Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs.

Freschet, G. T., Aerts, R., and Cornelissen, J. H. C. (2012). A plant economics spectrum of litter decomposability. Funct. Ecol. 26, 56–65. doi: 10.1111/j.1365-2435.2011.01913.x.

Freschet, G. T., Cornwell, W. K., Wardle, D. A., Elumeeva, T. G., Liu, W., Jackson, B. G., et al. (2013). Linking litter decomposition of above- and below-ground organs to plant–soil feedbacks worldwide. J. Ecol. 101, 943–952. doi: 10.1111/1365-2745.12092.

Frouz, J. (2018). Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. Geoderma 332, 161–172. doi: 10.1016/j.geoderma.2017.08.039.

Fu, W., Jiang, P., Zhao, K., Zhou, G., Li, Y., Wu, J., et al. (2014). The carbon storage in Moso bamboo plantation and its spatial variation in Anji county of southeastern China. J. Soils Sediments 14, 320–329. doi:10.1007/s11368-013-0665-7

Fujii, S., and Takeda, H. (2012). Succession of collembolan communities during decomposition of leaf and root litter: Effects of litter type and position. Soil Biol. Biochem. 54, 77–85. doi: 10.1016/j.soilbio.2012.04.021.

Fujii, S., and Takeda, H. (2017). Succession of soil microarthropod communities during the aboveground and belowground litter decomposition processes. Soil Biol. Biochem. 110, 95–102. doi: 10.1016/j.soilbio.2017.03.003.

Fujii, S., Cornelissen, J. H. C., Berg, M. P., and Mori, A. S. (2018). Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient. Funct. Ecol. 32, 840–852. doi: 10.1111/1365-2435.13027.

Fujii, S., Makita, N., Mori, A. S., and Takeda, H. (2016). Plant species control and soil faunal involvement in the processes of above- and below-ground litter decomposition. Oikos 125, 883–892. doi: 10.1111/oik.02457.

Fukuzawa, K., Shibata, H., Takagi, K., Satoh, F., Koike, T., and Sasa, K. (2007). Vertical distribution and seasonal pattern of fine-root dynamics in a cool–temperate forest in northern Japan: implication of the understory vegetation, Sasa dwarf bamboo. Ecol. Res. 22, 485–495. doi:10.1007/s11284-006-0031-y

García‐Palacios, P., Maestre, F. T., Kattge, J., and Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecol. Lett. 16, 1045–1053. doi: 10.1111/ele.12137.

García-Palacios, P., Shaw, E. A., Wall, D. H., and Hättenschwiler, S. (2016). Temporal dynamics of biotic and abiotic drivers of litter decomposition. Ecol. Lett. 19, 554–563. doi:10.1111/ele.12590

Gill, R. A., and Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147, 13–31. doi: 10.1046/j.1469-8137.2000.00681.x.

Goebel, M., Hobbie, S. E., Bulaj, B., Zadworny, M., Archibald, D. D., Oleksyn, J., et al. (2011). Decomposition of the finest root branching orders: linking belowground dynamics to fine-root function and structure. Ecol. Monogr. 81, 89–102. doi: 10.1890/09-2390.1.

Goldin, S. R., and Hutchinson, M. F. (2014). Coarse woody debris reduces the rate of moisture loss from surface soils of cleared temperate Australian woodlands. Soil Res. 52, 637–644. doi: 10.1071/SR13337.

Goldin, S. R., and Hutchinson, M. F. (2015). Thermal refugia in cleared temperate Australian woodlands: coarse woody debris moderate extreme surface soil temperatures. Agric. For. Meteorol. 214–215, 39–47. doi: 10.1016/j.agrformet.2015.07.011.

Gonzalez-Polo, M., Fernández-Souto, A., and Austin, A. T. (2013). Coarse Woody Debris Stimulates Soil Enzymatic Activity and Litter Decomposition in an Old-Growth Temperate Forest of Patagonia, Argentina. Ecosystems 16, 1025–1038. doi: 10.1007/s10021-013-9665-0.

Guo, D. L., Mitchell, R. J., and Hendricks, J. J. (2004). Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140, 450–457. doi: 10.1007/s00442-004-1596-1.

Hair, J. F., Hult, G. T. M., Ringle, C. M., and Sarstedt, M. (2017). A primer on partial least squares structural equation modeling (PLS-SEM). Thousand Oaks, CA: Sage Publications.

Hanula, J. L., Horn, S., and Wade, D. D. (2006). The role of dead wood in maintaining arthropod diversity on the forest floor. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station Available at: http://www.fs.usda.gov/treesearch/pubs/24878 [Accessed November 17, 2021].

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., et al. (2004). “Ecology of Coarse Woody Debris in Temperate Ecosystems,” in Advances in Ecological Research Advances in Ecological Research: Classic Papers. (Academic Press), 59–234. doi: 10.1016/S0065-2504(03)34002-4.

Harrop-Archibald, H., Didham, R. K., Standish, R. J., Tibbett, M., and Hobbs, R. J. (2016). Mechanisms linking fungal conditioning of leaf litter to detritivore feeding activity. Soil Biol. Biochem. 93, 119–130. doi: 10.1016/j.soilbio.2015.10.021.

Hasegawa, M., and Takeda, H. (1995). Changes in feeding attributes of four collembolan populations during the decomposition process of pine needles. Pedobiologia 39, 155–169. Available at: https://ci.nii.ac.jp/naid/10027503320/ [Accessed August 21, 2020].

Hättenschwiler, S., and Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. Proc. Natl. Acad. Sci. 102, 1519–1524. doi: 10.1073/pnas.0404977102.

Hishi, T. (2007). Heterogeneity of individual roots within the fine root architecture: causal links between physiological and ecosystem functions. J. For. Res. 12, 126–133. doi: 10.1007/s10310-006-0260-5.

Hobbie, S. E. (1996). Temperature and Plant Species Control Over Litter Decomposition in Alaskan Tundra. Ecol. Monogr. 66, 503–522. doi: 10.2307/2963492.

Hobbie, S. E., Oleksyn, J., Eissenstat, D. M., and Reich, P. B. (2010). Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. Oecologia 162, 505–513. doi: 10.1007/s00442-009-1479-6.

Holub, S. M., Spears, J. D., and Lajtha, K. (2001). A reanalysis of nutrient dynamics in coniferous coarse woody debris. Can. J. For. Res. 31, 1894–1902. doi: 10.1139/x01-125.

Homet, P., Gómez-Aparicio, L., Matías, L., and Godoy, O. (2021). Soil fauna modulates the effect of experimental drought on litter decomposition in forests invaded by an exotic pathogen. J. Ecol. 109, 2963–2980. doi: 10.1111/1365-2745.13711.

Ichihashi, R., Komatsu, H., Kume, T., Onozawa, Y., Shinohara, Y., Tsuruta, K., et al. (2015). Stand-scale transpiration of two Moso bamboo stands with different culm densities. Ecohydrology 8, 450–459. doi: 10.1002/eco.1515.

Inoue, A., Sato, M., and Shima, H. (2018). Maximum size-density relationship in bamboo forests: case study of Phyllostachys pubescens forests in Japan. For. Ecol. Manag. 425, 138–144. doi:10.1016/j.foreco.2018.05.044

Irmler, U. (2000). Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two deciduous forests. Pedobiologia 44, 105–118. doi: 10.1078/S0031-4056(04)70032-3.

Isagi, Y., and Torii, A. (1997). Range expansion and its mechanisms in a naturalized bamboo species, Phyllostachys pubescens, in Japan. J. Sustain. For. 6, 127–141. doi:10.1300/J091v06n01_08

Isagi, Y., Kawahara, T., Kamo, K., and Ito, H. (1997). Net production and carbon cycling in a bamboo Phyllostachys pubescens stand. Plant Ecol. 130, 41–52. doi: 10.1023/A:1009711814070.

Jabin, M., Mohr, D., Kappes, H., and Topp, W. (2004). Influence of deadwood on density of soil macro-arthropods in a managed oak–beech forest. For. Ecol. Manag. 194, 61–69. doi: 10.1016/j.foreco.2004.01.053.

Jackson, R. B., Lajtha, K., Crow, S. E., Hugelius, G., Kramer, M. G., and Piñeiro, G. (2017). The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. Annu. Rev. Ecol. Evol. Syst. 48, 419–445. doi:10.1146/annurev-ecolsys-112414-054234

Jackson, R. B., Mooney, H. A., and Schulze, E.-D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sci. 94, 7362–7366. doi: 10.1073/pnas.94.14.7362.

Japan Meteorological Agency (2019). Records of 2008-2018 period. Available at: http://www.data.jma.go.jp/obd/stats/etrn/ [Accessed April 1, 2019].

Jastrow, J. D., and Miller, R. M. (1998). "Soil Aggregate Stabilization and Carbon Sequestration: Feedbacks through Organomineral Associations," in Soil Processes and the Carbon Cycle (Boca Raton, FL: CRC Press), 207–224.

Jobbágy, E. G., and Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol. Appl. 10, 423–436. doi:10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2

Johnston, J., and Crossley, D. (1993). in The significance of coarse woody debris for the diversity of soil mites Biodiversity and Coarse Woody Debris in Southern Forests: Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. (USDA Forest Service, Southern Forest Experiment Station), 82–87.

Joly, F.-X., Milcu, A., Scherer-Lorenzen, M., Jean, L.-K., Bussotti, F., Dawud, S. M., et al. (2017). Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. New Phytol. 214, 1281–1293. doi:10.1111/nph.14452

Joly, F.-X., Scherer-Lorenzen, M., and Hättenschwiler, S. (2023). Resolving the intricate role of climate in litter decomposition. Nat. Ecol. Evol. 7, 214–223. doi: 10.1038/s41559-022-01948-z.

Joo, S. J., Yim, M. H., and Nakane, K. (2006). Contribution of microarthropods to the decomposition of needle litter in a Japanese cedar (Cryptomeria japonica D. Don) plantation. For. Ecol. Manag. 234, 192–198. doi: 10.1016/j.foreco.2006.07.005.

Kampichler, C., and Bruckner, A. (2009). The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. Biol. Rev. Camb. Philos. Soc. 84, 375–389. doi: 10.1111/j.1469-185X.2009.00078.x.

Kappes, H. (2005). Influence of coarse woody debris on the gastropod community of a managed calcareous beech forest in western Europe. J. Molluscan Stud. 71, 85–91. doi: 10.1093/mollus/eyi011.

Kappes, H., Catalano, C., and Topp, W. (2007). Coarse woody debris ameliorates chemical and biotic soil parameters of acidified broad-leaved forests. Appl. Soil Ecol. 36, 190–198. doi: 10.1016/j.apsoil.2007.02.003.

Katayama, A., Endo, I., Makita, N., Matsumoto, K., Kume, T., and Ohashi, M. (2021). Vertical variation in mass and CO2 efflux of litter from the ground to the 40m high canopy in a Bornean tropical rainforest. Agric. For. Meteorol. 311, 108659. doi: 10.1016/j.agrformet.2021.108659.

Kay, B. D. (1998). “Soil Structure and Organic Carbon: A Review,” in Soil Processes and the Carbon Cycle (Boca Raton, FL: CRC Press), 169-197.

Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O., and Garnier, E. (2009). Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply. Ann. Bot. 104, 1151–1161. doi: 10.1093/aob/mcp202.

Keuskamp, J. A., Dingemans, B. J. J., Lehtinen, T., Sarneel, J. M., and Hefting, M. M. (2013). Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. Methods Ecol. Evol. 4, 1070–1075. doi:https://doi.org/10.1111/2041-210X.12097

Kobayashi, K., Ohashi, M., Fujihara, M., Kitayama, K., and Onoda, Y. (2023). Rhizomes play significant roles in biomass accumulation, production and carbon turnover in a stand of the tall bamboo Phyllostachys edulis. J. For. Res. 28, 42–50. doi: 10.1080/13416979.2022.2090669.

Kögel-Knabner, I. (2017). The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter: Fourteen years on. Soil Biol. Biochem. 105, A3–A8. doi: 10.1016/j.soilbio.2016.08.011.

Komatsu, H., Onozawa, Y., Kume, T., Tsuruta, K., Kumagai, T., Shinohara, Y., et al. (2010). Stand-scale transpiration estimates in a Moso bamboo forest: II. Comparison with coniferous forests. For. Ecol. Manag. 260, 1295–1302. doi: 10.1016/j.foreco.2010.06.040.

Krantz, G. M., and Walter, D. E. (Eds.) (2009). A Manual of Acarology. Third Edition. Lubbock, Texas: Texas Tech University Press.

Laiho, R., and Prescott, C. E. (2004). Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Can. J. For. Res. 34, 763–777. doi: 10.1139/x03-241.

Liao, C., Long, C., Zhang, Q., and Cheng, X. (2022). Stronger effect of litter quality than micro-organisms on leaf and root litter C and N loss at different decomposition stages following a subtropical land use change. Funct. Ecol. 36, 896–907. doi: 10.1111/1365-2435.13999.

Lin, D., Dou, P., Yang, G., Qian, S., Wang, H., Zhao, L., et al. (2020). Home-field advantage of litter decomposition differs between leaves and fine roots. New Phytol. 227, 995–1000. doi: 10.1111/nph.16517.

Lin, D., Pang, M., Fanin, N., Wang, H., Qian, S., Zhao, L., et al. (2019). Fungi participate in driving home-field advantage of litter decomposition in a subtropical forest. Plant Soil 434, 467–480. doi: 10.1007/s11104-018-3865-5.

Lin, D., Wang, F., Fanin, N., Pang, M., Dou, P., Wang, H., et al. (2019). Soil fauna promote litter decomposition but do not alter the relationship between leaf economics spectrum and litter decomposability. Soil Biol. Biochem. 136, 107519. doi: 10.1016/j.soilbio.2019.107519.

Lin, M. Y., Hsieh, I. F., Lin, P. H., Laplace, S., Ohashi, M., Chen, T. H., et al. (2017). Moso bamboo (Phyllostachys pubescens) forests as a significant carbon sink? A case study based on 4-year measurements in central Taiwan. Ecol. Res. 32, 845–857. doi: 10.1007/s11284-017-1497-5

Liu, C., Zhou, Y., Qin, H., Liang, C., Shao, S., Fuhrmann, J. J., et al. (2021). Moso bamboo invasion has contrasting effects on soil bacterial and fungal abundances, co-occurrence networks and their associations with enzyme activities in three broadleaved forests across subtropical China. For. Ecol. Manag. 498, 119549. doi: 10.1016/j.foreco.2021.119549

Liu, G., Cornwell, W. K., Cao, K., Hu, Y., Van Logtestijn, R. S. P., Yang, S., et al. (2015). Termites amplify the effects of wood traits on decomposition rates among multiple bamboo and dicot woody species. J. Ecol. 103, 1214–1223. doi: 10.1111/1365-2745.12427.

Liu, G., Shi, P., Xu, Q., Dong, X., Wang, F., Wang, G. G., et al. (2016). Does the size–density relationship developed for bamboo species conform to the self-thinning rule? For. Ecol. Manag. 361, 339–345. doi: 10.1016/j.foreco.2015.11.030.

Liu, X., Lin, T.-C., Vadeboncoeur, M. A., Yang, Z., Chen, S., Xiong, D., et al. (2019). Root litter inputs exert greater influence over soil C than does aboveground litter in a subtropical natural forest. Plant Soil 444, 489–499. doi:10.1007/s11104-019-04294-5

Liu, X., Siemann, E., Cui, C., Liu, Y., Guo, X., and Zhang, L. (2019). Moso bamboo (Phyllostachys edulis) invasion effects on litter, soil and microbial PLFA characteristics depend on sites and invaded forests. Plant Soil 438, 85–99. doi: 10.1007/s11104-019-04010-3

Liu, Y., Wang, L., He, R., Chen, Y., Xu, Z., Tan, B., et al. (2019). Higher soil fauna abundance accelerates litter carbon release across an alpine forest-tundra ecotone. Sci. Rep. 9, 10561. doi: 10.1038/s41598-019-47072-0.

Long, J. A. (2021). interactions: comprehensive, user-friendly toolkit for probing interactions. Available at: https://CRAN.R-project.org/package=interactions

Long, K., Yin, R., Kardol, P., Wei, Q., Li, Y., and Huang, J. (2023). Bamboo invasion alters Collembola community composition varying with life-forms. Pest Manag. Sci. 79, 2517–2526. doi: 10.1002/ps.7434.

Luan, J., Liu, S., Li, S., Whalen, J. K., Wang, Y., Wang, J., et al. (2021). Functional diversity of decomposers modulates litter decomposition affected by plant invasion along a climate gradient. J. Ecol. 109, 1236–1249. doi: 10.1111/1365-2745.13548.

Lussenhop, J. (1992). “Mechanisms of microarthropod-microbial interactions in soil,” in Advances in Ecological Research, eds. M. Begon and A. H. Fitter (Academic Press), 1–33. doi: 10.1016/S0065-2504(08)60145-2.

Magnússon, R. Í., Tietema, A., Cornelissen, J. H. C., Hefting, M. M., and Kalbitz, K. (2016). Tamm Review: Sequestration of carbon from coarse woody debris in forest soils. For. Ecol. Manag. 377, 1–15. doi: 10.1016/j.foreco.2016.06.033.

Makkonen, M., Berg, M. P., Logtestijn, R. S. P. van, Hal, J. R. van, and Aerts, R. (2013). Do physical plant litter traits explain non-additivity in litter mixtures? A test of the improved microenvironmental conditions theory. Oikos 122, 987–997. doi: 10.1111/j.1600-0706.2012.20750.x.

Manzoni, S., Jackson, R. B., Trofymow, J. A., and Porporato, A. (2008). The Global Stoichiometry of Litter Nitrogen Mineralization. Science 321, 684–686. doi: 10.1126/science.1159792.

Mathers, N. J., Jalota, R. K., Dalal, R. C., and Boyd, S. E. (2007). 13C-NMR analysis of decomposing litter and fine roots in the semi-arid Mulga Lands of southern Queensland. Soil Biol. Biochem. 39, 993–1006. doi: 10.1016/j.soilbio.2006.11.009.

McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., et al. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. New Phytol. 207, 505–518. doi: 10.1111/nph.13363.

Meentemeyer, V. (1978). Macroclimate and lignin control of litter decomposition rates. Ecology 59, 465–472. doi:https://doi.org/10.2307/1936576

Minerovic, A. J., Valverde-Barrantes, O. J., and Blackwood, C. B. (2018). Physical and microbial mechanisms of decomposition vary in importance among root orders and tree species with differing chemical and morphological traits. Soil Biol. Biochem. 124, 142–149. doi: 10.1016/j.soilbio.2018.06.006.

Minnich, C., Peršoh, D., Poll, C., and Borken, W. (2021). Changes in Chemical and Microbial Soil Parameters Following 8 Years of Deadwood Decay: An Experiment with Logs of 13 Tree Species in 30 Forests. Ecosystems 24, 955–967. doi: 10.1007/s10021-020-00562-z.

Morel, J. L., Habib, L., Plantureux, S., and Guckert, A. (1991). Influence of maize root mucilage on soil aggregate stability. Plant Soil 136, 111–119. doi:10.1007/BF02465226

Mori, T., Aoyagi, R., Taga, H., and Sakai, Y. (2021). Effects of water content and mesh size on tea bag decomposition. Ecologies 2, 175–186. doi:10.3390/ecologies2010010

Mueller, P., Schile-Beers, L. M., Mozdzer, T. J., Chmura, G. L., Dinter, T., Kuzyakov, Y., et al. (2018). Global-change effects on early-stage decomposition processes in tidal wetlands – implications from a global survey using standardized litter. Biogeosciences 15, 3189–3202. doi:10.5194/bg-15-3189-2018

Na, M., Sun, X., Zhang, Y., Sun, Z., and Rousk, J. (2021). Higher stand densities can promote soil carbon storage after conversion of temperate mixed natural forests to larch plantations. Eur. J. For. Res. 140, 373–386. doi:10.1007/s10342-020-01346-9

Neher, D. A., Weicht, T. R., and Barbercheck, M. E. (2012). Linking invertebrate communities to decomposition rate and nitrogen availability in pine forest soils. Appl. Soil Ecol. 54, 14–23. doi: 10.1016/j.apsoil.2011.12.001.

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2020). Vegan: Community Ecology Package. R package version 2.5-7. Available at: https://cran.r-project.org/web/packages/vegan/vegan.pdf [Accessed May 17, 2021].

Okutomi, K., Shinoda, S., and Fukuda, H. (1996). Causal analysis of the invasion of broad-leaved forest by bamboo in Japan. J. Veg. Sci. 7, 723–728. doi:https://doi.org/10.2307/3236383

Olson, J. S. (1963). Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. Ecology 44, 322–331. doi: 10.2307/1932179.

Ono, K., Hiradate, S., Morita, S., and Hirai, K. (2013). Fate of organic carbon during decomposition of different litter types in Japan. Biogeochemistry 112, 7–21. doi: 10.1007/s10533-011-9682-z.

Osler, G. H. R., and Sommerkorn, M. (2007). Toward a Complete Soil C and N Cycle: Incorporating the Soil Fauna. Ecology 88, 1611–1621. doi: 10.1890/06-1357.1.

Ouyang, M., Yang, Q., Chen, X., Yang, G., Shi, J., and Fang, X. (2016). Effects of the expansion of Phyllostachys edulis on species composition, structure and diversity of the secondary evergreen broad-leaved forests. Biodivers. Sci. 24, 649. doi: 10.17520/biods.2015290.

Palviainen, M., Finér, L., Laiho, R., Shorohova, E., Kapitsa, E., and Vanha-Majamaa, I. (2010). Carbon and nitrogen release from decomposing Scots pine, Norway spruce and silver birch stumps. For. Ecol. Manag. 259, 390–398. doi: 10.1016/j.foreco.2009.10.034.

Palviainen, M., Laiho, R., Mäkinen, H., and Finér, L. (2008). Do decomposing Scots pine, Norway spruce, and silver birch stems retain nitrogen? Can. J. For. Res. 38, 3047–3055. doi: 10.1139/X08-147.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., et al. (2011). A Large and Persistent Carbon Sink in the World's Forests. Science 333, 988–993. doi: 10.1126/science.1201609.

Parton, W., Silver, W. L., Burke, I. C., Grassens, L., Harmon, M. E., Currie, W. S., et al. (2007). Global-Scale Similarities in Nitrogen Release Patterns During Long-Term Decomposition. Science 315, 361–364. doi: 10.1126/science.1134853.

Penne, C., Ahrends, B., Deurer, M., and Böttcher, J. (2010). The impact of the canopy structure on the spatial variability in forest floor carbon stocks. Geoderma 158, 282–297. doi:10.1016/j.geoderma.2010.05.007

Perreault, L., Forrester, J. A., Mladenoff, D. J., and Lewandowski, T. E. (2021). Deadwood Reduces the Variation in Soil Microbial Communities Caused by Experimental Forest Gaps. Ecosystems. doi: 10.1007/s10021-021-00624-w.

Peršoh, D., and Borken, W. (2017). Impact of woody debris of different tree species on the microbial activity and community of an underlying organic horizon. Soil Biol. Biochem. 115, 516–525. doi: 10.1016/j.soilbio.2017.09.017.

Petersen, H., and Luxton, M. (1982). A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. Oikos 39, 288–388. doi: 10.2307/3544689.

Petraglia, A., Cacciatori, C., Chelli, S., Fenu, G., Calderisi, G., Gargano, D., et al. (2019). Litter decomposition: effects of temperature driven by soil moisture and vegetation type. Plant Soil 435, 187–200. doi:10.1007/s11104-018-3889-x

Pettit, N. E., and Naiman, R. J. (2005). Flood-deposited wood debris and its contribution to heterogeneity and regeneration in a semi-arid riparian landscape. Oecologia 145, 434–444. doi: 10.1007/s00442-005-0143-z.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team (2019). nlme: Linear and nonlinear mixed effects models. R package version 3.1-141.

Poirier, V., Roumet, C., and Munson, A. D. (2018). The root of the matter: Linking root traits and soil organic matter stabilization processes. Soil Biol. Biochem. 120, 246–259. doi: 10.1016/j.soilbio.2018.02.016.

Powers, J. S., Montgomery, R. A., Adair, E. C., Brearley, F. Q., DeWalt, S. J., Castanho, C. T., et al. (2009). Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. J. Ecol. 97, 801–811. doi: https://doi.org/10.1111/j.1365-2745.2009.01515.x.

Pregitzer, K. S., DeForest, J. L., Burton, A. J., Allen, M. F., Ruess, R. W., and Hendrick, R. L. (2002). Fine Root Architecture of Nine North American Trees. Ecol. Monogr. 72, 293–309. doi: 10.1890/0012-9615(2002)072[0293:FRAONN]2.0.CO;2.

Prescott, C. E. (2002). The influence of the forest canopy on nutrient cycling. Tree Physiol. 22, 1193–1200. doi:10.1093/treephys/22.15-16.1193

Prescott, C. E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101, 133–149. doi:10.1007/s10533-010-9439-0

Qin, H., Niu, L., Wu, Q., Chen, J., Li, Y., Liang, C., et al. (2017). Bamboo forest expansion increases soil organic carbon through its effect on soil arbuscular mycorrhizal fungal community and abundance. Plant Soil 420, 407–421. doi: 10.1007/s11104-017-3415-6

R Core Team (2021). R: A Language and Environment for Statistical Computing. R Found. Stat. Comput. Vienna Austria. Available at: https://www.R-project.org/.

Remsburg, A. J., and Turner, M. G. (2006). Amount, position, and age of coarse wood influence litter decomposition in postfire Pinus contorta stands. Can. J. For. Res. doi: 10.1139/x06-079.

Ringle, C. M., Wende, S., and Becker, J.M. (2015). SmartPLS 3. Version 3.3.6. Germany: SmartPLS GmbH.

Rinne, K. T., Rajala, T., Peltoniemi, K., Chen, J., Smolander, A., and Mäkipää, R. (2017). Accumulation rates and sources of external nitrogen in decaying wood in a Norway spruce dominated forest. Funct. Ecol. 31, 530–541. doi: 10.1111/1365-2435.12734.

Sarneel, J. M., Sundqvist, M. K., Molau, U., Björkman, M. P., and Alatalo, J. M. (2020). Decomposition rate and stabilization across six tundra vegetation types exposed to >20 years of warming. Sci. Total Environ. 724, 138304. doi:10.1016/j.scitotenv.2020.138304

Schädler, M., and Brandl, R. (2005). Do invertebrate decomposers affect the disappearance rate of litter mixtures? Soil Biol. Biochem. 37, 329–337. doi: 10.1016/j.soilbio.2004.07.042.

Scheu, S., Ruess, L., and Bonkowski, M. (2005). "Interactions between microorganisms and soil micro- and mesofauna," in Microorganisms in Soils: Roles in Genesis and Functions Soil Biology., eds. A. Varma and F. Buscot (Berlin, Heidelberg: Springer), 253–275. doi: 10.1007/3-540-26609-7_12.

Schuur, E. A. G. (2001). The effect of water on decomposition dynamics in mesic to wet Hawaiian montane forests. Ecosystems 4, 259–273. doi:10.1007/s10021-001-0008-1

Seastedt, T. R. (1984). The role of microarthropods in decomposition and mineralization Processes. Annu. Rev. Entomol. 29, 25–46. doi: 10.1146/annurev.en.29.010184.000325.

Seethepalli, A., Dhakal, K., Griffiths, M., Guo, H., Freschet, G. T., and York, L. M. (2021). RhizoVision Explorer: open-source software for root image analysis and measurement standardization. AoB PLANTS 13, plab056. doi: 10.1093/aobpla/plab056.

Setälä, H. (2002). Sensitivity of ecosystem functioning to changes in trophic structure, functional group composition and species diversity in belowground food webs. Ecol. Res. 17, 207–215. doi: 10.1046/j.1440-1703.2002.00480.x.

Shimada, N., Tsuyama, T., and Kamei, I. (2019). Rapid determination of Thioglycolic Acid Lignin for various biomass samples. J. Wood Sci. Soc. Jpn. 65, 25–32. doi: 10.2488/jwrs.65.25.

Shimono, K., Katayama, A., Abe, H., and Enoki, T. (2021). Carbon and nitrogen storage of dead woody debris in an abandoned Moso bamboo forest. Bull. Kyushu Univ. For., 9–14. doi: https://doi.org/10.15017/4377826.

Shimono, K., Katayama, A., Kume, T., Enoki, T., Chiwa, M., and Hishi, T. (2022). Differences in net primary production allocation and nitrogen use efficiency between Moso bamboo and Japanese cedar forests along a slope. J. For. Res. 27, 28–35. doi: 10.1080/13416979.2021.1965280.

Shinohara, Y., and Otsuki, K. (2015). Comparisons of soil-water content between a Moso bamboo (Phyllostachys pubescens) forest and an evergreen broadleaved forest in western Japan. Plant Species Biol. 30, 96–103. doi: 10.1111/1442-1984.12076.

Shinohara, Y., Kume, T., Ichihashi, R., Komatsu, H., and Otsuki, K. (2014). Moso bamboo forests in Japan: what are the effects of their area expansion on ecosystem services? J. Jpn. For. Soc. 96, 351–361. doi:10.4005/jjfs.96.351

Silver, W. L., and Miya, R. K. (2001). Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129, 407–419. doi: 10.1007/s004420100740.

Six, J., Bossuyt, H., Degryze, S., and Denef, K. (2004). A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil Tillage Res. 79, 7–31. doi:10.1016/j.still.2004.03.008

Six, J., Conant, R. T., Paul, E. A., and Paustian, K. (2002). Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241, 155–176. doi:10.1023/A:1016125726789

Smith, V. C., and Bradford, M. A. (2003). Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. Appl. Soil Ecol. 24, 197–203. doi: 10.1016/S0929-1393(03)00094-5.

Soane, B. D. (1990). The role of organic matter in soil compactibility: A review of some practical aspects. Soil Tillage Res. 16, 179–201. doi:10.1016/0167-1987(90)90029-D

Song, Q., Lu, H., Liu, J., Yang, J., Yang, G., and Yang, Q. (2017). Accessing the impacts of bamboo expansion on NPP and N cycling in evergreen broadleaved forest in subtropical China. Sci. Rep. 7, 40383. doi: 10.1038/srep40383.

Song, Q., Ouyang, M., Yang, Q., Lu, H., Yang, G., Chen, F., et al. (2016). Degradation of litter quality and decline of soil nitrogen mineralization after Moso bamboo (Phyllostachys pubescens) expansion to neighboring broadleaved forest in subtropical China. Plant Soil 404, 113–124. doi:10.1007/s11104-016-2835-z

Song, X., Wang, Z., Tang, X., Xu, D., Liu, B., Mei, J., et al. (2020). The contributions of soil mesofauna to leaf and root litter decomposition of dominant plant species in grassland. Appl. Soil Ecol. 155, 103651. doi: 10.1016/j.apsoil.2020.103651.

Song, X., Zhou, G., Jiang, H., Yu, S., Fu, J., Li, W., et al. (2011). Carbon sequestration by Chinese bamboo forests and their ecological benefits: assessment of potential, problems, and future challenges. Environ. Rev. 19, 418–428. doi: 10.1139/a11-015.

Spears, J. D., Holub, S. M., Harmon, M. E., and Lajtha, K. (2003). The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. Can. J. For. Res. 33, 2193–2201. doi: 10.1139/x03-148.

Sun, T., Dong, L., Zhang, L., Wu, Z., Wang, Q., Li, Y., et al. (2016). Early Stage Fine-Root Decomposition and Its Relationship with Root Order and Soil Depth in a Larix gmelinii Plantation. Forests 7, 234. doi: 10.3390/f7100234.

Sun, T., Hobbie, S. E., Berg, B., Zhang, H., Wang, Q., Wang, Z., et al. (2018). Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. Proc. Natl. Acad. Sci. 115, 10392–10397. doi: 10.1073/pnas.1716595115.

Sun, T., Mao, Z., Dong, L., Hou, L., Song, Y., and Wang, X. (2013). Further evidence for slow decomposition of very fine roots using two methods: litterbags and intact cores. Plant Soil 366, 633–646. doi: 10.1007/s11104-012-1457-3.

Suzuki, S. (2015). Chronological location analyses of giant bamboo (Phyllostachys pubescens) groves and their invasive expansion in a satoyama landscape area, western Japan. Plant Species Biol. 30, 63–71. doi:10.1111/1442-1984.12067

Suzuki, S. N., Ataka, M., Djukic, I., Enoki, T., Fukuzawa, K., Hirota, M., et al. (2019). Harmonized data on early stage litter decomposition using tea material across Japan. Ecol. Res. 34, 575–576. doi: 10.1111/1440-1703.12032

Suzuki, S., and Nakagoshi, N. (2008). Expansion of bamboo forests caused by reduced bamboo-shoot harvest under different natural and artificial conditions. Ecol. Res. 23, 641–647. doi: http://dx.doi.org/10.1007/s11284-007-0422-8.

Swift, M. J., Heal, O. W., and Anderson, J. M. (1979). Decomposition in Terrestrial Ecosystems. Oxford: Blackwell Scientific Publications.

Taiwan Central Weather Bureau. (2019). Records of 2008-2018 period. https://www.cwb.gov.tw/V8/E/index.html [Accessed January 13, 2019].

Takano, K. T., Hibino, K., Numata, A., Oguro, M., Aiba, M., Shiogama, H., et al. (2017). Detecting latitudinal and altitudinal expansion of invasive bamboo Phyllostachys edulis and Phyllostachys bambusoides (Poaceae) in Japan to project potential habitats under 1.5°C–4.0°C global warming. Ecol. Evol. 7, 9848–9859. doi:10.1002/ece3.3471

Taylor, P. G., Cleveland, C. C., Wieder, W. R., Sullivan, B. W., Doughty, C. E., Dobrowski, S. Z., et al. (2017). Temperature and rainfall interact to control carbon cycling in tropical forests. Ecol. Lett. 20, 779–788. doi:10.1111/ele.12765

Traoré, O., Groleau-Renaud, V., Plantureux, S., Tubeileh, A., and Boeuf-Tremblay, V. (2000). Effect of root mucilage and modelled root exudates on soil structure. Eur. J. Soil Sci. 51, 575–581. doi:10.1111/j.1365-2389.2000.00348.x

Tresch, S., Frey, D., Le Bayon, R.-C., Zanetta, A., Rasche, F., Fliessbach, A., et al. (2019). Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. Sci. Total Environ. 658, 1614–1629. doi: 10.1016/j.scitotenv.2018.12.235.

Tripathi, S. K., and Singh, K. P. (1992). Nutrient immobilization and release patterns during plant decomposition in a dry tropical bamboo savanna, India. Biol. Fertil. Soils 14, 191–199. doi: 10.1007/BF00346060.

Ugawa, S., Miura, S., Matsuura, Y., Takahashi, M., and Kaneko, S. (2011). Characteristics of culm structure and carbon and nitrogen concentrations in dead bamboo culms of two Phyllostachys species. Plant Soil 347, 269–278. doi: 10.1007/s11104-011-0844-5.

Ulyshen, M. D., and Hanula, J. L. (2009). Responses of Arthropods to Large-Scale Manipulations of Dead Wood in Loblolly Pine Stands of the Southeastern United States. Environ. Entomol. 38, 1005–1012. doi: 10.1603/022.038.0407.

Ulyshen, M. D., Klooster, W. S., Barrington, W. T., and Herms, D. A. (2011). Impacts of emerald ash borer-induced tree mortality on leaf litter arthropods and exotic earthworms. Pedobiologia 54, 261–265. doi: 10.1016/j.pedobi.2011.05.001.

Veen, G. F. (Ciska), Freschet, G. T., Ordonez, A., and Wardle, D. A. (2015). Litter quality and environmental controls of home-field advantage effects on litter decomposition. Oikos 124, 187–195. doi:https://doi.org/10.1111/oik.01374

von Lützow, M., and Kögel-Knabner, I. (2009). Temperature sensitivity of soil organic matter decomposition—what do we know? Biol. Fertil. Soils 46, 1–15. doi:10.1007/s00374-009-0413-8

Wall, D. H., Bradford, M. A., John, M. G. S., Trofymow, J. A., Behan‐Pelletier, V., Bignell, D. E., et al. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Glob. Change Biol. 14, 2661−2677. doi: 10.1111/j.1365-2486.2008.01672.x.

Wallace, K. J., Laughlin, D. C., Clarkson, B. D., and Schipper, L. A. (2018). Forest canopy restoration has indirect effects on litter decomposition and no effect on denitrification. Ecosphere 9, e02534. doi:https://doi.org/10.1002/ecs2.2534

Wang, B., Wei, W.J., Liu, C.J., You, W.Z., Niu, X., Man, R.Z. (2013). Biomass and carbon stock in moso bamboo forest in subtropical China: characteristics and implications. J. Trop. For. Sci. 25(1), 137-148.

Wang, P., Liu, X., Mou, P., Guo, J., and Li, S. (2019). Root order and initial moisture status influenced root decomposition in a subtropical tree species Liquidambar formosana. Plant Soil 443, 539–548. doi: 10.1007/s11104-019-04248-x.

Wang, Z., Yin, X., and Li, X. (2015). Soil mesofauna effects on litter decomposition in the coniferous forest of the Changbai Mountains, China. Appl. Soil Ecol. 92, 64–71. doi: 10.1016/j.apsoil.2015.03.010.

Wardle, D. (2002). Communities and ecosystems: Linking the aboveground and belowground components.

Wardle, D. A., and Lavelle, P. (1997). “Linkages between soil biota, plant litter quality and decomposition,” in Driven by Nature: Plant litter quality and decomposition (London: CAB International.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., and Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633. doi:10.1126/science.1094875

Warton, D. I., Duursma, R. A., Falster, D. S., and Taskinen, S. (2012). smatr 3– an R package for estimation and inference about allometric lines. Methods Ecol. Evol. 3, 257–259. doi: 10.1111/j.2041-210X.2011.00153.x.

Watanabe, T., Fukuzawa, K., and Shibata, H. (2013). Temporal changes in litterfall, litter decomposition and their chemical composition in Sasa dwarf bamboo in a natural forest ecosystem of northern Japan. J. For. Res. 18, 129–138. doi: 10.1007/s10310-011-0330-1.

Xiao, H., Liu, J., and Li, F. (2023). Both alpha and beta diversity of nematode declines in response to moso bamboo expansion in south China. Appl. Soil Ecol. 183, 104761. doi: 10.1016/j.apsoil.2022.104761.

Xiong, Y., Fan, P., Fu, S., Zeng, H., and Guo, D. (2013). Slow decomposition and limited nitrogen release by lower order roots in eight Chinese temperate and subtropical trees. Plant Soil 363, 19–31. doi: 10.1007/s11104-012-1290-8.

Xu, M., Ji, H., and Zhuang, S. (2018). Carbon stock of Moso bamboo (Phyllostachys pubescens) forests along a latitude gradient in the subtropical region of China. PLOS ONE 13, e0193024. doi:10.1371/journal.pone.0193024

Xu, S., Liu, L. L., and Sayer, E. J. (2013). Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments. Biogeosciences 10, 7423–7433. doi:10.5194/bg-10-7423-2013

Yang, C., Wang, A., Zhu, Z., Lin, S., Bi, Y., and Du, X. (2021). Impact of extensive management system on soil properties and carbon sequestration under an age chronosequence of Moso bamboo plantations in subtropical China. For. Ecol. Manag. 497, 119535. doi:10.1016/j.foreco.2021.119535

Yang, X., and Chen, J. (2009). Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. Soil Biol. Biochem. 41, 910–918. doi: 10.1016/j.soilbio.2008.12.028.

Yen, T.-M., and Lee, J.-S. (2011). Comparing aboveground carbon sequestration between moso bamboo (Phyllostachys heterocycla) and China fir (Cunninghamia lanceolata) forests based on the allometric model. For. Ecol. Manag. 261, 995–1002. doi: 10.1016/j.foreco.2010.12.015.

Yin, J., Ge, Z., Deng, X., Shi, Y., Xu, L., Zhou, G., et al. (2019). Abandonment lead to structural degradation and changes in carbon allocation patterns in Moso bamboo forests. For. Ecol. Manag. 449, 117449. doi:10.1016/j.foreco.2019.117449

Yuan, J., Hou, L., Wei, X., Shang, Z., Cheng, F., and Zhang, S. (2017). Decay and nutrient dynamics of coarse woody debris in the Qinling Mountains, China. PLOS ONE 12, e0175203. doi: 10.1371/journal.pone.0175203.

Yuen, J. Q., Fung, T., and Ziegler, A. D. (2017). Carbon stocks in bamboo ecosystems worldwide: Estimates and uncertainties. For. Ecol. Manag. 393, 113–138. doi:10.1016/j.foreco.2017.01.017

Zhang, H., Zhuang, S., Qian, H., Wang, F., and Ji, H. (2015). Spatial Variability of the Topsoil Organic Carbon in the Moso Bamboo Forests of Southern China in Association with Soil Properties. PLOS ONE 10, e0119175. doi: 10.1371/journal.pone.0119175

Zhang, J., Zhang, D., Jian, Z., Zhou, H., Zhao, Y., and Wei, D. (2019). Litter decomposition and the degradation of recalcitrant components in Pinus massoniana plantations with various canopy densities. J. For. Res. 30, 1395–1405. doi:10.1007/s11676-018-0715-5

Zhou, B., Fu. M. (2008). Fine root production and turnover of Phyllostachys pubescens stands in Miaoshanwu Nature Reserve. Acta Agriculturae Universitatis Jiangxiensis 30, 239-245.

Zimmer, M., Kautz, G., and Topp, W. (2003). Leaf litter-colonizing microbiota: supplementary food source or indicator of food quality for Porcellio scaber (Isopoda: Oniscidea)? Eur. J. Soil Biol. 39, 209–216. doi: 10.1016/j.ejsobi.2003.07.001.

Zukswert, J. M., and Prescott, C. E. (2017). Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. Oecologia 185, 305–316. doi: 10.1007/s00442-017-3951-z.

Appendix

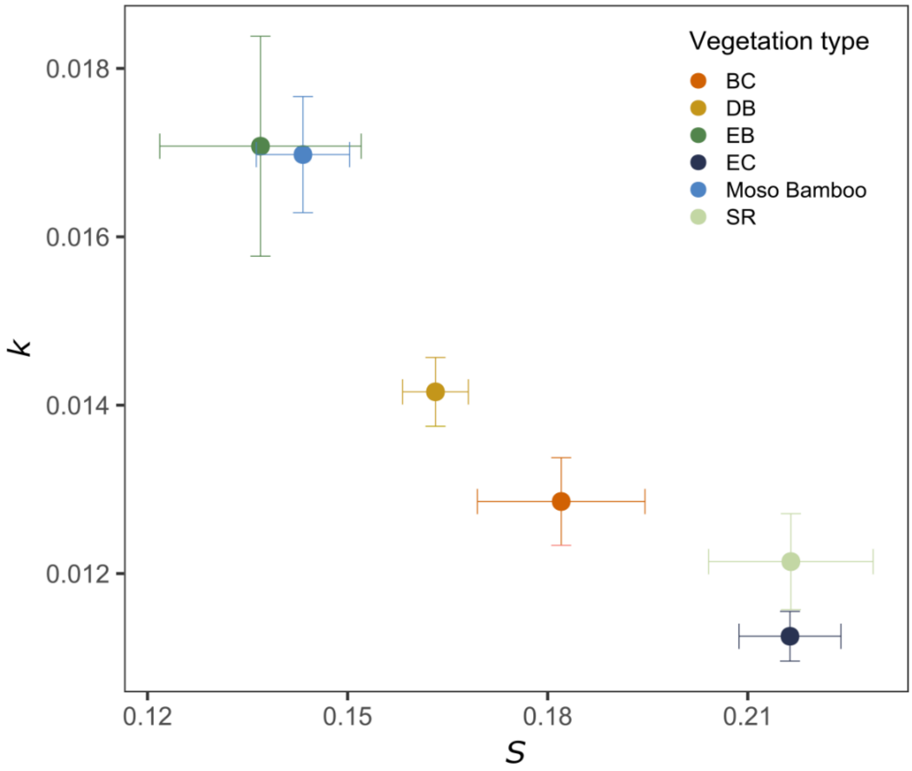

Figure S2.1 Comparison of Tea Bag Index parameters (*k* and *S*) in Moso bamboo stands (this study) and those obtained from the dataset of Suzuki et al. (2019) of tea bags incubated in five vegetation types across Japan. BC (Broadleaf-conifer forest), DB (Deciduous broadleaf forest), EB (Evergreen broadleaf forest), EC (Evergreen conifer forest), SR (Alpine shrub).

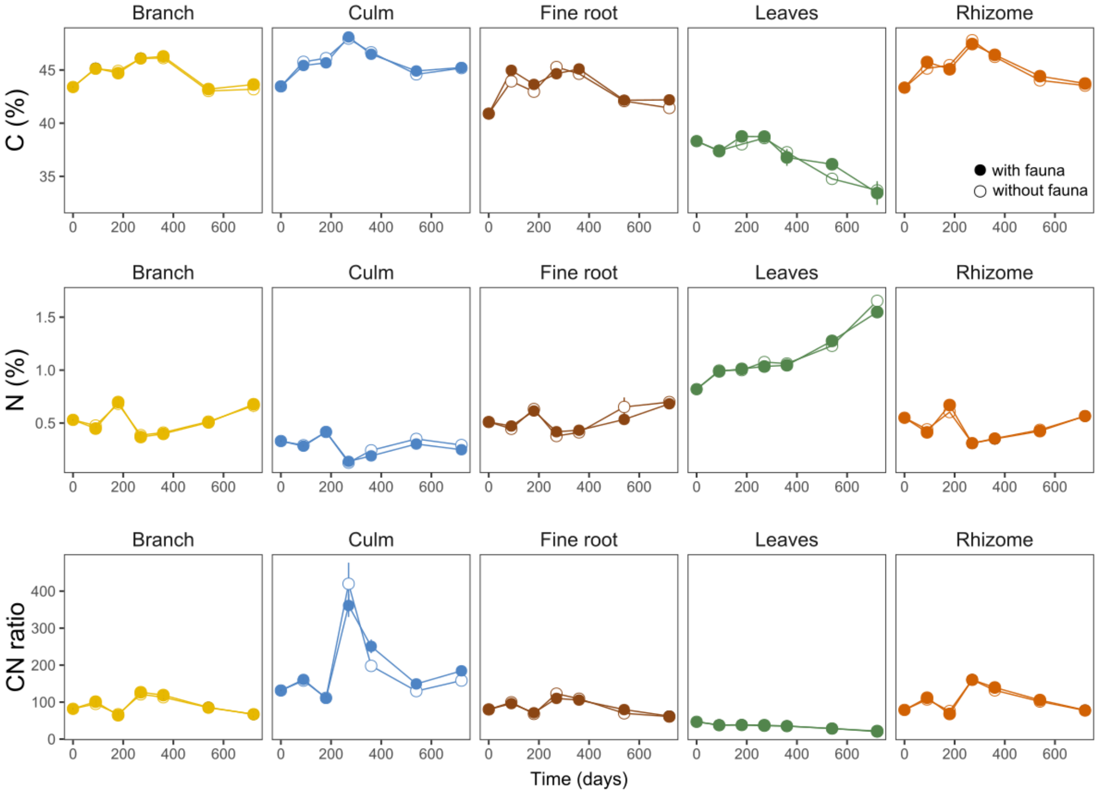

Figure S3.1 Litter C and N concentrations (%), and C/N dynamics in different bamboo litter (branch, culm, fine root, leaves and rhizome litter) in the presence and absence of soil mesofauna during decomposition.

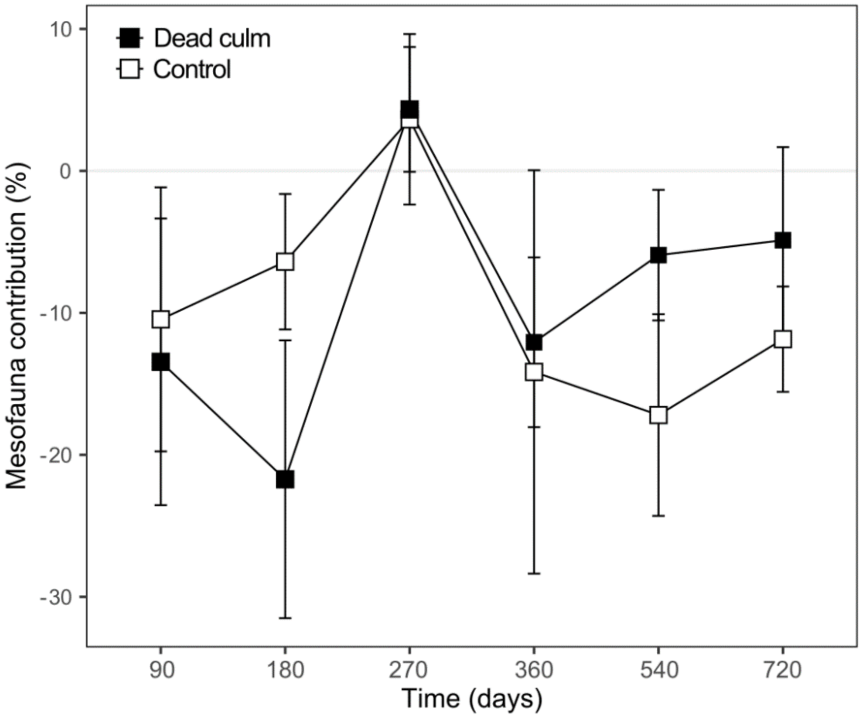

Figure S5.1 Changes in mesofaunal contributions (%) to litter mass loss in control and dead culms. No significant differences were found between treatments at each decomposition period (one-way ANOVA, *P* > 0.05).

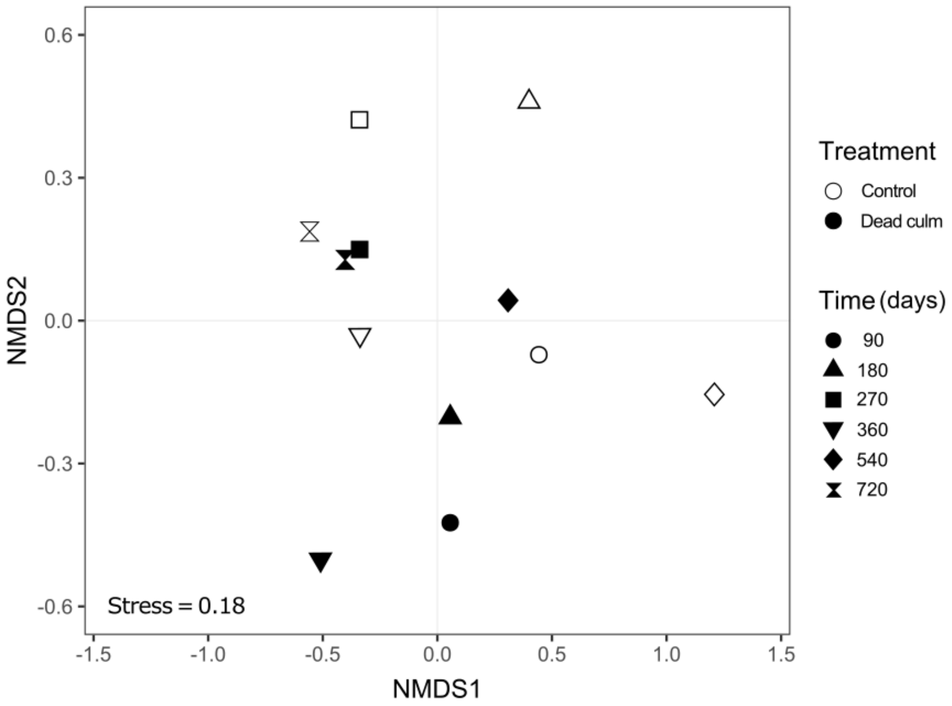

Figure S5.2 Non-Metric Multidimensional Scaling (NMDS) ordination of soil mesofauna community composition showing the effects of dead culms and decomposition time. NMDS plot is based on Bray-Curtis dissimilarities.