博士学位论文

毛乌素沙地不同植物器官凋落物分解的驱动机制研究

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Abstract

Litter decomposition plays an important role in carbon and nutrient cycling in terrestrial ecosystems. It is well known that litter decomposition in wet to mesic ecosystems is driven by biotic factors due to higher decomposer abundance and favorable moisture conditions. However, arid and semiarid ecosystems are characterized by lower vegetation cover, strong solar radiation nearby soil surface and lower precipitation amount. Thus, litter decomposition in semiarid and arid ecosystems is controlled by both abiotic and biotic factors. In addition, wind erosion and sand burial are common phenomena in these regions due to lower soil stability. However, it still remains uncertain on the relative importance of solar radiation or UV radiation and sand burial on litter decomposition and how they interact with litter quality with diverse species on litter decomposition in semiarid Mu Us Sandland. It has seldom been examined on how different plant organs respond to UV radiation and sand burial. In this thesis, there are three scientific questions to be solved: (1) How would UV radiation affect carbon and nutrient fluxes of surface and suspended (simulated standing) leaf litters? Whether would litter quality with different species affect the effects of UV radiation on litter decomposition? (2) How would the effects of UV radiation and litter positions influence the decomposition of woody litters with different diameter classes? (3) How would litter quality and incubation environment impact litter decomposition of leaves and fine roots? Whether would the coordination exist between leaf and fine root turnover? There are several progresses as follows.

(1) A field experiment was carried out in semiarid Mu Us Sandland of Inner Mongolia, China to investigate the effects of UV radiation and litter position on leaf litter decomposition of eight contrasting species (three perennial grasses, three shrubs, and two annual forbs) representing different litter qualities over whole year of incubation. The results showed that UV radiation increased the mass loss of suspended litters for two perennial grasses and two annual forbs, but had no significant effect on the other four species considered; the percentage increase in mass loss across eight species ranged from 4.5 to 27.3% with an average of 13.7%. Nitrogen (N) release from litters on the soil surface was lower than in suspended position because the former was involved in N immobilization driven by microbial decomposition. There were no net effects of UV radiation on decomposition rates of

surface litters possibly due to the positive effects of photochemical process offsetting negative effects on microbes. Multiple linear regressions showed that the C: N ratio of initial leaf litter and leaf dry matter content (LDMC) could predict the rate of litter decomposition, in which litter C: N ratio had a stronger influence. The findings, based on multiple species, highlight the importance of photodegradation on litter nitrogen and/or carbon mineralization in drylands as mediated by different abiotic and biotic drivers.

(2) I explored the relative importance of litter position (sand burial vs surface vs suspended above the surface), UV radiation (block vs pass), and woody diameter class (φ <2, 2-4, 4-8, 8-13, and 13-20 mm) on the mass loss of woody litters of four shrub species in semiarid Mu Us Sandland of Inner Mongolia, China. I found that after 34 months of *in situ* incubation, the mass loss of buried woody litters was over three times as those of suspended and surface woody litters (53.5 ± 2.7 %, 17.0 ± 1.0 % and 14.4± 1.2 % for sand burial, suspended and surface positions, respectively). In surface and suspended positions, litter decomposition rates were almost equally low and most of mass loss occurred during the first two years. UV radiation had no significant effect on woody litter mass loss. These findings suggest that sand burial is the main environmental driver of wood decomposition via providing optimal incubation environment for microbial activity. Several structural and chemical traits including initial bark thickness, wood dry matter content, wood diameter, and wood N and C: N ratio were correlated with *k* values for woody litter decomposition, among which wood N and diameter classes were the predominant factors driving woody litter decomposition. This study highlights the importance of belowground organic matter fluxes in accelerating biogeochemical processes in shrub-encroachment grasslands or shrub-dominated semiarid and arid ecosystems, where woody litter often becomes buried. The accuracy and confidence of global carbon cycling model would be improved by incorporating belowground wood decomposition processes in drylands.

(3) I incubated leaf and fine root litters under sand burial environment and leaf litter on soil surface across 25 species in semiarid Mu Us Sandland of Inner Mongolia, China and examined the relative importance of litter quality and incubation environment on litter decomposition and whether there exists coordination between leaf litter and fine root turnover. The results showed that after 2 years of incubation, the average loss rate of leaf litter on the soil surface and buried positions were 64.0 ±

1.2%, 73.4 ± 1.4%, respectively. However, buried fine root loss rate was 56.8 ± 1.3%. When they were incubated in a unified underground sand burial environment, the greater difference in decomposition rates was observed between leaves and fine roots. Herbs had faster litter decomposition rates than shrubs. The N concentrations of litters increased with increasing incubation time in all treatments, which may be due to the soluble matter in the litter with relatively faster turnover. At the same time, the nitrogen immobilization of the microorganism causes the increasing N concentration of the litter with the incubation time. During the decomposition, the C concentration and C: N ratio of fine roots were significantly higher than those of surface and buried leaves, which means that the decomposition rate of fine roots is slower than that of leaf litters. The stronger relationship was observed between the surface and buried leaf litter decomposition rates, implying that litter quality with diverse species had predominant control on litter decomposition in contrast with decomposing environments. Multiple trait pairs between leaf and fine roots covaried, i.e. green leaf or leaf litter N, Ca, Mg - root N, Ca, Mg, respectively and leaf litter N, C: N ratio, P, K - root N, C: N ratio, P, K, respectively. In addition, there was coordination between the decomposition rates of surface leaf litter and buried fine roots; the relationship decoupled when leaf litter and fine root were incubated under same sand burial condition. According to these findings, the coupling/decoupling of leaf litter and fine root decomposition rates indicates that there is limitation when the plant economic spectrum theory is extended to litter turnover.

In summary, these studies have shown that the relative importance of UV radiation and sand burial on litter decomposition are quite different for different plant organs: photodegradation is important on litter nitrogen and/or carbon mineralization in drylands; sand burial rather than UV radiation is the predominant factor in wood decomposition in drylands. This implies that sand burial can be a potential mechanism driving wood decomposition in drylands. The finding that strong coordination relationship between surface and buried leaf litter decomposition rates, implying that litter quality predominantly controls litter decomposition in contrast with microclimate environment. These studies can aid in understanding the litter turnover of different tissues and their driving mechanisms in drylands and can provide important data on building the global carbon cycle and ecosystem management in drylands.

Key Words: Dryland, Litter Decomposition, UV Radiation, Fine Root, Leaf, and Wood Decomposition

摘 要

凋落物分解在陆地生态系统的碳和养分循环中起着重要作用。众所周知，由于分解者丰度高和有利的水分条件，潮湿到中等湿度的生态系统中凋落物分解主要是由生物因素驱动的。干旱半干旱生态系统具有植被覆盖率低、地表附近太阳辐射强，降水量低，以及由于土壤稳定性较差而导致的风蚀和沙埋等特点，该系统中凋落物分解可能受这些非生物和生物因素的共同控制。然而，对于太阳辐射或紫外线辐射和沙埋对凋落物分解的相对重要性以及它们如何与凋落物质量互作对凋落物分解影响的认识，仍然存在着不确定性。有关不同的植物器官对太阳辐射或紫外线辐射和沙埋的响应仍认识不足。在本文中，拟解决如下三个科学问题：(1) 紫外线辐射如何影响地表和悬挂（模拟立枯）叶凋落物的碳和养分周转？不同物种的凋落物质量是否会影响紫外线辐射对凋落物的分解？(2) 紫外线辐射和凋落物位置如何影响不同直径大小的木质残体凋落物的分解？(3) 凋落物质量和分解环境如何影响叶和细根的凋落物分解？叶与细根周转之间是否存在耦合关系？研究结果如下：

(1) 研究了紫外线辐射和凋落物位置对毛乌素沙地具有不同凋落物质量的 8 种植物（包括 3 种多年生禾本科植物、3 种灌木、2 种一年生草本植物）叶凋落物分解的影响。结果表明，紫外线辐射增加了两种多年生禾本科植物和两种一年生草本植物悬挂叶凋落物的质量损失，但对其它四种植物没有显著影响；在物种间，紫外线辐射提高凋落物质量损失率 4.5-27.3%，平均为 13.7%。土壤表层凋落物的氮 (N) 释放量低于悬挂位置，其原因是前者存在微生物分解驱动的氮固定过程。由于光化学过程的正效应抵消了对微生物的负效应，紫外线辐射对地表凋落物分解率没有影响。多元线性回归分析表明，初始叶凋落物 C: N 比和叶干物质含量 (LDMC) 可以预测凋落物分解速率，其中凋落物 C: N 比的影响较大。基于多物种的研究结果强调了光降解在不同的非生物和生物驱动因素介导下对旱区凋落物氮和/或碳矿化的重要性。

(2) 研究了凋落物位置（沙埋，地表，悬挂），紫外线辐射（阻挡，通过）和直径大小 (φ <2，2-4，4-8，8-13 和 13-20 mm) 对毛乌素沙地 4 种灌木质

量损失的相对重要性。结果表明，经过 34 个月的原位分解实验，沙埋条件下木质残体凋落物的质量损失是悬挂和地表条件下的三倍（沙埋、悬挂和地表分别为 53.5±2.7%，17.0±1.0% 和 14.4±1.2%），但是，在前两年的分解过程中，地表和悬挂位置条件下却表现出相对较快的凋落物分解率。紫外线辐射对木质残体凋落物质量损失无显著影响。这些结果都表明沙埋是驱动微生物控制的木质残体分解的主要环境因素。木质残体凋落物分解速率常数 *k* 值与初始树皮厚度，木质残体干物质含量，直径大小，N 含量和 C: N 比等形态化学性状有关，其中木质残体 N 含量和直径大小是驱动茎秆凋落物分解的主要因素。本研究结果表明地下有机残体分解在灌丛化草原或灌木为主的半干旱和干旱生态系统中加速生物地球化学过程的重要性。结合干旱地区地下木质残体分解过程可以提高全球碳循环模型的准确性。

(3) 通过毛乌素沙地 25 种植物在沙埋环境下的叶和细根凋落物和土壤表面的叶片凋落物的原位野外分解实验，研究了凋落物质量和分解环境对凋落物分解的相对重要性，以及叶凋落物与细根周转的协同变异。结果表明，经过 2 年的野外分解，地表和沙埋条件下叶凋落物平均损失率分别为 64.0±1.2% 和 73.4±1.4%，然而沙埋细根损失率为 56.8±1.3%。当它们在统一的地下沙埋环境中时，叶和细根之间分解速率的差异更大。草本的凋落物分解速率比灌木快。各处理中，随着分解时间的延长，凋落物中 N 浓度增加，可能是由于凋落物中的可溶性物质分解较快，同时微生物的固氮作用使凋落物中 N 浓度随分解时间的增加而增加。而在分解过程中，细根 C 和 C: N 比明显高于地表和沙埋的叶凋落物，解释了细根的分解速度为何慢于叶凋落物。地表与沙埋叶凋落物分解速率的关系更强，说明不同植物物种的凋落物质量对凋落物分解有强的控制作用。叶和细根之间的多个性状都存在协同变异，例如，鲜叶和叶凋落物 N，Ca，Mg – 细根 N，Ca，Mg 之间，叶凋落物 N，C: N 比，P，K –根 N，C: N 比，P，K 之间显著正相关。此外，地表叶凋落物与沙埋细根的分解速率存在耦合关系；当叶凋落物和细根放在相同沙埋环境下培养时，叶和细根分解速率发生解耦合。叶凋落物与细根分解速率的耦合/解耦合关系表明，植物经济谱理论推广到凋落物周转具有一定局限性。

综上所述，这些研究表明太阳辐射或紫外线辐射和沙埋对不同植物器官的凋落物分解的相对重要性是不同的：光降解对干旱地区凋落物的氮和/或碳矿化很重要；沙埋而非紫外线辐射是干旱地区木质残体分解的主要因素，这意味着沙埋可能是驱动干旱地区木质残体周转的潜在机制。地表和沙埋的叶凋落物分解速率存在更强的耦合关系，这说明，相比于微气候环境，凋落物质量在凋落物分解的调控中更为重要。这些研究结果有助于认识干旱地区不同植物器官的凋落物周转及其驱动机制，也可以为全球碳循环构建和干旱地区生态系统管理提供重要的数据。

关键词：旱区，凋落物分解，紫外辐射，细根，叶和木质残体分解

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Chapter 1. General introduction: the effects of multiple environmental factors on litter decomposition

1.1 Litter decomposition

1.1.1 The litter decomposition process

As two important ecosystem processes, litter decomposition is equal in its importance compared with photosynthesis (Berg and McClaugherty, 2008; Moorhead and Sinsabaugh, 2006). Green plants can grow and propagate by photosynthesis via assimilating CO_2. Conversely, CO_2 is released into air and nutrient is returned to the soil during decomposition processes. In terrestrial ecosystems, dead organic matter plays an important role in the supply of nutrients in the soil and also as an energy source of microorganisms (Bhatt et al., 1986). More than 50% of net primary production (NPP) is returned to the soil (Wardle et al., 2004) and 58 Pg C $year^{-1}$ is released to the atmosphere through litter decomposition (Houghton, 2007). Therefore, litter decomposition is a key process for the transfer of carbon and nutrients in ecosystems (Jiang et al., 2014; Berg and McClaugherty, 2008). It consists of three concurrent processes: fragmentation, leaching of water-soluble compounds and microbial catabolism (Kutsch et al., 2009; Sanderman and Amundson, 2003; Waring and Schlesinger, 1985). In past decades, understanding of litter decomposition process has been devoted to identify both abiotic and biotic factors that control litter decay rates and determine dynamics of nutrient and organic carbon compounds during litter decomposition (Liu et al., 2018; King et al., 2012; Austin and Vivanco, 2006; Swift et al., 1979). The litter decomposition process is regulated by individual and interacting factors including climate, litter quality and the abundance of the decomposing organisms (Cotrufo et al., 2010; Coûteaux et al., 1995; Swift et al., 1979; Meentemeyer, 1978; Figure 1.1).

The climate may indirectly influence the rate of litter decomposition by changing the properties of the litter, or directly control the activity of the decomposition organisms. Moreover, the direct impacts of climate on the litter decomposition arise from the increased activity of decomposing organisms supported by higher temperature and humidity, which increase the rates of litter decomposition and nutrients loss (Petraglia et al., 2018; Wang et al., 2017a; Baker and Allison, 2015). In

the dryland ecosystem, the temperature is high and the relative humidity is low. Thus, the litter chemistry becomes the most important determinant of litter decomposition rate (Shaw and Harte, 2001; Aerts, 1997). The second main factor controlling litter decomposition is litter quality (Melillo et al., 1982). The nutrient concentrations have been usually linked to litter quality. High nitrogen (N) and phosphorus (P) concentrations, as well as lower C: N and lignin: N ratio has been associated to higher litter quality, which may be used to correlate with decomposition rates (Li et al., 2011; Brandt et al., 2010). In addition, initial litter chemistry can affect the rates of nutrient immobilization and mineralization and the amount of net nutrient immobilization is related to the initial N content of litter (Parton et al., 2007; Scott and Binkley, 1997; Aber and Melillo, 1980).

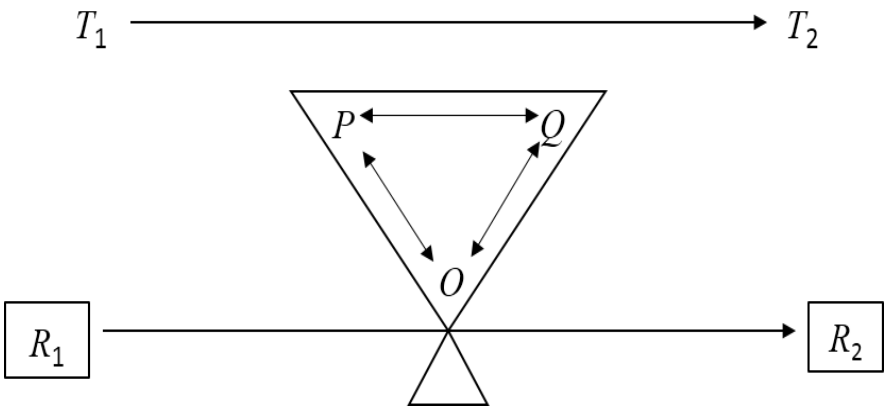


Figure 1.1 Regulation of decomposition processes by three driving variables

图 1.1 三类驱动变量对凋落物分解过程的调节

Physical-chemical environment (*P*), resource quality (*Q*) and decomposer organisms (*O*), and their interlinked action. The three variables and their interaction control the dynamics of resource (i.e. changing from R_1 to R_2) decomposition along time (i.e. moving from time T_1 to T_2). It is adapted from Cotrufo et al., 2010 and Swift et al., 1979.

物理化学环境（*P*）,资源质量（*Q*）和生物分解者（*O*）及其相互关联性。 这三个变量及其相互作用控制沿分解时间（即从时间 T_1 移动到 T_2）的资源动态（即从 R_1 变为 R_2）。它改编自 Cotrufo et al., 2010 和 Swift et al., 1979。

The decomposing organisms including microbe and soil arthropod fauna such as beetles, termites, etc. are the third main factor regulating litter decomposition. These organisms metabolize litter components and remove, mix, break the organic matter,

mineralize and make nutrients to plant utilization (Hättenschwiler and Gasser, 2005). Decomposing litter N concentration commonly increased via colonized decomposers transferring N from soil to litter (Wood, 1974; Gosz et al., 1973). The relative effects of these factors on litter decomposition differ in different ecosystems and there exist strong interaction effects between those factors (Liu et al., 2015a; Bradford et al., 2014).

1.1.2 Dryland litter decomposition

Litter decomposition plays an important role in regulating C accumulation in the terrestrial ecosystems (Le Quéré et al., 2015; Le Quéré, 2009) and the capacity of the global terrestrial carbon (C) sink is growing and it is mostly determined by highly productive ecosystems (Ballantyne et al., 2012; Sitch et al., 2003). However, the relatively higher turnover rates of carbon pools in semiarid ecosystems are a significant driver in inter-annual variability of the global C cycle (Ahlström et al., 2015; Poulter et al., 2014). Arid and semiarid ecosystems differ from other ecosystems in structure and in the rate and regulation of ecosystem processes. High temperature, low precipitation or rainfall, high potential evaporation rate, poor soil fertility, and serious land degradation processes are the distinctive characteristics of dryland (Reynolds et al., 2007). Dryland ecosystems cover 41% of the Earth's land surface (Maestre et al., 2012) and account for about 20% of the soil organic carbon pool (Lal, 2004). It is still challenging that which predominant factors control litter turnover in dryland ecosystems. Some previous studies indicated that photodegradation by ultraviolet (UV) radiation can be a significant driver of dryland litter decomposition (Huang et al., 2017; Wang et al., 2015; Austin and Vivanco, 2006). However, other studies suggested that soil–litter mixing controlled litter decomposition in arid and semiarid ecosystems (Liu et al., 2018; Gliksman et al., 2017; Barnes et al., 2015; Austin and Ballaré, 2010). Moreover, some researchers have suggested that photodegradation indirectly increases microbial decomposition which is called the positive photo-priming effect (Huang et al., 2017; Lin and King, 2014). In addition, there exists a strong interaction between UV radiation and litter quality on litter decomposition (King et al., 2012; Austin and Ballaré, 2010; Brandt et al., 2007). For example, UV increased litter decomposition rates with lower litter quality (higher C: N ratio), but no effect on a litter with higher litter quality (Brandt et al., 2007). Additionally, most studies on litter decomposition in water-limited

ecosystems focus on the only leaf or herb materials. Fine root turnover is seldom investigated although fine root turnover is also important in the carbon and nutrient cycling of belowground processes (McCormack et al., 2015; Freschet et al., 2013). Moreover, it is quite scarce on wood decomposition in arid and semiarid ecosystems possibly due to very slow turnover of wood material with the lowest surface area to volume ratio. These imply the complexity and scarcity for fine root and woody litter in litter decomposition in drylands.

1.1.3 Effects of litter quality, plant organ and growth form on litter decomposition

Morphological and chemical traits could be considered as a proxy of litter quality and its important drivers of litter decomposition. The commonly used morphological and chemical traits are DMC (dry mass content), SLA (specifies leaf area), N, C: N ratio and lignin, etc. in predicting leaf litter decomposition. The relationships between the rate of decomposition and initial litter traits depend on plant organs (Hobbie et al., 2010; Aerts, 1997). For wood decomposition, the predictor variables are wood density, bark thickness, wood N and P concentration, C: N ratio, lignin, lignin: N ratio, etc. For fine root decomposition, the predictors are SRL (specific root length), root diameter, root N concentration, Ca concentration etc. (Smith et al., 2018; Weedon et al., 2009; Cornwell et al., 2008; Silver and Miya, 2001; Aber et al., 1990; Melillo et al., 1982). Litter chemistry and morphological traits may vary widely in plant tissues and thus the large difference in sizes between plant tissues affects microbially or abiotically driven decomposition. Many previous studies have investigated that the leaf litter decomposed faster than woody litter or fine roots (Helsen et al., 2018; Ma et al., 2016; Freschet et al., 2013; Liu et al., 2010; Bedford, 2005). These are owed to contrasting litter quality between different plant organs. For example, initial lignin concentration and lignin: N ratio was lower but N and P concentrations were higher in leaf litter than woody litter or fine roots (Liu et al., 2019; Li et al., 2016; Lü et al., 2012).

Many previous studies have shown that decomposition rates and associated with functional trait variation differ across different plant organs (leaves, stem/branch, and root), which is critical to predict how future global changes affecting C and nutrient cycling through mechanisms of biological response (Pietsch et al., 2014; Brovkin et al., 2012; Wirth and Lichstein, 2009). The leaf litter decomposition has been substantially studied but other organs such as stem/branch or roots have been seldom

studied. Generally, the leaf litter decomposed faster than woody litter or roots, it is poorly known that whether species with fast decaying leaves also have fast decaying wood or roots (Li et al., 2016; Freschet et al., 2013; Wang et al., 2010; Vivanco and Austin, 2006; Kemp et al., 2003). Species trait had a substantial influence on litter decomposition (Weedon et al., 2009; Cornwell et al., 2008; Silver and Miya, 2001). Plant organs having lower concentrations of nutrients (e.g. N and P) and higher stoichiometry (lignin: N and C: N ratios) decay more slowly (Cornwell et al., 2008; Moore et al., 1999). Moreover, the litter decomposition of the same organs decomposed differently under different environmental conditions such as sand burial or on the soil surface position or the litter decomposition of different plant organs decomposed differently under the same environmental conditions. For one of the reasons, each plant organ has different litter quality and same plant organ also differ across specific species (Freschet et al., 2012b; Cornwell et al., 2008; Santiago, 2007). The difference in litter quality of species is relevant to plant growth form. The forbs decomposed more quickly than that of grass and shrubs because the latter retained a lower N content and higher lignin and C content (Hobbie, 1996). Other studies found similar results between plant growth forms (Erdenebileg et al., 2018; Liu et al., 2015b; Chapin et al. 1996). However, how incubation environment and litter quality with different morphological and chemical traits affect decomposition rates of litter decomposition particularly woody litters or fine roots turnovers are controversial.

1.2 Environmental changes in drylands

1.2.1 Effects of solar radiation on litter decomposition

Many studies have focused on litter decomposition in terrestrial ecosystems that how soil organisms interact with climate and litter quality to regulate mass loss and nutrient release of plant litter materials (Petraglia et al., 2018; Eichenberg et al., 2017; Zhang et al., 2009). The rate of litter decomposition is positively correlated with microclimates such as annual temperature and annual precipitation (Davies et al., 2013; Meentemeyer, 1978). Initial morphological (DMC, SLA) and chemical (e. g. N, P, C: N) traits were good predictors of interspecific variation in decomposition of litter at the regional scale (Helsen et al., 2018; Erdenebileg et al., 2018; Liu et al., 2018; Pietsch et al., 2014; Freschet et al., 2012a). Therefore, the decomposition model based on potential evaporation and litter quality could predict litter decomposition in

wet to mesic ecosystems, while it fails to predict litter decomposition in drylands (Meentemeyer, 1978). Dryland had unexpected higher litter decomposition. These imply that mechanisms driving litter decomposition in dryland are quite different from those in wet to mesic ecosystems. There is a unique factor affecting litter decomposition in arid and semiarid ecosystems, which may contain abiotic controls such as photodegradation by UV radiation. UV radiation has been an important issue in global environmental change (Pancotto et al., 2005). Solar UV radiation could directly or indirectly affect litter decomposition and nutrient cycling in terrestrial ecosystems. Many previous studies investigated that UV radiation had a significant effect on the decomposition of litter (Ma et al., 2017; Wang et al., 2015; Brandt et al., 2010; Austin and Vivanco, 2006). UV radiation comprised of UV-A and UV-B (280-400 nm) could accelerate litter decomposition by photochemical processes. Austin and Vivanco (2006) found that attenuation of Ultraviolet-B and total radiation causes 33% and 60% reduction in decomposition rates, respectively and due to the photochemical mineralization of the litter, the individual UV-B radiation can account for nearly 50% of the carbon loss. In addition, Wang et al. (2015) found that UV radiation increased litter mass loss by 1.44% (95% CI: 0.85% to 2.08%), and increased the concentration of dissolved organic carbon (DOC) by 14.01%. Although UV-B radiation could directly increase the litter decomposition rate via photochemical breakdown of lignin and it could also indirectly reduce litter decomposition by altering species composition, abundance and colonization of decomposers including microbes exposed to solar radiation (Erdenebileg et al., 2018; Song et al., 2013; Pancotto et al., 2005; Moody et al., 2001). In conclusion, the effects of UV radiation (both direct and indirect) on litter decomposition depends on specific species due to differences in litter type or experimental approaches affecting UV radiation intensity.

1.2.2 Effects of litter position on litter decomposition

Due to lower soil stability, wind erosion and sand burial are common phenomena in arid and semiarid ecosystems. Litter may be buried by soil due to wind transport or raindrop. Additionally, some litters particularly woody stem stands for a relatively long time in a suspended position. The possible fate of litters would determine its carbon and nutrient release dynamics. Therefore, litter position is one of the important environmental factors that can regulate the litter decomposition processes in diverse

ecosystems. However, there are only a few studies assessing the effects of litter position on litter decomposition (Liu et al., 2015b; Lin and King, 2014; Dukes and Field, 2000; Holland and Coleman, 1987). In arid and semiarid ecosystems, plant litter materials placed below soil surface decomposes more rapidly than litter that is placed on the soil surface and in the air suspended due to optimal temperature and moisture (Liu et al., 2015b; Danger et al., 2012; Smith and Lake, 1993; Moorhead and Reynolds, 1989b; Thurow, 1989). By contrast, Moroni et al. (2015) found buried wood decomposed slowly in forests due to the fact that cool moist environments provide conditions capable of generating the anaerobic condition. Lin and King (2014) found that surface litter decomposed faster than suspended litters. It is believed that the closeness of litter to the soil surface mainly affects the decomposition of litter by affecting microbial activity. These findings were in contrast to the studies informed that photodegradation as an important abiotic mechanism for the decomposition of litter without microbial activity in surface litter decomposition (Lee et al., 2012; King et al., 2012; Smith et al., 2010; Austin and Vivanco, 2006). On the other hand, there may have a physical fragmentation by direct windy effects on litter mass loss in suspended position and abiotic mechanisms, such as the photochemical degradation may have important direct effects on surface litter mass loss (Gliksman et al., 2017; Austin et al., 2016; Moorhead and Reynolds, 1989a). In many previous studies, interaction effects of litter position and litter qualities or plant organs significantly influenced the rates of litter decomposition (Liu et al., 2018; Erdenebileg et al., 2018; Austin et al., 2009; Zhang et al., 2009; Dukes and Field, 2000).

1.3 The research framework, contents, and innovation

1.3.1 The research framework and contents

This thesis brings together much of the current understanding of the litter decomposition process as it occurs in semiarid ecosystems. The main purpose of this thesis was to investigate the decomposition of different organs (leaf and woody litter and fine roots) of diverse species from Mu Us Sandland and how litter quality and environmental factors such as solar UV radiation, litter position affect the litter decomposition process in this semiarid ecosystem. This thesis contains the three experiment chapters (Figure 1.2) addressing these scientific questions which are indicated below. I used comparative ecology methods across multiple species to

investigate plant litter decomposition in Mu Us Sandland in responses to solar (UV) radiation and sand burial and simulated standing. For chapter 3, I incubated leaf litter from eight species for one year. For chapter 4, I incubated woody branches/twigs for 34 months, when is close to three years. Due to the slower decomposition of fine roots, for chapter 5 I incubated leaf and fine roots for two years covering six incubation times.

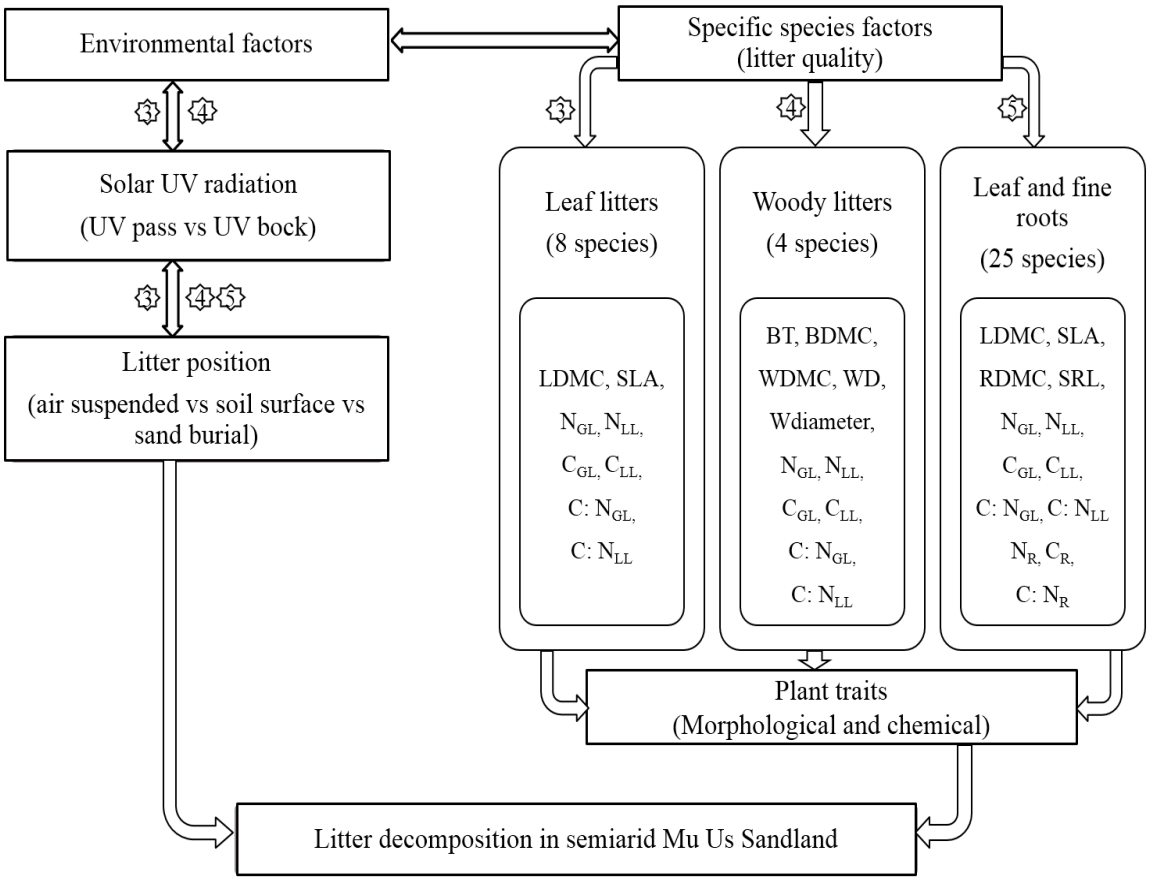


Figure 1.2 The framework of the thesis

图 1.2 论文的框架

In this figure, ③, ④ and ⑤ represents the framework of Chapter 3, 4 and 5, respectively. LDMC: leaf dry matter content; SLA: specific leaf area; BT: bark thickness; BDMC: bark dry matter content; WDMC: wood dry matter content; WD: wood density; Wdiameter: wood diameter; RDMC: root dry matter content; SRL: specific root length.

图中③,④ 和⑤ 分别表示第 3, 4 和 5 章的研究框架。LDMC：叶干物质含量; SLA：比叶面积; BT：树皮厚度; BDMC：树皮干物质含量; WDMC：木质茎干物质含量; WD: 木材密度； Wdiameter：木质茎直径; RDMC：根干物质含量; SRL：比根长。

There were three questions to be solved in this thesis. They are as follows:

(1) How would UV radiation affect carbon and nutrient fluxes of surface and suspended leaf litters in Mu Us Sandland? Whether would litter quality with different species affect the effects of UV radiation on litter decomposition?

To answer this question, chapter 3 compares decomposition of leaf litters of eight contrasting species in a semiarid ecosystem in responses to experimentally manipulated UV radiation using specially designed screens (UV pass versus UV block), and positions both at the surface and suspended above the surface for one year. Due to distinct abiotic and biotic environmental conditions between the surface and suspended positions, there should be a strong interaction between litter position and UV exposure on litter decomposition across eight species with different litter qualities. Thus, it is hypothesized that UV radiation would increase litter decomposition rates and C and nitrogen (N) mineralization of suspended leaf litters compared with UV block treatment, but it would decrease decomposition rates and C mineralization and microbial N immobilization of surface litters due to a negative effect on microbial composition and activity for most species.

(2) How would the effects of UV radiation and litter positions influence the decomposition of woody litters with different diameter classes in Mu Us Sandland?

The aim of chapter 4 is to examine the effects of litter position (sand burial, suspended, and surface) on woody litters from four shrub species with different diameter classes (φ: <2, 2-4, 4-8, 8-13, 13-20 mm) in a semiarid sandland, where the effects of UV radiation on wood decomposition on soil surface and suspended positions were examined for three years' experiments. I hypothesized that the following: (i) buried woody litters would have higher decomposition rates than surface and suspended woody litters due to stable and favourable moisture regime and well-developed microbial community; (ii) UV radiation would increase the decomposition rate of woody litters; (iii) bark thickness would be negatively correlated with the rate of wood decomposition; (iv) woody litters of smaller diameter, with higher relative surface exposure to external microbes and sunlight, and possibly higher resource quality, should be decomposed faster than wider ones.

(3) How would litter quality and decomposing environments impact litter decomposition of leaves and fine roots in Mu Us Sandland?

The aim of chapter 5 is to examine how litter quality and incubation environment impacted litter decomposition of leaves and fine roots in semiarid ecosystems. Therefore, to answer above question, I carried out long-term (two years) *in situ* decomposition experiments by incubating leaf litter and the fine root of 25 herbaceous and shrub species under sand burial and leaf litter of 25 species on the surface positions in the semiarid ecosystem in Ordos, Inner Mongolia. I tested the following hypothesis that (i) leaf litter would decompose faster on the soil surface and much faster under sand burial than buried fine roots; (ii) leaf litter and fine roots of herbs would decompose faster than these of shrub litters due to their higher initial N concentrations and lower C: N ratios; (iii) there would be coordination between decomposition rates of leaf litter and fine roots.

In closing chapter 6 of this thesis, I synthesized that the most important results of previous chapters in answer to scientific research questions introduced above.

1.3.2 The research innovation

First, I examined the effects of UV radiation on leaf litter using eight species. I found UV radiation has inconsistent effects on leaf litter decomposition rates in the same experiment, in which it increased suspended leaf litter decomposition rates of four species but no effect on the other four species. Leaf litter N concentration and C: N ratio were stronger predictors of leaf decomposition rates in this dryland. The lack of overall net effect of UV on surface litter decomposition across eight species indicates the complexity of UV effect on litter decomposition due to dual UV radiation effect on surface litters decomposition via direct UV breakdown of plant litters and indirect changes via microbial processes.

Second, our results from woody litter decomposition experiment showed that buried woody litter had the fastest decomposition rates, which are as triple times as these of aboveground woody litters. The finding demonstrates that sand burial, as a common phenomenon in arid and semiarid regions, is a predominant factor in woody litter decomposition. This is quite a different mechanism with buried wood decomposition in forests that buried wood can be preserved for a relatively long period due to anaerobic condition (Moroni et al., 2015). Litter traits, as a proxy of litter quality, could correlate with the rates of wood decomposition, which initial wood N concentration and diameter classes were predominant factors in driving wood decomposition. These findings highlight the importance of belowground organic

fluxes in accelerating biogeochemical processes in shrub-encroachment grasslands or shrub-dominated semiarid and arid ecosystems. The accuracy and uncertainty of global carbon cycling model would be improved by incorporating belowground wood decomposition processes in drylands.

Third, I incubated leaf and fine root litters under sand burial environment and leaf litter on soil surface across 25 species in a semiarid Mu Us Sandland and examined the relative importance of litter quality and incubation environment on litter decomposition and whether there exists coordination between leaf litter and fine root turnover. I found that the decomposition rate of leaf litter was faster under sand burial and on the soil surface position than that of buried fine roots. Herbs had faster litter decomposition rates than shrubs. Several trait pairs between leaf and fine roots covaried. For example, the nitrogen concentration of green leaf or leaf litter was positively correlated with fine root N. In addition, there was coordination between the decomposition rates of surface (or buried) leaf litter and fine roots. The stronger relationship was observed between the surface and buried leaf litter decomposition rates, implying that litter quality with diverse species had predominant control on litter decomposition in contrast with decomposing environments. Different plant traits control litter decomposition of leaf and fine root, respectively. The coupling of decomposition of surface leaf litter and buried fine roots and decoupling of decomposition of buried leaf and roots were observed. According to these findings, the coupling and decoupling of leaf litter and fine root decomposition rates indicate that there is limitation when plant economic spectrum theory can be extended to litter turnover.

Further studies are required to consider incubation time, litter layer thickness and other abiotic factors, i.e. precipitation pulse and air moisture, that the interaction between UV and litter position on litter decomposition in semiarid dryland ecosystems.

Chapter 2. Materials and Methods

2.1 Study site

The field work was conducted at the Ordos Sandland Ecological Research Station (OSERS) in Mu Us Sandland, Institute of Botany, Chinese Academy of Sciences (Inner Mongolia, China, 39°29′ 37.6″N, 110°11′29.4″E, 1290 m a.s.l.). This site experiences a continental climate with extreme seasonal and diurnal temperature variation and low annual rainfall amount. Briefly, in this site mean annual temperature is 6.2 °C and mean annual precipitation is 369 mm, 80% of which falls during the growing season from April to August (Liu et al., 2010). The soil in this area is the sandy texture that the percentage of sand is over 90% (see Gao et al., 2016). Soil N fertility is low (N concentration 0.081 ± 0.009 g N kg^{-1} versus 0.405 ± 0.031 ~ 0.491± 0.028 g N kg^{-1} for other vegetation types such as desert, desert steppe and typical steppe across Ordos Plateau; authors' unpublished data). Since strong winds occur in winter and early spring, both wind erosion and sand burial are common processes in this area. Nowadays the landscape in this region is characterized by mobile, semi-fixed and fixed inland dunes, where vegetation comprises perennial shrubs (dominated by *Artemisia ordosica* Krasch., *Hedysarum laeve* Maxim.) and annual herbs (dominated by *Agriophyllum pungens* (Vahl) Link ex A. Dietr, *Corispermum chinganicum* Iljin) together accounting for 30–50% coverage. In order to combat land desertification, two shrubs, i.e. *Salix psammophila* C. Wang et Ch. Y. Yang and *Caragana korshinskii* Kom., have been planted by local governments for over 20 years in some areas in order to stabilize the dunes, among which large areas with lower vegetation coverage remain in this region. Therefore, burial of dead wood of all four shrubs mentioned is a widespread phenomenon.

2.2 Litter collection and functional trait measurements

2.2.1 Leaf litter collection and morphological trait measurements of initial and decomposed litters

For the vegetation described above, recently senesced leaf litters of eight species had been collected from the plants or the soil surface from the beginning of October through mid-November 2015. Leaf litters sampled from the soil surface could be

recognized as recently senesced based on leaf color and texture. The species used were three shrubs *Salix psammophila* C. Wang et Ch. Y. Yang, *Caragana korshinskii* Kom., *Atraphaxis bracteata* A. Los., three perennial grasses *Psammochloa villosa* (Trin.) Bor, *Calamagrostis pseudophragmites* (Hall. f.) Koel., *Pennisetum centrasiaticum* Tzvel., two annual forbs *Corispermum chinganicum* Iljin and *Agriophyllum pungens* (Vahl) Link ex A. Dietr. For measurements of functional traits that may correlate with litter decomposition rates across species, green leaves of the eight species were sampled at the end of August 2015 within an area of about 5 ha around OSERS. These samples were put into nylon bags and immersed into water to be rehydrated. They were fully saturated for one night, then wiped gently with filter paper, weighed and scanned with a resolution of 300 dpi using a plane scanner (UNIS Uniscan D6810, Tsinghua Unisplendour Co., Ltd.); their leaf areas were measured using ImageJ software (https://imagej.nih.gov/ij/index.html). They were then oven-dried at 65 °C for 48 h to obtain the dry weights. Leaf dry matter content (LDMC, g g^{-1}) was determined as green leaf dry mass divided by its saturated mass and specific leaf area (SLA, cm^2 g^{-1}) as green leaf area divided by its dry mass (Cornelissen et al., 2003). LDMC and SLA (or its inverse, leaf mass per area) are now commonly used as negative and positive indicators of litter decomposability, respectively (Fortunel et al., 2009; Cornwell et al., 2008).

2.2.2 Woody litter collection and functional trait measurements of initial and decomposed litters

The four shrub species used in the second experiment are *Salix psammophila*, *Caragana korshinskii, Hedysarum leave* and *Artemisia ordosica*. For each species, recently senesced woody litters were collected from the plants from the beginning of October through the middle of November 2015. For each species, I collected branches and twigs with five diameter classes (φ <2, 2-4, 4-8, 8-13, 13-20 mm), where the total length collected per class was inversely related to diameter in order to obtain broadly equal total mass across the diameter classes (see Figure 2.1). For measurements of initial or decomposed woody litter density that may correlate to woody litter decomposition rates, initial (i.e. undecomposed) and decomposed woody litter subsamples (collected at subsequent harvests; see below) were immersed in water in plastic containers for 4 days to be fully saturated and to ensure homogeneous filling of air spaces (Freschet et al., 2012b; also see wood water absorption curve based on the

largest wood class, Figure 2.2).



Figure 2.1 Collection of branch and twig litters

图 2.1 茎和枝条凋落物收集

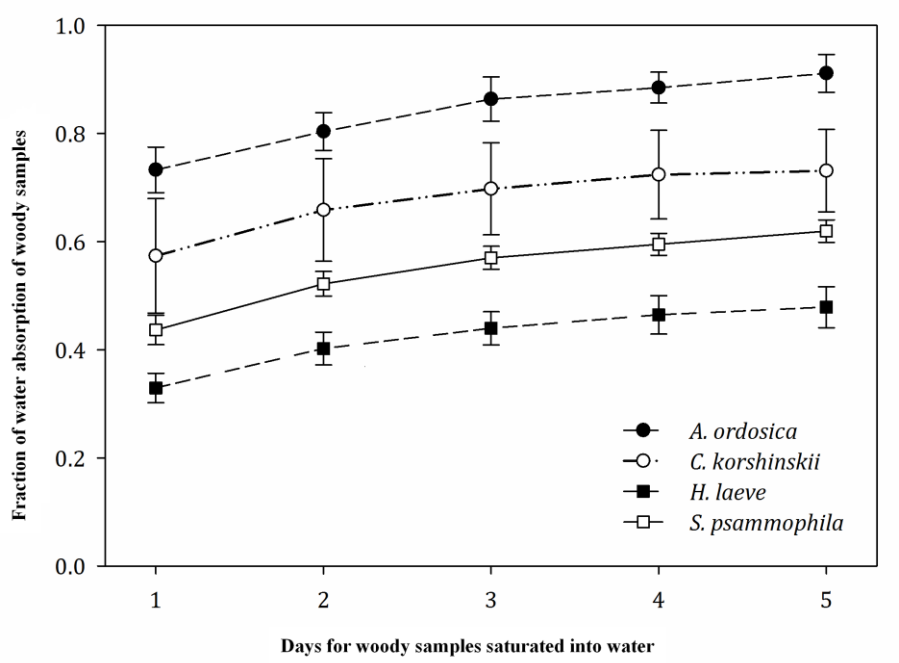


Figure 2.2 Woody samples with maximum diameter class were saturated into water up to 5 days in the laboratory and fraction of water absorption was measured

图 2.2 在实验室中将最大径级样品在水中饱和至5天，并测量水分吸收率

Initial and decomposed litter volumes were measured using Archimedes' principle of water displacement (details in Williamson and Wiemann, 2010). The saturated samples were then gently blotted dry with filter paper and weighed to obtain saturated mass, subsequently oven-dried at 65 °C for 72 h to obtain dry mass. Wood dry matter content (WDMC, g g^{-1}) was calculated as dry mass divided by its saturated

mass and initial or decomposed wood density (g cm^{-3}) was calculated as litter dry mass divided by saturated litter volume (Figure 2.3). Because bark could affect wood decomposition by providing a protective barrier around the wood (Dossa et al., 2018; Cornwell et al., 2009), bark thickness (mm) and bark dry matter content (BDMC, g g^{-1}) were also determined. Bark thickness was measured using digital calipers. Bark was separated from the initial wood subsamples and then was immersed in water to be saturated for one day. The saturated bark samples were gently blotted dry with filter paper and weighed to obtain saturated bark mass, subsequently oven-dried at 65 °C for 24 h to obtain its dry mass.

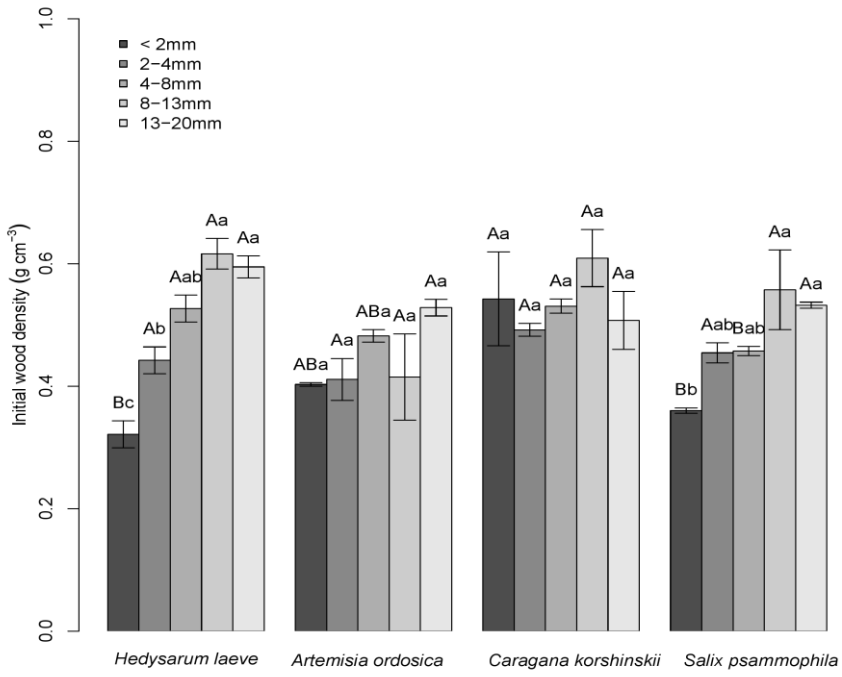


Figure 2.3 Initial woody density of four shrub species with different diameter classes

图 2.3 四种灌木不同径级的初始茎密度

The same lowercase denotes no significant difference in initial wood density between diameter classes for each species and the same uppercase denotes no significant difference between species for each diameter at $P < 0.05$.

相同小写字母表示某一物种初级木质残体密度在不同径级间没有显著差异，相同大写字母表示某一径级下初级木质残体密度在不同物种间没有显著差异（$P < 0.05$）。

2.2.3 Leaf and fine root collection and morphological traits measurements

Leaf litter and the fine root of 25 species including herbaceous and shrub growth forms were collected from September to November 2015 in the Mu Us Sandland, Ordos, Inner Mongolia, China (Table 2.1). Litters were air dried in the laboratory for at least 10 days. Then, I filled c. 5 g leaf litter and 4-5g fine root into a nylon litterbag with a size of 15 × 20 cm; the top and bottom layers considered of 2 mm and a 0.5 mm mesh sizes, respectively.

Table 2.1 25 common plant species list and their families and growth forms in Mu Us Sandland. Growth information comes from the Flora of China

表 2.1 毛乌素沙地 25 种常见植物物种及其科和生长型。生长型信息来自中国植物志

物种编号 Species code	物种 Species in Chinese	拉丁名 Species in Latin	科 Family	生长型 Growth form
1	白草	*Pennisetum centrasiaticum*	Poaceae	Herb
2	瓣蕊唐松草	*Thalictrum petaloideum*	Ranunculaceae	Herb
3	糙隐子草	*Cleistogenes squarrosa*	Poaceae	Herb
4	寸草苔	*Carex duriuscula*	Cyperaceae	Herb
5	鹅绒藤	*Cynanchum chinense*	Apocynaceae	Herb
6	假苇拂子茅	*Calamagrostis pseudophragmites*	Poaceae	Herb
7	赖草	*Leymus secalinus*	Poaceae	Herb
8	芦苇	*Phragmites australis*	Poaceae	Herb
9	牛心朴子	*Cynanchum komarovii*	Apocynaceae	Herb
10	沙鞭	*Psammochloa villosa*	Poaceae	Herb
11	沙米	*Agriophyllum pungens*	Amaranthaceae	Herb
12	兴安虫实	*Corispermum chinganicum*	Amaranthaceae	Herb
13	羽茅	*Achnatherum sibiricum*	Poaceae	Herb
14	针茅	*Stipa bungeana*	Poaceae	Herb
15	北沙柳	*Salix psammophila*	Salicaceae	Shrub
16	草麻黄	*Ephedra sinica*	Ephedraceae	Shrub
17	达乌里胡枝子	*Lespedeza davurica*	Fabaceae	Shrub
18	甘草	*Glycyrrhiza uralensis*	Fabaceae	Shrub
19	宽叶沙木蓼	*Atraphaxis bracteata var. latifolia*	Polygonaceae	Shrub
20	蒙古莸	*Caryopteris Mongolica*	Lamiaceae	Shrub
21	柠条锦鸡儿	*Caragana korshinskii*	Fabaceae	Shrub
22	沙地柏	*Sabina vulgaris*	Cupressaceae	Shrub
23	乌柳	*Salix cheilophila*	Salicaceae	Shrub
24	羊柴	*Hedysarum laeve*	Fabaceae	Shrub
25	油蒿	*Artemisia ordosica*	Asteraceae	Shrub

For each species, 3–20 freshly senesced leaves for each of three replicates were saturated for 2 hours into the water. The saturated samples were gently blotted dry with filter paper and weighed to obtain saturated weight. Then those samples were dried at 70°C for 48 hours to measure dry weight. Litter leaf dry matter content (LDMC, mg/g) was calculated as dry weight divided by saturated weight. SLA (mm^2/mg) of the litter was calculated as the leaf area divided by dry weight using 3–20 freshly senesced leaves for each of three replicates. For fine root samples, I collected commonly used live fine roots ($\varphi < 2mm$) due to its difficulty to obtain newly dead root and different decay stages of the dead root (Hobbie et al., 2010) and measured root functional traits. Specific root length (SRL, $m\ g^{-1}$) was calculated as the ratio root length divided by root dry mass and root dry matter content (RDMC, mm/mg) was calculated as dry weight divided by saturated weight.

2.3 Decomposition experiments

2.3.1 Leaf litter experimental design

In order to assess the influences of UV radiation and litter position (soil surface versus suspended above the surface) on litter decomposition, a plot at OSERS with a size of 20 × 23 m was established near the meteorological station to host 10 subplots with a size of 2.4 × 4.4 m each. The standing plants and litters were removed by hand (Figure 2.4). In this study, four subplots (two UV treatments × two litter positions) were used to examine responses of leaf litter decomposition. A UV screen treatment design was adopted based on the method reported by Brandt et al. (2010). UV radiation received by the litter layer was manipulated by utilizing two pairs of steel frames (l × w × h: 440 × 240 × 50 cm) carrying plastics with removable louver sheets that either block or allow pass UV radiation (Figure 2.4). In short, considering the distinct optical properties, two types of plastic materials were used: UV-transparent acrylic (UV pass, which transmits approximately 90% of UV radiation, Zhongshan Good Life Sun Sheet Co., Ltd., China) and UV- absorbing polycarbonate (UV block, which blocks approximately 95% of UV radiation, Zhongshan Good Life Sun Sheet Co., Ltd., Guangzhou, China). The removable louver sheets (125 per screen, each 240 cm length and 7 cm width and 2 mm thickness) were fixed at an angle of 60° with a horizontal line as a reference. Screens were custom-made and constructed in a

louvered design to allow for penetration of rainfall to the litter layer, allow free air movement and avoid heating.

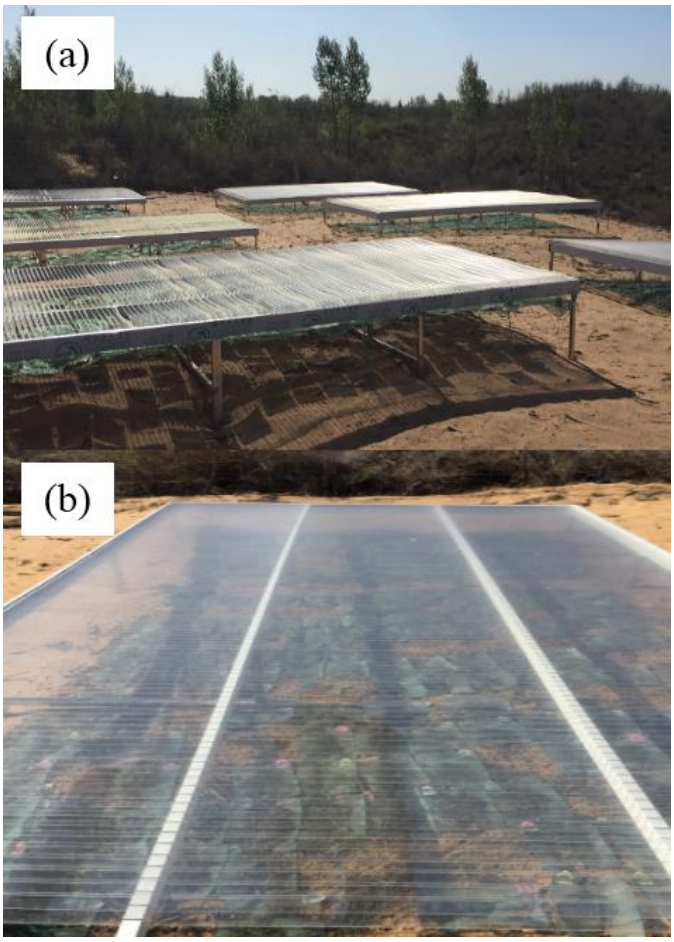


Figure 2.4 Leaf litter experimental design

图 2.4 叶凋落物分解实验设计

In this figure, (a) frames were custom-designed from steels with removable plastic louvers that either blocked or passed UV radiation and a total of 240 litterbags were placed at the suspended or surface position in each subplot. (b) screens were oriented southward to achieve the greatest possible UV treatment effect.

在该图中，(a)架子是由具有可移除塑料百叶窗的钢材定制设计的，塑料百叶窗阻挡或通过UV辐射，并且在每个架子下悬挂或表面位置处放置总共240个分解袋。(b) 亚克力板南向斜插入(60°倾角) 以实现最大可能的UV处理效果。

UV radiation (UV-A and UV-B) were measured in various months at noon, on average once per month from March to October during 2016 using a UV radiometer (280 to 400 nanometers, UV Products, Sentry ST-513, UVAB, Taiwan, China). UV radiation under screens for UV block and UV pass treatments decreased by an

average of 34.8 and 87.3%, respectively (Figure 3.1). To evaluate impacts of UV radiation and position treatments on the microclimate of the litter layer, button-type recorders (ibutton recorders) were placed on the surface and in suspended positions during the incubation time from December 2015 to November 2016. These sensors were set to record temperature and relative humidity every two hours. Data on temperature and relative humidity were downloaded once per 3 months. It should be acknowledged that one year does not cover the entire decomposition trajectory of most species, and it is of interest to study the fate of the less readily decomposed fraction beyond one year of incubation; the interactions between species traits, UV radiation and litter position on mass loss and element dynamics were expected to be relatively important especially in the first year of decomposition.

The litter bag approach was adopted to determine mass loss of litter at different harvest periods, i.e. 3, 6, 9, 12 months of incubation. A litterbag size 15 cm × 20 cm with a mesh size of 2 mm for the top side exposed to the sun, and a 0.5 mm mesh for the bottom side in order to prevent loss of small litter fragments was used (Baker and Allison, 2015). The number of litterbags used was 768 (8 species × 4 subplots × 4 harvest times × 6 replicates). Approximately 5 g of pre-weighed air-dried litter was sealed into each litterbag. Three subsamples for each species were used to correct air-dried litter weight via initial air-dried and oven-dried weights (at 65°C for 48 h). One hundred ninety-two litterbags were placed in each of 4 subplots either in suspended position supported by a fishing net 10 cm below the screen layer or on the soil surface. For each species, six litterbags from each subplot were harvested after 3, 6, 9, and 12 months, respectively. Any visible gravel, green plants, and arthropods were removed from the litters. Samples were then oven dried at 65 °C for 48 h before weighing. During the decomposition period, living plants in the subplots were removed periodically to prevent unwanted shading effects. The cumulative solar radiation and UV radiations were 5932.8 and 279.7 MJ m^{-2}, respectively during the whole incubation year (Figure 2.5). To account for some overlap of standing green leaves, twigs and leaf litter in vertical projection from above in the natural situation, which was assumed to reduce the relative exposure of the surface of an average dead leaf to direct solar radiation, broadly representative overlap of leaf litter particles was implemented within the litterbags. In other words, the present study did not capture

the maximum effect of solar radiation on litter decomposition, but an effect relevant to the natural situation.

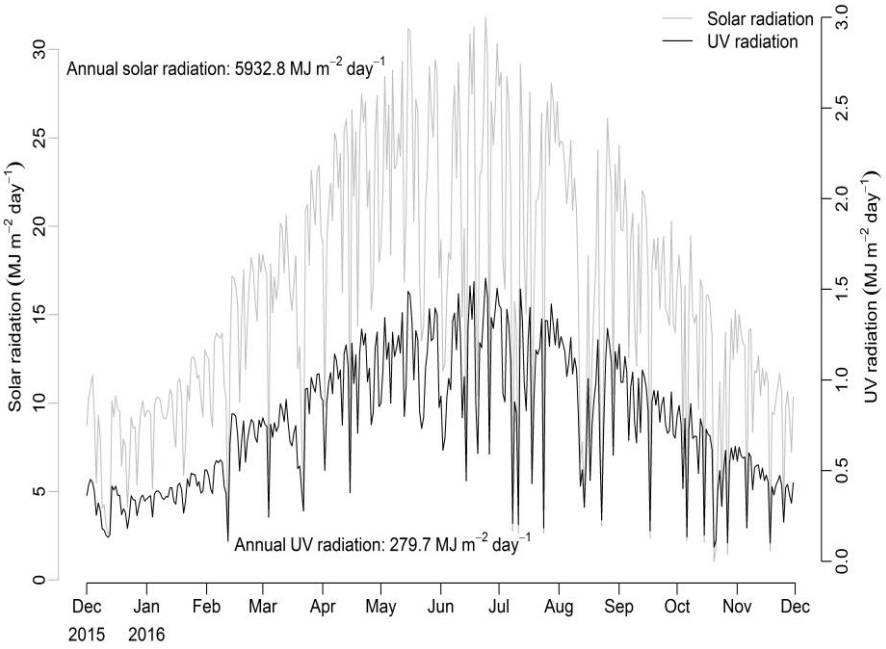


Figure 2.5 The monthly solar radiation and UV radiation data of meteorological station adjacent to the incubation experiment, during the experimental period

图 2.5 邻近分解实验的气象站的太阳辐射和紫外线辐射的每月动态

2.3.2 Woody litter experimental design

In order to assess the influences of UV radiation and litter position (i.e. suspended above the surface to represent the position of the litter still attached to the shrub; on the soil surface; buried below the sand) on woody litter decomposition, I used five subplots (two UV treatments × two aboveground positions and one sand burial) to examine responses of woody litter decomposition to litter position or UV radiation. The detailed description could be seen in the above section. I used the litterbag approach to capture the mass loss of woody litter of four species with five diameter classes at different harvests, i.e. 6, 12, 18, 24 and 34 months (from December 2015 through October 2018) by sealing more than 5 g of pre-weighed air-dried woody litter into each litterbag. This amount should depend on the actual situation because woody litters are quite distinct from leaf litters. That is to say, I cut shrub wood into fixed 10 cm long segments before filling litters into bags. Three subsamples for each species were used to correct air-dried litter mass via initial air-dried and oven-dried mass (at 65°C for 48 h). The size of the litterbags was 10 cm ×

15 cm with a mesh size of 2-mm for the top side exposed to the sun, and a 0.5-mm mesh for the bottom side in order to prevent loss of small woody litter fragments (Baker and Allison, 2015). The number of replicates was 5. Therefore, the number of litterbags used was 2500 (4 species × 5 diameter classes × 5 treatments × 5 harvest times × 5 replicates). The five hundred litterbags were placed in each of the 5 subplots either in suspended position supported by a fishing net at 10 cm distance below the UV screen (see Figure 2.6a), on the soil surface (see Figure 2.6b) or buried in the sandy soil at 10 cm depth. This 10-cm layer of soil had first been cleared of plant material and removed before the litterbags were laid out, after which the soil layer was mixed and put back on, (see Figure 2.6c, d). I retrieved litterbags after 5 periods of incubation (see above), cleaned the samples in the laboratory by brushing, oven-dried them at 65°C for 72 h to obtain dry masses.

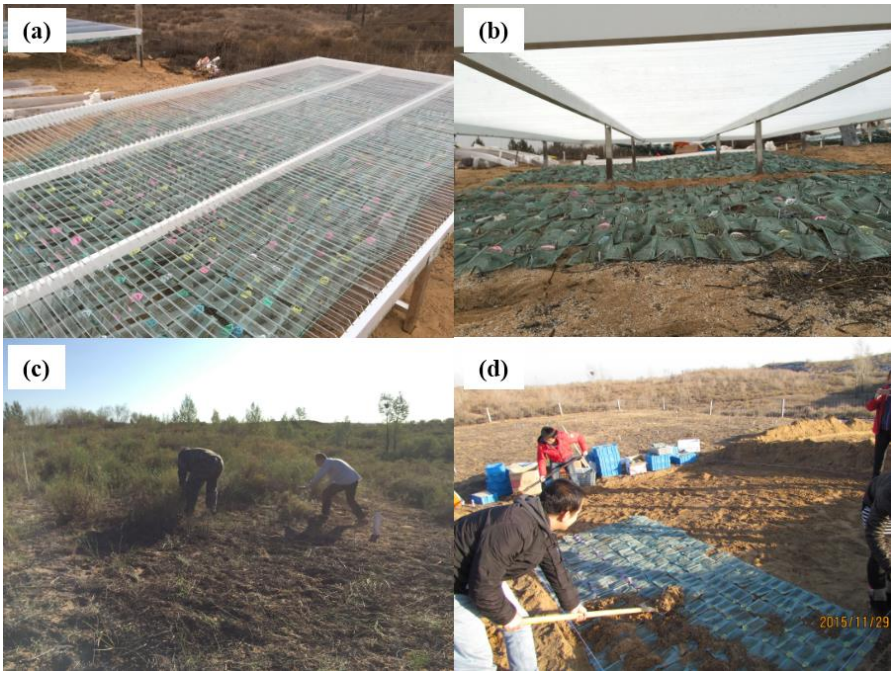


Figure 2.6 The process of setting up experiments in the field

图 2.6 野外实验设置步骤

Woody litters were placed (a) suspended above the surface; (b) on the soil surface; (c) cleared of plant material and removed before the litterbags were laid out; (d) after which the soil layer was mixed and put back on buried below the sand.

木本凋落物放置在（a）悬空；（b）土壤表面；（c）凋落物袋布置之前清除地表植物；（d）将土壤混合把凋落物袋埋在土壤下面。

2.3.3 Leaf and fine root experimental design

This prevented litter falling through the bottom while it maximized light penetration at the top. I setup two litter treatments by placing litterbags including on the soil surface under solar radiation and 10 cm depth below the soil surface (sand burial). The poor soil stability is an important phenomenon in the Mu Us Sandland, therefore, the root decomposition process only occurs in underground sand-burial position and the leaf litter is carried out under sand-buried position and also placed to the soil surface position. For each leaf litter and fine root treatment, there were five litterbags (replicates) per species on average for each of six harvest times, i.e. after 3, 6, 9, 12, 18 and 24 months of incubation. The leaf litter and fine root incubation experiment started in early December 2015 and lasted 2 years.

2.4 Chemical analysis

For each of the green leaf, leaf, woody litter, and fine root samples, three replicate initial and decomposed litter samples were randomly taken from each combination of UV (UV block *vs* UV pass) and position (sand burial *vs* surface *vs* suspended) treatments for chemical analyses in the laboratory. These samples were ground using a Wiley mill with U.S. standard (#20 meshes). For the green leaves, initial and decomposed leaf, woody litters and fine root samples, carbon (% C) and nitrogen (% N) concentrations of the three replicates were determined by an element analyzer (Vario EL III) (Westerman, 1990). The C: N ratios of green leaf, leaf, woody litter, and fine root samples were determined using the C and N concentrations above. The loss rates of C or N over different incubation periods were determined by the formula $(M_0 \cdot Con_0 - M_t \cdot Con_t)/(M_0 \cdot Con_0)$, where M_0, M_t, and Con_0, Con_t are dry masses, the C or N concentrations of initial litter and of decomposed litter during the incubation period *t*, respectively. P, Ca, K, Mg and Mn concentrations for green leaves, initial leaf litter and fine roots were measured by inductively coupled plasma mass spectrometry (ICP-MS, Agilent 7700X).

2.5 Data analysis

All statistical analyses were performed using R software (v3.2.3, R Core Team, 2016). Repeated - measures (incubation period) three-way ANOVAs were used to examine the effects of species, UV radiation, litter position, diameter classes and all

their interactions on a leaf, woody litter and fine root mass loss and C and N loss. For each of the harvests, the ordinary linear regression model was used to explore whether there were significant differences in mass loss, concentrations, and losses of C and N between UV radiation treatments under different positions and between litter positions under different UV radiation treatments, with Bonferroni correction (Hothorn et al., 2008). One-way ANOVAs and Tukey's HSD multiple contrasts were used to examine the difference between green leaves and initial leaf and woody litter traits among the species; Bonferroni correction was used to control the overall type I error rate. Nonlinear regressions were carried out to calculate the *k* value (yr^{-1}) Olson's (1963) negative exponential model ($Y_t = Y_0 e^{-kt}$) across all harvest times and replicates each of the species (where *Y* represents mass remaining and *t* is incubation time). Pearson correlation analyses were used to examine whether green leaves or initial leaf litter, woody litter, and fine root traits were correlated with each other or whether they were correlated with the *k* values under different combinations of UV and litter position treatments. Ordinary least square (OLS) regression was used to examine whether the relationship between C and N losses for each of the species was significant. Multiple linear regressions were used to explore how the effects of multiple influential traits affected litter decomposition rates for different treatments; the influential traits were standardized using the formula (x-m)/sd, where x is the value of a trait, m and sd are the mean and standard deviation of a trait, respectively. Then a best-fit model was chosen based on the lowest AIC criteria. The level of statistical significance was set at $P < 0.05$.

All I used multi-model inference to determine how changes in rates of wood decomposition were related to bark and wood traits. I carried out all possible combinations of predictors using the Dredge function of MUMIn package (Barton, 2009). Prior to running full models, I standardized the predictor variables using the standardize function in the arm package, which is essential for interpreting parameter estimates (Grueber et al., 2011). I excluded models with highly correlated predictor variables ($|r|>0.5$) to reduce any collinearity problem among explanatory variables so that the candidate models only contained one of a pair of highly correlated variables (Dormann et al., 2013). The best candidate models were ordered based on AICc and I used the model averaging procedure on top order models with $\Delta AICc \leq 4$ criteria (Anderson and Burnham, 2002). In the multi-model inference, I transformed the five

diameter classes into a continuous predictor variable using the simple mean of each range (also see Abbott and Crossley, 1982). The significance level was set at P <0.05.

For leaf and fine root experiments, SLA was square-root-transformed and leaf C: N ratio, leaf litter N, SRL, and root N were log10-transformed to meet normality. Additionally, P, K, Ca, Mg, Mn for leaves, initial leaf litters, and fine roots were Log10-transformed to satisfy normality of ANOVA. Principal components analysis (PCA) was used to show associated leaf or leaf litter traits for leaf and fine roots traits, respectively. Ordinary least squares were carried out to test whether green leaf and initial litter traits could determine the k values under the three litter treatments. The significant level is set at $P < 0.05$.

Chapter 3. Effects of UV exposure and litter position on leaf litter decomposition

3.1 Introduction

Decomposition of plant litter plays a crucial role in the cycling of carbon (C) and nutrients (Berg and McClaugherty, 2008; Swift et al., 1979). In and across most terrestrial ecosystems and climatic regions, litter decomposition is controlled by three main factors: incubation environment, litter quality and decomposer community composition (Coûteaux et al., 1995). These three factors modulate the fluxes of carbon and nutrients with different relative contributions in different ecosystem types or regions (Liu et al., 2018; 2015a; Bradford et al., 2014; Cornwell et al., 2008; Gholz et al., 2000; Swift et al., 1979). Drylands comprise approximately 40% of global land cover and account for roughly 20% of the soil organic carbon pool (Reynolds et al., 2007; Lal, 2004). In contrast with biotically driven litter decomposition in mesic ecosystems (Liu et al., 2015a; Bradford et al., 2014), abiotic photodegradation is a predominant control on the cycling of C and nutrients in dryland ecosystems (Austin, 2011; Austin and Vivanco, 2006). The different contributions of these competing pathways between mesic and xeric ecosystems have challenged accurate predictions of global litter decomposition rates and associated nutrient fluxes (Throop and Archer, 2009; Parton et al., 2007).

One of the most documented effects of human activity on the environment is the reduction of stratospheric ozone resulting in an increase of biologically harmful ultraviolet (UV) radiation, especially UV-B (Bornman et al., 2015). Many researchers have investigated direct and indirect effects of UV, particularly UV-B effects on plant growth, litter decomposition (Pancotto et al., 2003; Rozema et al., 1997) and terrestrial carbon and nutrient cycling (Smith et al., 2009). In contrast with microbial decomposition, UV radiation affects litter decomposition by direct photochemical degradation of the litter (Brandt et al., 2007). Photodegradation is the photochemical mineralization of photo-reactive compounds such as lignin or cellulose (Bornman et al., 2015; King et al., 2012). Generally, UV radiation has been demonstrated to stimulate litter decomposition in arid and semiarid terrestrial ecosystems (Gaxiola and Armesto, 2015; Day et al., 2017; 2007; Lin and King, 2014; Austin and Ballaré, 2010; Brandt et al., 2010; Austin and Vivanco, 2006). However, direct exposure to UV-B

radiation can also reduce microbial decomposition by inhibiting the microbial activity or altering microbial community composition (Robson et al., 2005; Johnson, 2003). Additionally, some studies reported that photodegradation by UV radiation could increase subsequent microbial decomposition, which is called the photopriming effect (Lin et al., 2017; Huang et al., 2017; Gaxiola and Armesto, 2015). However, Kirschbaum et al. (2011) did not find such an effect of UV radiation on subsequent microbial decomposition. The net effect of UV radiation on the litter decomposition rates thus largely depends on the balance between the positive effect on abiotic photodegradation or subsequent microbial decomposition and the negative effect on microbial activity and composition (Wang et al., 2017b; 2015; Smith et al., 2010).

The impact of UV radiation on leaf litter decomposition also depends on litter chemistry (King et al., 2012; Uselman et al., 2011; Brandt et al., 2007). However, the effects of UV radiation on litter decomposition as dependent on litter quality are inconsistent (Liu et al., 2018; King et al., 2012; Uselman et al., 2011; Brandt et al., 2007). Litter position, either falling onto the surface versus intercepted or standing above the surface, can also affect decomposition rates and could possibly modify the relative contribution of photodegradation and microbial decomposition to the cycling of C and nutrients. In semiarid and arid ecosystems, most litter, particularly that of grasses and forbs, can remain standing for several months or seasons (Wang et al., 2017a). Thus standing litter decomposition also plays important roles in C and nutrient cycling of drylands. Most studies have found that suspended litters were decomposed more slowly than litters placed on the soil surface (Almagro et al., 2017; Dukes and Field, 2000; Thurow, 1989). It was thought that the proximity of litter to the soil surface increased litter decomposition mostly due to effects of the microbial activity. However, faster litter decomposition above the surface than on the soil surface has been found too and attributed to a stronger effect of wind abrasion (Lin and King, 2014).

Up to now, the interactive effects of UV radiation, litter position, and species (with different litter qualities) on dryland litter decomposition are unclear. To answer this question, leaf litters of eight contrasting species were exposed in a semiarid ecosystem to experimentally manipulated UV radiation using specially designed screens (UV pass versus UV block), in positions both at the surface and suspended above the surface, for one year. Due to distinct abiotic and biotic environmental

conditions between the surface and suspended positions, there should be a strong interaction between litter position and UV exposure on litter decomposition across eight species with different litter qualities. Thus, the hypothesis is that UV radiation would increase litter decomposition rates and C and nitrogen (N) mineralization of suspended leaf litters compared with UV block treatment, but it would decrease decomposition rates and C mineralization and microbial N immobilization of surface litters due to a negative effect on microbial composition and activity for most species.

3.2 Results

3.2.1 UV radiation and microclimate

UV pass and UV block treatments differed in their exposure to UV radiation. On average, the UV block treatment transmitted 12.7% of UV radiation, whereas the UV pass transmitted 65.2% (Figure 3.1a). From December 2015 to November 2016, UV treatment did not affect daily mean temperature or relative humidity (RH) for either of the litter positions (Figure 3.1b, c). RH was affected by position with slightly higher values at the surface as compared with the suspended position (Figure 3.1b, c).

3.2.2 Green leaf and initial leaf litter traits

The morphological and chemical traits of green leaves and initial leaf litter differed among the eight species (Table 3.1). The perennial grass species (*P. villosa*, *P. centrasiaticum*, and *C. pseudophragmites*) had lower N concentration of both green leaves and initial litter but higher C: N than two shrub species (*S. psammophila* and *C. korshinskii*) (Table 3.1). The shrub *A. bracteata* had lower litter N and higher litter C: N ratio compared with the other two shrubs (Table 3.1). Two annual forb species (*A. pungens* and *C. chinganicum*) had lower leaf dry matter content (LDMC) and larger specific leaf area (SLA) than most species (Table 3.1).

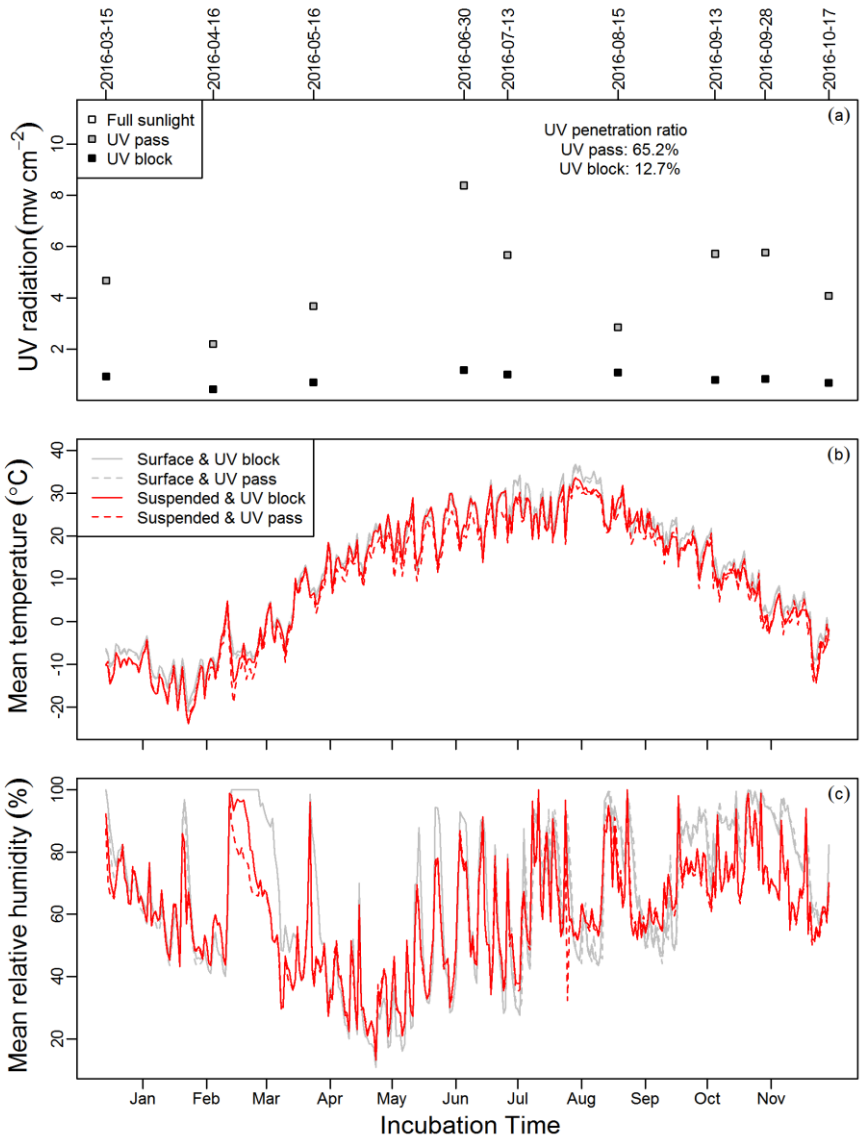


Figure 3.1 Microclimate characteristics during the experimental period from December 2015 through November 2016

图 3.1 2015 年 12 月至 2016 年 11 月实验期间的微气候特征

In this figure, (a) UV radiation (mw cm^{-2}) under ambient and reduced UV conditions (UV pass versus UV block) compared with full sunlight (b) Mean daily air temperature (°C) and (c) Mean daily air relative humidity (%) respectively based on data from each of the four subplots.

在该图中(a)与全日照相比，在对照和减少的紫外线条件下(紫外线通过与紫外线阻挡)的紫外线辐射(mw cm^{-2})，(b)平均每日空气温度(°C)和(c)平均每日空气 相对湿度(%)。

Table 3.1 The morphological and chemical traits of green and initial leaf litter of eight species (mean ± 1SE, n = 3)

表 3.1 八个物种活体和初始叶凋落物的形态和化学性状（平均值±1SE，n = 3）

	Green leaf					Initial leaf litter		
Species	LDMC ($g\ g^{-1}$)	SLA ($cm^2\ g^{-1}$)	N (%)	C (%)	C: N ratio	N (%)	C (%)	C: N ratio
Psammochloa villosa	0.43±0.01a	74.33±0.68c	2.56 ± 0.09b	47.18 ± 0.74a	18.49 ± 0.61bcd	0.90 ± 0.15bc	45.98 ± 0.42a	53.92 ± 8.28abc
Pennisetum centrasiaticum	0.34±0.01b	254.53±15.56a	1.73 ± 0.04de	41.57 ± 0.48bc	24.00 ± 0.34b	0.62 ± 0.01c	38.87 ± 0.81c	62.54 ± 2.49ab
Calamagrostis pseudophragmites	0.36±0.01ab	156.55±13.25bc	1.29 ± 0.04e	43.64 ± 0.07abc	33.99 ± 1.14a	0.65 ± 0.08c	44.25 ± 0.98ab	70.03 ± 6.97a
Salix psammophila	0.37±0.00ab	116.43±7.18bc	2.53 ± 0.01b	47.05 ± 0.38a	18.59 ± 0.12bcd	1.36 ± 0.12ab	45.46 ± 0.66a	33.92 ± 2.70bc
Caragana korshinskii	0.37±0.00ab	119.93±7.55bc	3.17 ± 0.04a	45.43 ± 0.37a	14.32 ± 0.13d	1.96 ± 0.07a	44.92 ± 0.09ab	22.99 ± 0.83c
Atraphaxis bracteata	0.34±0.01b	92.23±4.57bc	2.27 ± 0.05bc	44.17 ± 0.42abc	19.48 ± 0.57bcd	0.61 ± 0.03c	42.23 ± 0.25abc	69.56 ± 3.63a
Agriophyllum pungens	0.24±0.02c	154.50±20.52bc	1.99 ± 0.15cd	40.71 ± 0.79c	20.74 ± 1.74bc	0.62 ± 0.00c	38.05 ± 0.32c	61.26 ± 0.67ab
Corispermum chinganicum	0.14±0.01d	167.27±10.14b	2.62 ± 0.04b	44.82 ± 0.47ab	17.12 ± 0.21cd	0.67 ± 0.01c	40.54 ± 0.00bc	60.40 ± 0.51ab

In this table, different lowercase denotes significant differences among species at $P < 0.05$. The P values in many Tukey's HSD multiple contrasts were adjusted by Bonferroni correction.

在该表中，不同的小写字母表示物种之间的显著差异（$P < 0.05$）。 Tukey HSD 多重比较中的 P 值通过 Bonferroni 校正进行了矫正。

3.2.3 Litter decomposition rates under UV and litter position treatments

The three-way repeated-measures ANOVA showed that species ($F = 724.26$, $P < 0.001$), litter position ($F = 75.61$, $P < 0.001$), UV radiation ($F = 20.77$, $P < 0.001$), and all their interactions had significant effects on litter mass loss except for the interaction of species and UV (Figure 3.2; Table 3.2); the different species had broadly similar UV response.

During the first three months of incubation, there was little litter decomposition (Figure 3.2). When incubation progressed, the two shrubs (*S. psammophila* and *C. korshinskii*) and two annual forbs (*A. pungens* and *C. chinganicum*) showed faster decomposition (Figure 3.2d, e, g, h); the other four species, however, showed lower decomposition rates over time (Figure 3.2a-c, f). All species showed faster decomposition rates from June through August as associated with a favorable combination of temperature and moisture (Figure 3.2b, c); especially the three grass species (*P. villosa, P. centrasiaticum,* and *C. pseudophragmites*) and one shrub (*A. bracteata*) showed much faster decomposition rates during the summer period (Figure 3.2a-c, f). For the suspended treatment, UV radiation significantly increased mass loss of two perennial grasses (*P. villosa* and *P. centrasiaticum*) and two annual forbs (*A. pungens* and *C. chinganicum*) over one year of incubation, but had no significant effect on the other four species; across species the percentage increase in mass loss ranged from 4.5 to 27.3% with an average of 13.7% (Figure 3.2). For the surface treatment, UV radiation had no influence on leaf litter decomposition of any of the species considered except for *P. centrasiaticum* and *C. pseudophragmites* after 9 and 6 months of incubation, respectively. For the UV block treatment, leaf litter decomposition rates of two grasses (*P. villosa* and *C. pseudophragmites*) were faster on the surface than in suspended position, but the opposite pattern was measured for *C. korshinskii* (Figure 3.2a, c, e). For UV radiation, decomposition rates of *C. korshinskii* and *C. chinganicum* litters were faster in suspended than in surface position (Figure 3.2e, h). In contrast, *C. pseudophragmites* had faster litter decomposition in surface than in suspended position (Figure 3.2c).

Table 3.2 Results of three-way repeated ANOVA with incubation period as a repeated measure on the fractions of litter mass loss in responses to the position, UV radiation, species, and all their interactions

表 3.2 物种、位置和UV辐射及其互作对叶凋落物分解影响的可重复性三因素方差分析表

	Predictor variables	Dfn, Dfd	F	*P*
Between-subjects effects	Species	7, 106	528.57	< 0.001
	Position	1, 106	6.28	0.014
	UV radiation (UV)	1, 106	16.20	< 0.001
	Species × position	7, 106	15.00	< 0.001
	Species × UV	7, 106	1.04	0.408
	Position × UV	1, 106	21.09	< 0.001
	Species × position × UV	7, 106	8.78	< 0.001
Within-subjects effects	Time	3, 318	4197.97	< 0.001
	Time × species	21, 318	60.51	< 0.001
	Time × position	3, 318	10.45	< 0.001
	Time × UV	3, 318	3.94	0.009
	Time × species × position	21, 318	5.65	< 0.001
	Time × species × UV	21, 318	1.42	0.104
	Time × position × UV	3, 318	5.39	0.001
	Time × species × position × UV	21, 318	2.87	< 0.001

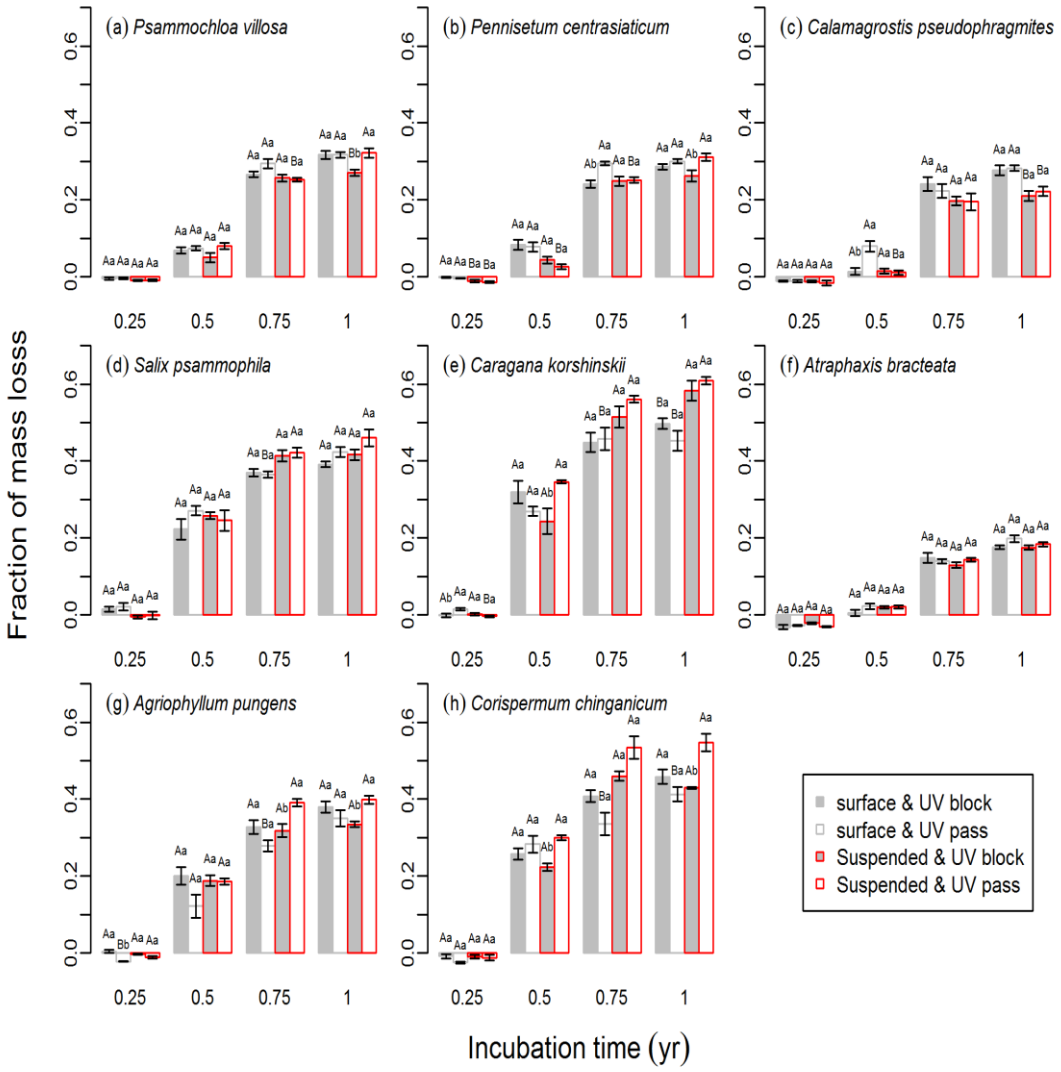


Figure 3.2 Effects of UV radiation (UV pass versus UV block) and position (surface versus suspended) on cumulative mass loss over four incubation periods for each of eight species

图 3.2 紫外线辐射（紫外线通过与紫外线阻挡）和位置（表面与模拟立枯）对八个物种叶凋落物分解的影响

In this figure, the different lowercase letters denote significant differences between UV treatments under different positions and different uppercase letters denote significant difference between positions under different UV treatments for each of four incubation periods at $P < 0.05$. The bar represents Mean ± 1SE (n = 6).

在该图中，某一分解时间条件下，不同小写字母表示在不同位置下 UV 处理之间损失率存在显著差异，不同大写字母表示在不同 UV 处理下位置之间损失率存在显著差异（P <0.05）。柱状图表示平均值±1SE（n = 6）。

3.2.4 Correlations of green leaf or leaf litter traits and decomposition rates

Pearson correlation analyses showed that N or C between the green leaves and initial leaf litters were significantly positively correlated (Table 3.3). The *k* values for litter decomposition increased with increasing N or decreasing C: N of both green leaves and initial leaf litters (Table 3.4). The other variables (LDMC, SLA, green leaf C, and initial leaf litter C) were not significantly correlated with the *k* values under any of the treatments of UV radiation and litter position (Table 3.4). In addition, multiple linear regressions showed that the best-fit model contained C: N ratio of initial leaf litters and LDMC as predictors of *k* values for each treatment, in which litter C: N ratio had a stronger influence on litter decomposition (Table 3.5).

Table 3.3 Pearson correlation matrix between eight traits of green leaf and initial leaf litters across eight species

表 3.3 八个绿叶和初始叶凋落物性状之间的 Pearson 相关矩阵（n =8）

	LDMC (mg g^{-1})	SLA (cm^2 g^{-1})	Green leaf N (%)	Green leaf C (%)	Green leaf C: N ratio	Litter N (%)	Litter C (%)	Litter C: N ratio
LDMC (mg g^{-1})		0.345	0.991	0.296	0.737	0.350	0.056	0.475
SLA (cm^2 g^{-1})	-0.39		0.205	0.057	0.360	0.414	0.056	0.499
Green leaf N (%)	0.00	-0.50		0.108	**0.001ξ**	**0.040**	0.361	**0.028**
Green leaf C (%)	0.42	-0.69	0.61		0.329	0.171	**0.004**	0.171
Green leaf C: N ratio	0.14	0.37	**-0.93ξ**	-0.40		0.179	0.842	0.105
Litter N (%)	0.38	-0.34	**0.73**	0.54	-0.53		0.124	**<0.001ξ**
Litter C (%)	0.70	-0.70	0.37	**0.88**	-0.08	0.59		0.198
Litter C: N ratio	-0.30	0.28	**-0.76**	-0.54	0.62	**-0.97**ξ	-0.51	

In this table, the lower and upper triangles represent correlation coefficient and *P* value, respectively. The values in bold denote a significant relationship with ecological implication at $P < 0.05$. ξ denotes an intrinsic relationship between N and C: N ratio of green leaves or initial leaf litters.

在该表中，下三角和上三角分别表示相关系数和 *P* 值。粗体值表示具生态学意义的显著关系，$P < 0.05$。ξ表示绿叶或初始叶凋落物的 N 和 C: N 比之间的内在关系。

Table 3.4 Pearson correlation analysis between 8 traits of green leaf and initial leaf litters and *k* values (n = 8) of litter decomposition for different treatments

表 3.4 不同处理下八个绿叶和初始叶凋落物性状和凋落物分解速率 *k* 值（n = 8）之间的 Pearson 相关性分析

	Surface				Suspended			
	UV block		UV pass		UV block		UV pass	
	R	*P*	R	*P*	r	*P*	r	*P*
LDMC (mg g^{-1})	-0.348	0.398	-0.173	0.682	-0.26	0.534	-0.388	0.342
SLA (cm^2 g^{-1})	0.003	0.994	-0.011	0.98	-0.049	0.908	-0.018	0.966
Green leaf N (%)	*0.679*	*0.064*	*0.685*	*0.061*	**0.746**	**0.034**	**0.739**	**0.036**
Green leaf C (%)	0.235	0.576	0.386	0.344	0.309	0.456	0.258	0.537
Green leaf C: N ratio	-0.585	0.128	-0.559	0.15	*-0.643*	*0.086*	*-0.657*	*0.077*
Litter N (%)	*0.683*	*0.062*	**0.773**	**0.025**	**0.772**	**0.025**	*0.676*	*0.066*
Litter C (%)	0.08	0.851	0.242	0.564	0.156	0.712	0.064	0.88
Litter C: N ratio	**-0.755**	**0.03**	**-0.852**	**0.007**	**-0.833**	**0.01**	**-0.743**	**0.035**

In this table, the values in bold denote a significant relationship at $P < 0.05$ and the italic values denotes a marginally significant relationship at $P < 0.1$.

在该表中, 粗体值表示P <0.05时的显著相关，斜体值表示P <0.1时的边际显著相关。

Table 3.5 The best-fit model for each treatment from multiple linear regression models on litter decomposition rates (*k* values) in response to green leaf and initial leaf traits

表3.5 绿叶和初始叶凋落物性状对叶凋落物分解速率影响的最优多元线性回归分析模型

	Estimate	Std. Error	t value	Pr(>|t|)	r^2
Surface *and* UV block					0.929
Intercept	0.410	0.019	21.19	<0.001	
LDMC (g g^{-1})	-0.109	0.022	-5.04	0.004	
Initial litter C: N ratio	-0.164	0.022	-7.55	0.001	
Surface *and* UV pass					0.925
Intercept	0.401	0.017	23.36	<0.001	
LDMC (g g^{-1})	-0.070	0.019	-3.64	0.015	
Initial litter C: N ratio	-0.148	0.019	-7.72	0.001	
Suspended *and* UV block					0.976
Intercept	0.411	0.014	30.30	<0.001	
LDMC (g g^{-1})	-0.118	0.015	-7.73	0.001	
Initial litter C: N ratio	-0.211	0.015	-13.86	<0.001	
Suspended *and* UV pass					0.958
Intercept	0.475	0.022	21.36	<0.001	
LDMC (g g^{-1})	-0.173	0.025	-6.96	0.001	
Initial litter C: N ratio	-0.244	0.025	-9.81	<0.001	

In this table, LDMC denotes green leaf dry matter content; C: N ratio denotes ratio of carbon to nitrogen of initial litter.

在该表中, LDMC 表示绿叶干物质含量; C: N 比表示初始叶凋落物 C: N 比。

3.2.5 C and N concentrations and losses of decomposed litters

There was an increase in N concentration for *P. villosa*, *P. centrasiaticum*, *C. pseudophragmites*, *S. psammophila*, and *A. bracteata* during litter decomposition (Figure 3.3). N concentrations were slightly higher on the surface than in a suspended position (Figure 3.3). In addition, N concentration of suspended litters was slightly higher in the UV pass than in the UV block treatment for most species except *A. pungens* (Figure 3.3). The fraction of (mass loss corrected) N loss during decomposition was affected by an incubation period, species, UV treatment, position, and all their interactions except for the interaction between position and UV (Table 3.6). UV radiation did not increase N loss of suspended litters for most species during the experiment (Figure 3.4); for suspended treatment, UV radiation increased N loss of *A. pungens* litter but decreased N loss of *C. pseudophramites* (Figure 3.4c, g). UV treatment increased N loss of surface litters for most species (Figure 3.4). The C loss

was affected by the incubation period, species, UV treatment, position, and all their interactions except for the interaction between the incubation period and UV (Table 3.6). The two shrubs (*S. psammophil*a and *C. korshinskii*) had higher C concentration in a suspended position than on the surface (Figure 3.5). For the suspended treatment, UV radiation increased C losses of *P. villosa, P. centrasiaticum, A. pungens* and, to a lesser degree, *C. chinganicum* (Figure 3.6 a, b, g, h).

The C loss was positively correlated with N loss in both UV and litter position treatments for most species (Figure 3.7). The stronger positive relationships between C and N losses were observed for the suspended position, but these response variables were decoupled or became negative for the surface litters of *P. centrasiaticum, C. pseudophragmites, S. psammophila,* and *A. bracteata*, except for *C. pseudophragmites* under UV radiation (Figure 3.7).

Table 3.6 Results of three-way ANOVA with incubation period as a repeated measure on the fractions of C and N losses in responses to the position, UV radiation, species, and all their interactions

表3.6 物种，位置和 UV 辐射及其互作对叶凋落物 C 和 N 损失影响的可重复性三因素方差分析

Effect	Dfn, Dfd	C loss		N loss	
		F	*P*	F	*P*
Between-subjects effects					
Species	7, 160	1329.53	<0.001	1116.01	**<0.001**
Position	1, 160	23.75	<0.001	98.61	**<0.001**
UV radiation (UV)	1, 160	31.52	<0.001	16.46	**<0.001**
Species × position	7, 160	13.16	<0.001	25.4	**<0.001**
Species × UV	7, 160	2.93	0.006	8.53	**<0.001**
Position × UV	1, 160	33.9	<0.001	3.38	0.068
Species × position × UV	7, 160	8.86	<0.001	38.73	**<0.001**
Within-subjects effects					
Time	3, 414	8295.56	<0.001	1745.24	**<0.001**
Time × species	21, 414	129.5	<0.001	297.68	**<0.001**
Time × position	3, 414	24.73	<0.001	139.79	**<0.001**
Time × UV	3, 414	1.17	0.32	10.38	**<0.001**
Time × species × position	21, 414	5.97	<0.001	10.35	**<0.001**
Time × species × UV	21, 414	2.7	<0.001	8.31	**<0.001**
Time × position × UV	3, 414	7.35	<0.001	36.42	**<0.001**
Time × species × position × UV	21, 414	5.35	<0.001	16.4	**<0.001**

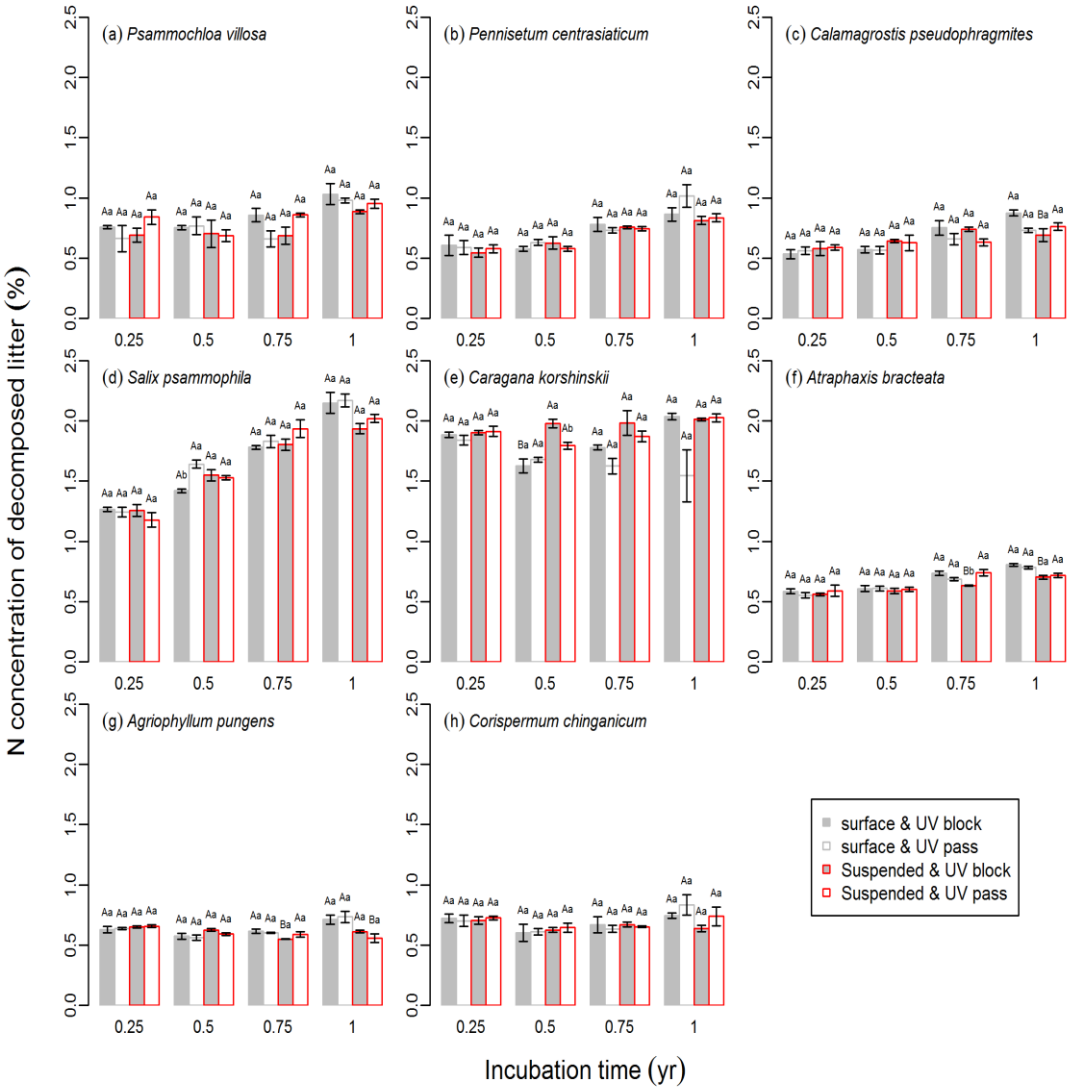


Figure 3.3 Effects of UV radiation (UV pass versus UV block) and position (surface versus suspended) on nitrogen (N) concentrations over 4 incubation periods for each of eight species. The meaning of lowercase and uppercase letters can be seen in the caption of Figure 3.2 The bar represents Mean ± 1SE (n = 3)

图 3.3 不同分解时间下，紫外线辐射（紫外线通过与紫外线阻挡）和位置的影响（表面与模拟立枯）对氮（N）浓度的影响。不同的大，小写字母表示含义见图 3.2 柱状图表示平均值 ± 1SE（n = 3）

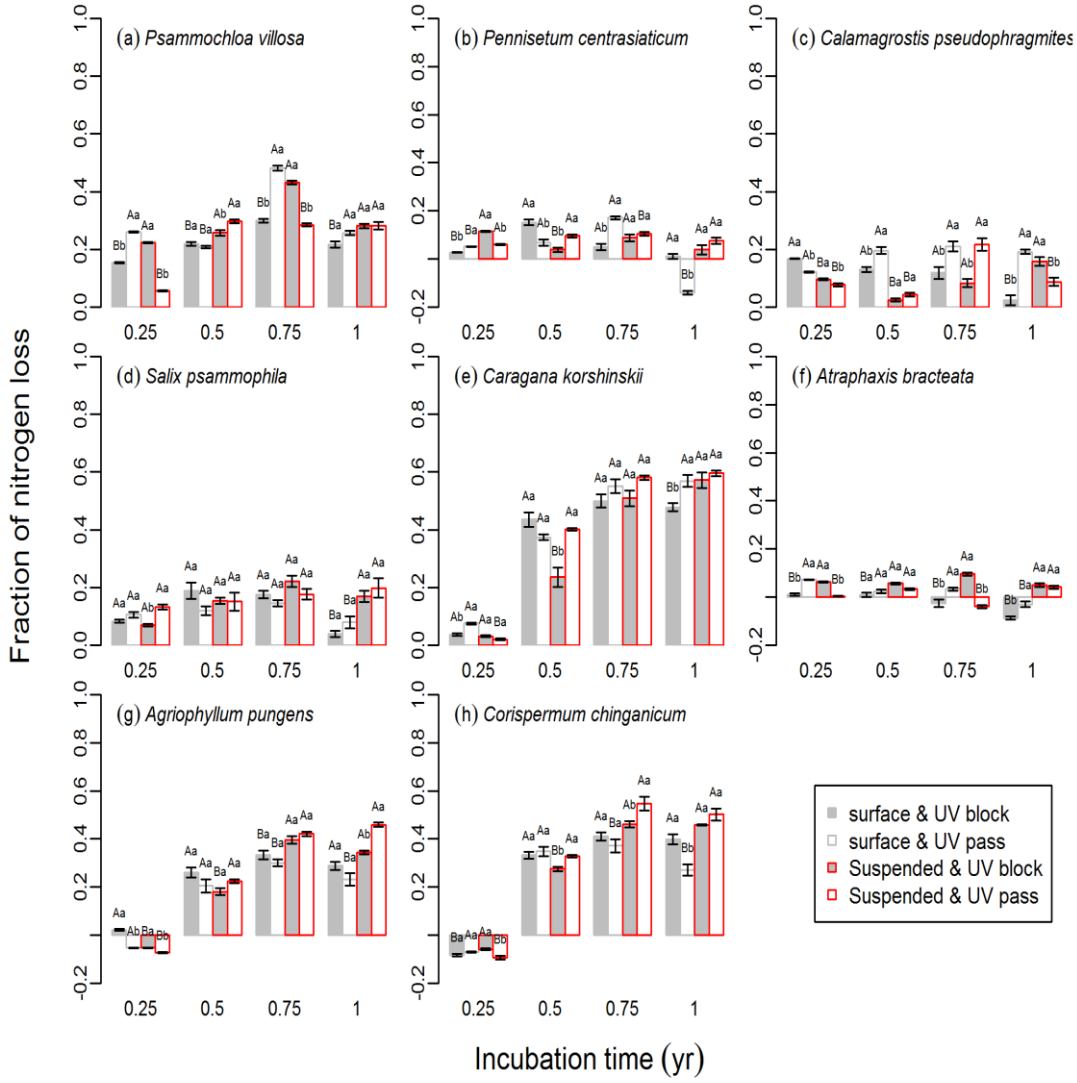


Figure 3.4 Effects of UV radiation (UV pass versus UV block) and position (surface versus suspended) on a fraction of nitrogen (N) losses of the decomposing litters over four incubation periods for each of the eight species. The meaning of lowercase and uppercase letters can be seen in the caption of Figure 3.2. The bar represents Mean ± 1 SE (n=6)

图 3.4 不同分解时间下紫外线辐射（紫外线传递与紫外线阻挡）和位置（表面与模拟立枯）对凋落物 N 损失的影响。不同的大，小写字母表示含义见图 3.2 柱状图表示平均值 ±1SE（n = 6）

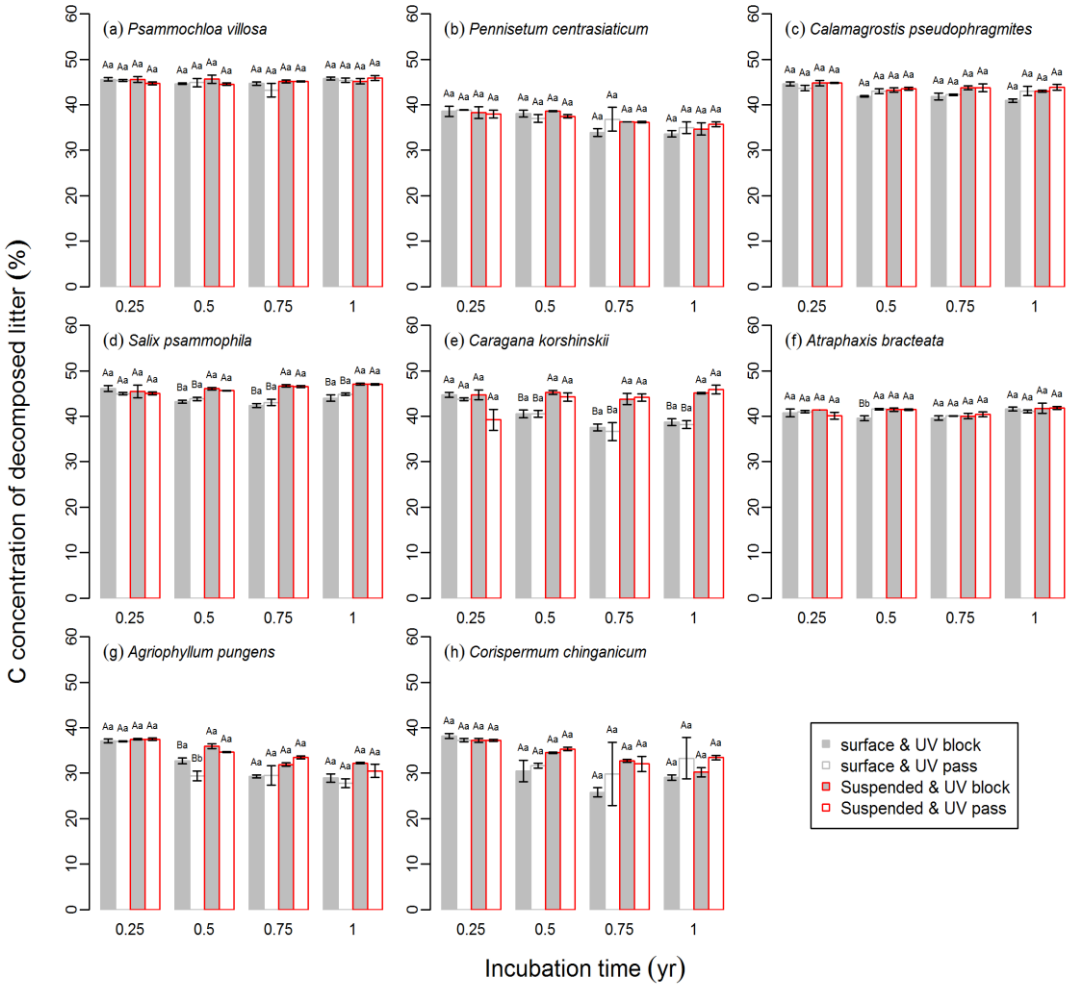


Figure 3.5 Effects of UV radiation (UV pass versus UV block) and position (surface versus suspended) on C concentration for each of eight species over 4 incubation periods. The meaning of lowercase and uppercase letters can be seen in the caption of Figure 3.2. The bar represents are Mean±1SE (n = 3)

图 3.5 紫外线辐射（紫外线传递与紫外线阻挡）和位置（表面与模拟立枯）对 4 种分解时间内 8 种物种中每种物种的 C 浓度的影响。不同的大、小写字母含义见图 3.2。柱状图表示平均值 ± 1SE（n = 3）

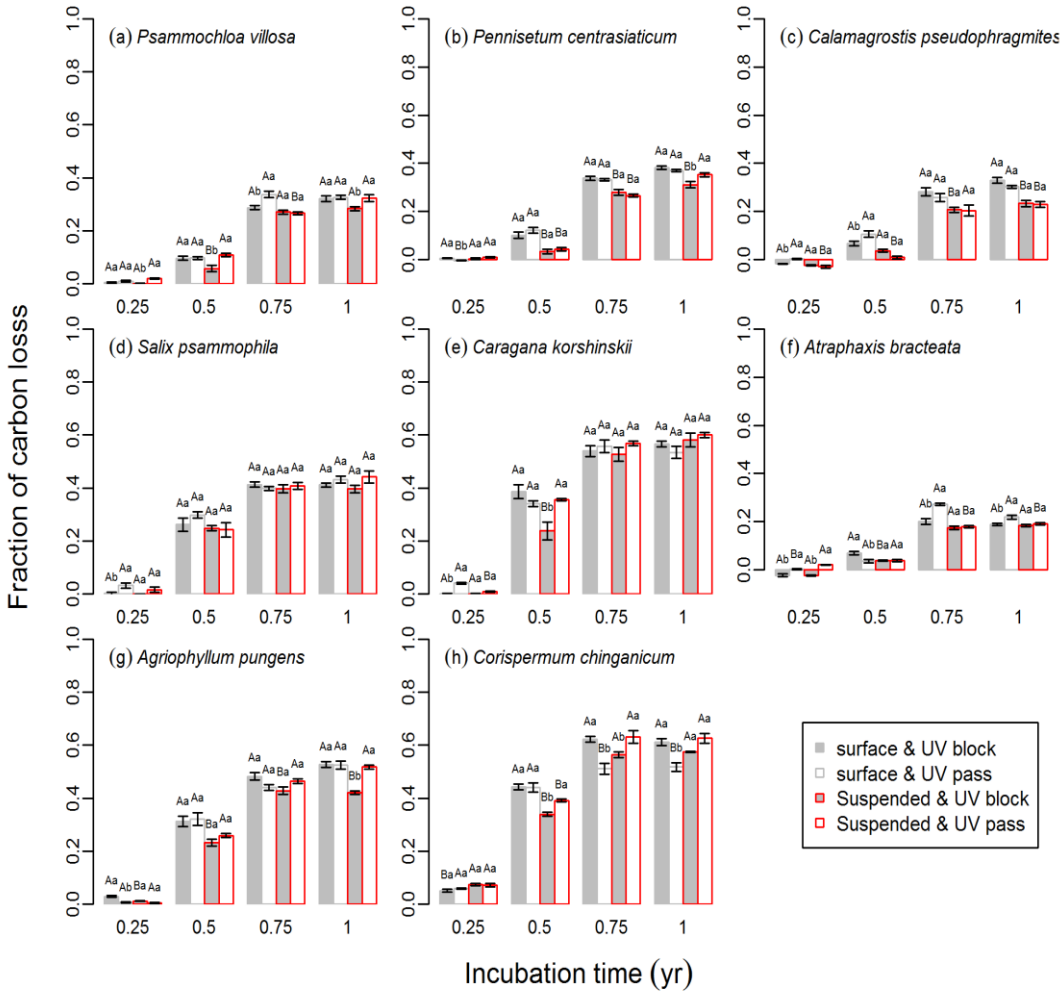


Figure 3.6 Effects of UV radiation (UV pass versus UV block) and position (surface versus suspended) on fraction C loss of the decomposed litters over 4 incubation periods, respectively. The meaning of lowercase and uppercase letters can be seen in the caption of Figure 3.2. The bar represents Means ± 1SE (n = 6)

图 3.6 紫外线辐射（紫外线传递与紫外线阻挡）和位置（表面与模拟立枯）叶凋落物 C 损失的影响。不同的大、小写字母表示含义见图 3.2。柱状图表示平均值 ± 1SE（n = 6）

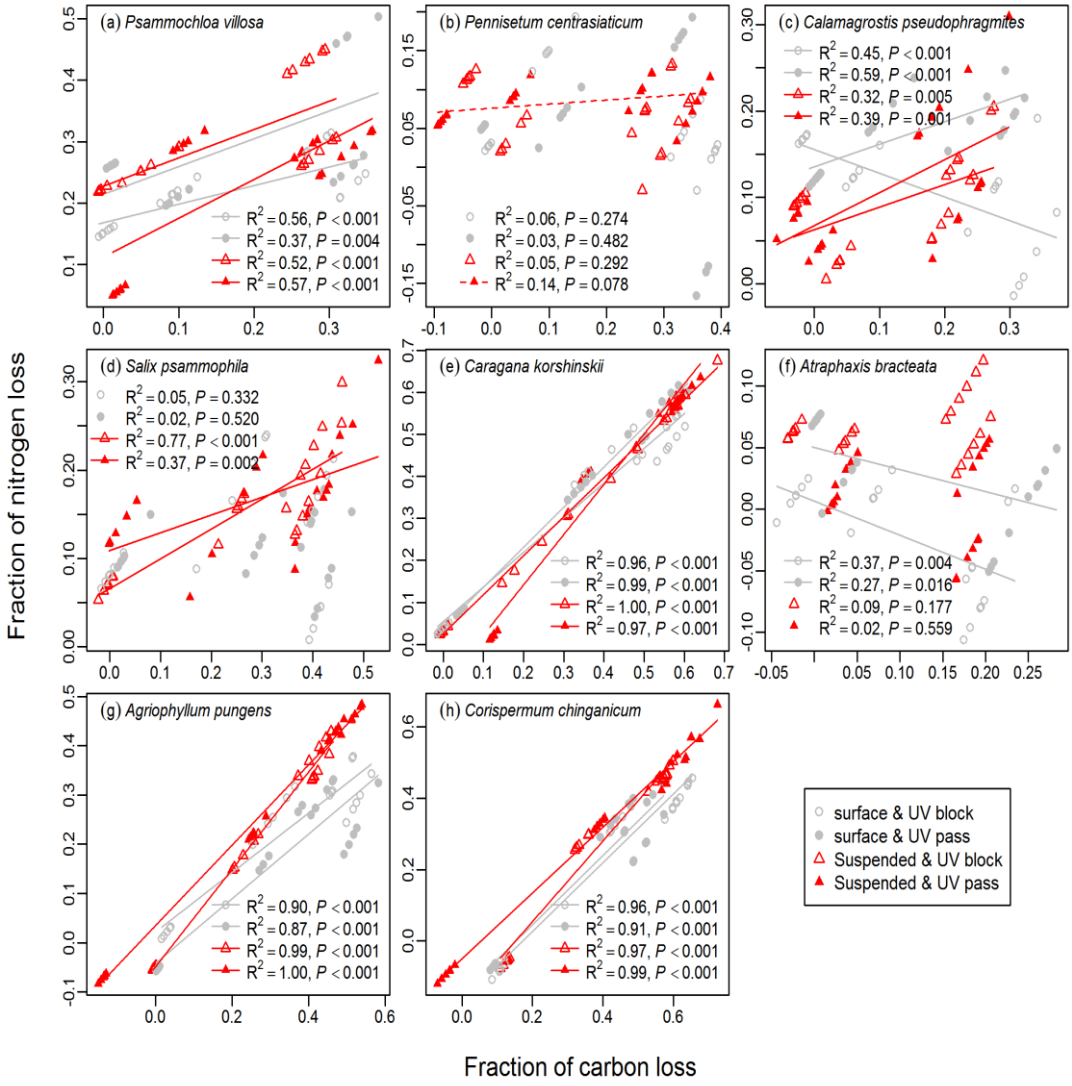


Figure 3.7 Correlations between fraction C loss and fraction N loss of decomposed litters under UV exposure (UV pass or UV block) and position (surface or suspended) treatments for each of the eight species. The solid and dotted lines denote a significant and marginally significant relationship at *P* < 0.05 and *P* <0.1

图 3.7 紫外线照射（紫外线传递或紫外线阻挡）和位置（土壤表面或模拟立枯）处理凋落物 C，N 损失之间的相关性。实线和虚线分别表示在*P* < 0.05 和 *P* < 0.1 时的显著和边际显著相关关系

3.3. Discussion

3.3.1 Changes in a mass loss during decomposition

In the present study, leaf litter decomposition in response to UV exposure and litter position in vertical space was investigated across multiple species in a semiarid region. In dryland ecosystems, differences in a mass loss during different incubation periods are related to litter decomposability (different fractions of labile and less readily decomposed organic material) and seasonal changes in decomposing environments in terms of solar radiation, temperature or moisture (Wang et al., 2015; Lin et al., 2015). The slowest (or even lack) mass loss was observed during the period from December through February possibly due to the very low solar radiation and temperature (Figures 3.1; 3.2), which likely inhibited photochemical and microbial degradation, respectively. When incubation progressed, the faster litter decomposition during spring and summer might be owed to the increase in the solar radiation and temperature and/or moisture. In addition, for litters with lower quality characterized by lower N and higher C: N ratio (Table 3.1), the faster decomposition occurred in summer rather than in spring, possibly due to relatively high proportion of less readily decomposed substances in litters for the three grasses (*P. villosa, P. centrasiaticum, C. pseudophragmites*) and a shrub (*A. bracteata*). While C: N ratio was a reasonable predictor of decomposition rates in this dryland, predictive power could still be improved by including the quality of C, e.g. by using lignin: N ratio as a predictor of the less readily decomposed fraction to decomposition. For instance, the shrub *A. bracteata* had very slow decomposition rate for both surface and buried treatments (46.4 ± 1.5 % and 46.7 ± 1.5% after two years of incubation, respectively) compared to the grass *C. pseudophragmites* (63.3 ± 0.5 % and 88.7 ± 2.2 % respectively; authors' unpublished data), even though these species had similar C: N ratio. This is likely because woody species tend to deposit relatively much C in cell walls as lignin, compared to grasses that tend to invest more C into less recalcitrant cellulose to reinforce cell walls.

Our results showed that UV radiation increased leaf litter decomposition rate of two grasses and two annual forbs in the suspended position (representing litter still attached to the plants) but there was no effect on the other four species (Figure 3.2). The finding of faster decomposition rates as induced by UV radiation is consistent with previous studies (Liu et al., 2015b; Lin and King, 2014; Austin and Vivanco,

2006). Decomposition of suspended litters is likely determined by abiotic factors, such as photochemical mineralization coupled with leaching. The lack of any UV effect on litter decomposition rates in the other four species was also consistent with previous reports (Song et al., 2011; Kirschbaum et al., 2011; Hoorens et al., 2004). These contrasting results for different species, even (in our study) within the same experiment, indicate that the effects of UV exposure on litter decomposition must be due to interspecific variation in morphological and or chemical properties. However, one has to be aware that other abiotic forces, particularly wind (and associated sand abrasion), may also cause litter degradation in relatively sparsely vegetated drylands. For two shrub species (*S. psammophila* and *C. korshinskii*), higher mass losses in suspended position than on the surface might be owed partly to wind-driven sand abrasion (Lin and King, 2014), which could have led to tiny litter fragments falling through the litterbag mesh. The interaction between different abiotic drivers of decomposition for litter attached to the plant, or otherwise suspended above the surface (and their possible interaction with biotic drivers; see below), would be an important topic for future research.

Compared to litter positioned above the surface, interactions between abiotic and biotic drivers of decomposition are likely more important on the soil surface under well-lit conditions. The evidence is accumulating that UV can increase litter decomposition on the soil surface due to photochemical mineralization and that, through photopriming, it can improve subsequent biodegradation (Lin et al., 2017; Austin et al., 2016; Wang et al., 2015). Meanwhile, UV, especially UV-B, inhibits microbial activity and composition (Pancotto et al., 2003). Thus the net effect of UV on surface litter decomposition depends on the balance between photodegradation and microbial decomposition (Wang et al., 2015). Our results showed that only two grass species, i.e. *P. centrasiaticum* and *C. pseudophragmites*, had a higher mass loss under UV radiation on the soil surface, and only after 9 and 6 months of incubation, respectively (Figure 3.2). Moreover, there was no net effect of UV radiation on decomposition rates of surface litters for any of the species considered, which partially conflicts with our hypothesis that UV radiation would decrease the mass loss of surface litters. The balance between photodegradation and microbial decomposition mediated by UV radiation may be modulated by moisture availability, i.e.

precipitation pulses or night-time humidity (Gliksman et al., 2017; King et al., 2012; Smith et al., 2010).

3.3.2 Carbon and nitrogen dynamics during decomposition

The increase in N concentrations of decomposed litter is a common phenomenon and has mainly been attributed to microbial N immobilization under low soil N availability (Tan et al., 2013; Manzoni et al., 2008). In the present study, there was a significant increase in N concentrations of the litters of *S. psammophila, C. pseudophragmites, P. villosa, P. centrasiaticum,* and *A. bracteata* during decomposition (Figure 3.3) due to slower N loss than C loss throughout decomposition (see also Manzoni et al., 2008). Generally, higher N concentrations and lower N losses were observed in surface than in suspended position (Figure 3.4; 3.3). This implies that the differential relative effects of abiotic and microbial factors in litter decomposition could affect N accumulation of decomposed litters. Lin et al. (2015) found that UV radiation decreased N concentration of simulated standing *Bromus diandrus* litter over the summer but not in other seasons of the year. In the present study, there was no UV effect on N concentration of suspended leaf litters across the eight species except for *C. korshinskii* during 6 months of incubation (Figure 3.4). Faster N loss in both UV treatments in suspended than in surface litters for most species partially supports our hypothesis. It also indicates that not only UV radiation but also visible radiation affects C and N dynamics of litters (Austin et al., 2016; Austin and Ballaré, 2010). As hypothesized, the finding on lower N loss or even higher N accumulation of the surface litters in UV block than in UV pass for most species suggests that UV indeed decreases microbial N immobilization.

The decoupled C and N dynamics of decomposing litters can be driven by photodegradation via decreasing microbial decomposition (Lin et al., 2015). Our finding that the release dynamics of C and N were coordinated strongly in suspended but not in surface treatments conflicts this viewpoint; the decoupling of C and N losses of litters on the soil surface was possibly due to microbial N immobilization for some species (Figure 3.7). This implies that the chemistry of decomposed litters can be modulated by the different relative contributions of abiotic and microbial drivers during litter decomposition. Although C concentrations were stable during litter decomposition, suspended litters' C concentrations were (slightly) higher in the UV pass than in the UV block treatment for two shrubs (*S. psammophila* and *C.*

korshinskii) and two annual species (*A. pungens* and *C. chinganicum*) associated with their faster mass losses (Figures 3.5; 3.6). This implies that faster litter decomposition of these four species was due to the release of easily decomposed organic compounds and the photochemical effect of UV radiation did not alter N dynamics of decomposed litters for most standing litter materials.

3.3.3 Litter quality affected over litter decomposition

Litter quality affects the contribution of solar radiation to litter decomposition (Liu et al., 2018; 2015b; Pan et al., 2015; King et al., 2012). Some studies showed that photodegradation increased with an increase of specific leaf area (Liu et al., 2018; Pan et al., 2015) or in litter C: N ratio (King et al., 2012; Brandt et al., 2007). In contrast to the latter finding, Uselman et al. (2011) found that greater UV-B exposure decreased decomposition of the litter with low litter quality. Similarly, Liu et al. (2015b) found that there was a strong negative relationship between C: N ratio of green leaf or initial leaf litters and decomposition rates as driven by photodegradation across 51 species. In the present study, and C: N ratios of green leaf and initial leaf litters, as a proxy for litter quality, controlled decomposition rates of both surface and suspended litters. Moreover, the multiple linear regressions showed that LDMC and litter C: N ratio determined litter decomposition rates and other chemistry traits may indirectly affect litter decomposition. Moreover, the finding in the present study showed that litter chemistry had a stronger influence on leaf litter decomposition. These further emphasized the importance of both morphological properties and chemistry of litters in modulating litter decomposition mediated by photochemical processes and microbes. Liu et al. (2018) suggest that SLA, as one of core leaf morphological traits, predominantly controls litter decomposition in drylands.

Altogether, differences in the predominant predictors controlling litter decomposition in arid and semiarid regions suggested that interactions between litter quality (leaf morphological or chemical traits) and UV radiation on litter decomposition are unclear up to now. The influence of further factors, e.g. solar radiation intensity, litter layer thickness and incubation period associated with temperature and moisture, need to be studied in depth for a full understanding of the interaction between photodecomposition and litter quality in drylands (but see Wang et al., 2017b). Additionally, since both UV and visible radiation can affect litter decomposition (Austin et al., 2016; Austin and Ballaré, 2010), it is not surprising that,

when UV radiation was blocked before reaching the litter layer, its decomposition rate increased during the incubation period (Figure 3.2). This implies that future studies on photochemically driven decomposition need to cover multiple wavelengths of solar radiation, as the C cycling in drylands would be underestimated by considering only the influence of UV radiation on litter decomposition.

3.4. Conclusion

This study emphasized the importance of interspecific morphological and chemical properties for the effect of UV radiation on leaf litter decomposition. While litter C: N ratio was a stronger predictor of decomposition rates in this dryland, predictive power could still be improved by including the quality of C, e.g. by using lignin: N ratio as a predictor of the less readily decomposed fraction to decomposition. The lack of overall net effect of UV on surface litter decomposition across eight species indicates the complexity of relationships due to dual UV radiation effect on surface litters decomposition via direct UV breakdown of plant litters and indirect changes via microbial processes. Further studies are required to consider incubation time litter layer thickness and other abiotic factors, i.e. precipitation pulse and air moisture, that the interaction between UV and litter position on litter decomposition in sun-lit dryland ecosystems.

Erdenebileg E, Ye XH, Wang CW, Huang ZY, Liu GF, Cornelissen JHC. 2018. Positive and negative effects of UV irradiance explain interaction of litter position and UV exposure on litter decomposition and nutrient dynamics in a semi-arid dune ecosystem. Soil Biology and Biochemistry, 124: 245–254.
https://doi.org/10.1016/j.soilbio.2018.06.013

Chapter 4. Effects of UV exposure and litter position on the decomposition of woody litters with different diameters

4.1 Introduction

Litter decomposition is a key process in the carbon (C) and nutrient cycles in terrestrial ecosystems (Berg and McClaugherty, 2008; Swift and Anderson, 1979). Generally, woody litter decomposition is mainly controlled by substrate quality, climate and decomposing organisms (Cornwell et al., 2009; Harmon et al., 1986; Swift et al., 1979). Wood decomposition within mesic temperate or tropical ecosystems is strongly modulated by biotic factors such as soil fauna and microbes due to their high abundances and activity at suitable environmental moisture regime (Bradford et al., 2014; González and Hollingsworth, 2008; Liu et al., 2015; Torres and González, 2005; Ulyshen, 2016). Microbial wood decomposition is mainly controlled by fungi that are highly specialized in resource requirements (Rayner and Boddy, 1988), although Wu et al. (2018; 2019) found that the decomposition rate of woody debris in subtropical forests was accelerated by an abiotic factor, that is, UV light. By contrast, lower vegetation canopy cover, that is, high irradiance, and lower annual precipitation could constrain decomposer abundances and activity. Therefore, there is accumulating evidence that litter decomposition in semi-arid and arid ecosystems are controlled by both biotic and abiotic factors (Austin and Vivanco, 2006; King and Adair, 2012; Liu et al., 2018). The abiotic conditions are a consequence of the dynamics of these ecosystems, where litter can either be strongly exposed to sunlight or get buried by wind-displaced soil material. This has been recognized in recent research on litter decomposition in sunny drylands, which has highlighted the importance of several abiotic mechanisms related to light exposure and burial, including photodegradation, photo priming effect and litter-soil mixing (Austin and Vivanco, 2006; Hewins and Throop, 2016; Lin and King, 2014; Liu et al., 2018). Austin and Ballaré (2010) suggested that lignin inhibits litter decomposition in mesic ecosystems while it enhances litter decomposition in arid ecosystems due to photochemical processes. Also, photodegradation of plant litter can reduce the structural and chemical bottleneck imposed by lignin in secondary cell walls, thereby increasing microbial driven litter decomposition (Austin and Ballaré, 2016). These are mechanisms that may explain why litter decomposition in drylands is faster than

expected from biotic mechanisms alone (Throop and Archer, 2009). Indeed, several studies reported that the rate of decomposition in sunny drylands is accelerated by stronger solar exposure including UV radiation (Austin and Vivanco, 2006; King et al., 2012) and also by burial under displaced soil material (Austin, Araujo, and Leva, 2009; Liu, Cornwell, Pan, et al., 2015; Liu et al., 2018) as compared to decomposition of surface litter.

Changes in plant species have strong effects on biogeochemical processes via plant–soil feedback (Hobbie, 2015) and this must certainly be true for changes in the relative abundance of herbaceous versus woody plants, which possibly mediate changes in incubation microclimate (Gottschall et al., 2019). Shrub encroachment, a common phenomenon in arid and semi-arid grasslands, affects soil C and N accumulation and turnover (Hibbard, Archer, Schimel, and Valentine, 2001). Moreover, there exist many vegetation types in drylands in which woody plants are common and likely important to biogeochemical cycling, such as desert, inland dunes, semi-desert, woodland, shrubland and savanna. It is therefore surprising that research on woody debris decomposition in arid and semi-arid ecosystems is scarce when compared with non-woody plant materials such as leaves or herbaceous stems. The sparse evidence that has accumulated suggests that, compared to mesic ecosystems, woody debris decomposes slowly in water-limited ecosystems such as in dry woodland, savanna, shrubland, semi-desert or desert, even if and where the decomposition rates are increased substantially due to termite activity (Andersen, Stricker, and Nelson, 2016; Ebert and Zedler, 1984; Milton and Dean, 1996). For example, Milton and Dean (1996) found that dead shrubs lying on the soil in an arid shrubland had woody litter mass half-lives of 9–18 years for different species. Moreover, Lyons and McCarth (2010) found there was no difference in Juniperus ashei wood decomposition in open and shaded habitats after 29 months of incubation. These observations seem a contradiction with the findings for herbaceous litter, which showed faster than expected decomposition due to sun exposure or burial, as explained above. Here we argue that the effect of solar radiation on wood decomposition should be weak or significantly decreased due to the lower surface area to volume ratio of wood, that is, its relatively low exposure to solar radiation compared to that of herbaceous litter in arid and semi-arid regions. Moreover, bark could provide a powerful protective layer against photodegradation of the wood

beneath. As for leaf litter, there is very scarce knowledge about the effects of burial on wood decomposition, but one desert study showed that soil movement mediated burial provides an optimal microclimate with higher moisture and relatively stable temperature for microbial wood degradation (Moorhead and Reynolds, 1993). In contrast, Moroni et al. (2015) suggested that wood buried by soil, litter or ground vegetation in wide-ranging forest ecosystems was efficiently preserved, that is, slowly decomposed.

However, this review included relatively few dryland sites and our understanding of decomposition processes of buried wood in drylands is still poor. While the above litter positions and related decomposition processes have focused on herbaceous versus woody litter in general terms, there is now much literature showing that species differ greatly in their traits as well as in the 'afterlife effects' these traits have on decomposition. This is the case both for leaf litter (Bakker and Poorter, 2011; Cornwell et al., 2008; Kazakou and Garnier, 2006) and for woody litter (Cornwell et al., 2009; Freschet and Cornelissen, 2012; Hu et al., 2018; Pietsch et al., 2014; Zuo et al., 2018). For instance, wood nitrogen was the best predictor of the decomposition rates of woody debris across angiosperm clades based on a global metaanalysis (Weedon et al., 2009). Also, thicker stems tend to be decomposed more slowly than thinner ones and this difference has been attributed to the lower surface to volume ratio of the former. Indeed, stem diameter could explain 41% of the variance of wood decomposition rates of 15 Neotropical tree species (van Geffen, and Cornelissen, 2010). Recently, Hu et al. (2018) found that wood nitrogen and diameter could explain approximately half of the global variation in wood decomposition rates. Moreover, wood density or wood dry matter content controlled the rate of wood decomposition in diverse forests (Freschet et al., 2012; Liu et al., 2015; Pietsch et al., 2014; Zuo et al., 2018). However, these studies have not considered the possibility that stem diameter and stem tissue quality traits (e.g. dry matter content) may be confounded. That is to say, stem diameter might affect decomposition rates not only via relative exposure but also because younger, narrower stems might have better resource quality to decomposers. Additionally, as the outermost covering of wood material, bark plays an important role in stem protection against insect or pathogen damage (Rosell, 2016). Moreover, bark may have a moisture-retention function in woody debris and it could increase microbial driven wood decomposition (Dossa,

Paudel, Cao, Schaefer, and Harrison, 2016; Ulyshen, Müller, and Seibold, 2016). Recently, Dossa et al. (2018) found that bark can enhance coarser WD decomposition but slows twig decomposition in some species. Bark thickness may affect both microbial invasion and microenvironment (Cornwell et al., 2009). Rosell (2016) showed that bark thickness is strongly positively correlated with stem sizes. Thus, it is likely that bark thickness affects woody litter decomposition, directly or via it relation with diameter, but empirical data are lacking. The same is true for the effect of bark traits on wood decomposition in general (but see Zuo et al., 2018). It still remains uncertain to which extent litter position versus initial litter traits of different species, or their interactions, predominantly control the decomposition of woody litter in arid and semiarid environments. Therefore, to fill this research gap, we designed an experimental study to examine the effects of litter position (sand burial, suspended above the surface and in a surface litter layer) on the decomposition of woody litters from four shrub species with different diameters (φ: <2, 2–4, 4–8, 8–13 and 13–20 mm) in an inland dune ecosystem, where the effects of litter position via UV radiation on above-ground wood decomposition were explicitly examined through experimental UV blocking.

Thus, the question is how UV radiation and litter positions together influence the decomposition of woody litters across different diameters in a semi-arid dune ecosystem? To answer this question, we hypothesized that (i) buried woody litters would have higher decomposition rates than surface and suspended woody litters due to stable and favourable moisture regime and well-developed microbial community; (ii) UV radiation would increase the decomposition rate of woody litters; (iii) bark thickness would be negatively correlated with the rate of wood decomposition; (iv) woody litters of smaller diameter, with higher relative surface exposure to external microbes and sunlight, and possibly higher resource quality, should be decomposed faster than wider ones.

4.2. Results

4.2.1 Initial woody litter traits

The morphological and chemical traits of initial wood litter differed among the four species and among five diameter classes (Figure 4.1). Overall, there was remarkable covariation of several wood and bark traits with diameter class. The initial bark thickness and wood DMC increased with increasing diameter class especially for

A. ordosica; initial wood DMC was significantly positively correlated to bark thickness or wood density (Figure 4.1a, c; Table 4.1). *A. ordosica* had lower bark DMC than the other species for most of the diameter classes (Figure 4.1b). Initial wood N decreased with increasing diameter class for most species (Figure 4.1d). The woody litter of *C. korshinskii* and *H. laeve* had higher N concentration of initial litter than the two other species for each of the five diameter classes (Figure 4.1d). Initial wood C: N ratio was a proxy for initial wood N concentration due to the stable C concentration (r = –1.00, $p < 0.001$; Table 4.1).

Table 4.1 The relationship coefficient matrix among initial bark and wood traits

表 4.1 树皮和茎干性状之间的关系系数矩阵

	Bark thickness	Bark DMC	Wood DMC	Wood density	Wood N	Wood C	Wood C: N ratio	Diameter
Bark thickness		0.971	**0.001**	**0.015**	0.265	0.413	0.276	**<0.001**
Bark DMC	-0.009		0.141	0.120	0.837	0.681	0.831	0.290
Wood DMC	**0.663**	0.341		**<0.001**	0.993	0.237	0.998	**0.001**
Wood density	**0.536**	0.359	**0.882**		0.522	0.065	0.521	**0.004**
Wood N	-0.262	0.049	-0.002	0.152		**0.049**	**<0.001**	0.256
Wood C	-0.194	-0.098	-0.277	-0.421	**-0.446**		**0.045**	0.403
Wood C: N ratio	0.256	-0.051	<0.001	-0.153	**-1.000**	**0.453**		0.272
Diameter	**0.870**	0.249	**0.705**	**0.612**	-0.266	-0.198	0.258	

Lower and upper triangles denote Pearson correlation coefficients and *P* values, respectively. Diameter classes were transformed into a continuous predictive variable before analysis (also see Abbott *and* Crossley 1982). The values in bold denote significant relationship at $P < 0.05$. DMC, Dry matter content; C, total carbon concentration; N, total nitrogen concentration.

表中的数据显示为下三角和上三角分别表示 Pearson 相关系数和 *P* 值。不同径级直径转化为连续预测变量（参见 Abbott 和 Crossley, 1982）。 粗体值表示 $P < 0.05$ 时显著的相关关系。

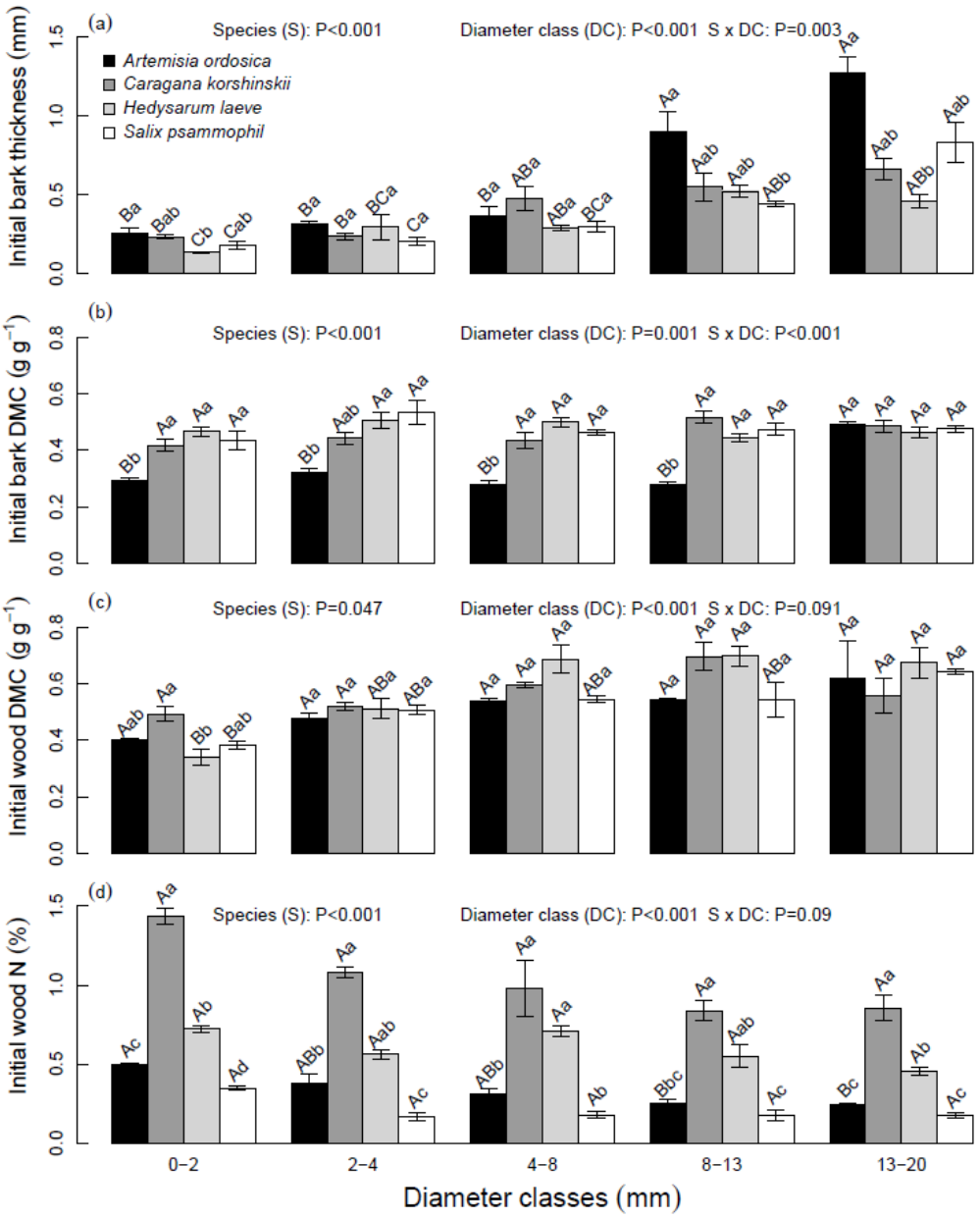


Figure 4.1 Differences in initial bark and wood traits among species and diameters in the semi-arid dune ecosystem. Bark DMC: bark dry matter content, Wood DMC: saturated wood dry matter content. The bars represent means ± SE (n = 5 for bark traits or n = 3 for other traits). The same lowercase denotes no significant difference in bark or wood traits among species within each of the diameter classes, while the same uppercase denotes no significant difference among diameter classes within each species at $p < 0.05$

图 4.1 半干旱沙丘生态系统中物种和直径之间初始树皮和木材性状的差异。 树皮 DMC：树皮干物质含量，木材 DMC：饱和木材干物质含量。 条形代表平均值±SE（树皮特征为 n = 5，其他特征为 n = 3）。 相同的小写字母表示在每个直径类别内的物种之间树皮或木材性状没有显着差异，而相同的大写字母表示在 p <0.05 时每个物种内的直径类别之间没有显着差异。

4.2.2 Rates of wood litter decomposition

The three-way repeated-measures ANOVA showed that position UV treatment ($F_{4,400} = 2{,}503$, $p < 0.001$), diameter class ($F_{4,400} = 549$, $p < 0.001$), species ($F_{3,400} = 87.6$, $p < 0.001$) and all their interactions had significant effects on woody litter mass loss (Table 4.2).

Table 4.2 Results from the three-way repeated measures ANOVA of predictive variables on wood mass losses in the semiarid dune ecosystem

表 4.2 物种，径级，处理及其相互作用对茎凋落物质量损失的影响的可重复性方差分析。粗体的 *P 值*表示该项具有显著影响

	Variation	Dfn, Dfd	F	*P*
Between-subjects effects	Species (S)	3, 400	87.63	< **0.001**
	Diameter classes (DC)	4, 400	548.51	< **0.001**
	Litter treatment (LT)	4, 400	2503.19	< **0.001**
	S × DC	12, 400	13.32	< **0.001**
	S × LT	12, 400	4.26	< **0.001**
	DC × LT	16, 400	33.32	< **0.001**
	S × DC × LT	48, 400	2.80	< **0.001**
Within-subjects effects	Time (T)	4, 1587	1324.03	< **0.001**
	T × S	12, 1587	5.19	< **0.001**
	T × DC	16, 1587	21.36	< **0.001**
	T × LT	16, 1587	100.99	< **0.001**
	T × S × DC	48, 1587	0.87	0.717
	T × S × LT	48, 1587	1.09	0.319
	T × DC × LT	64, 1587	2.38	< **0.001**
	T × S × DC × LT	192, 1587	1.18	**0.056**

The predictive variables include species, diameter class, litter treatment (i.e. environment in terms of position and UV exposure; see Table 2) and all their interactions. Dfn and Dfd denote numerator and denominator degrees of freedom, respectively. The *p* values in bold denote significant terms.

预测变量包括物种，直径等级，垫料处理（即环境的位置和紫外线照射；请参见表 2）及其所有相互作用。 Dfn 和 Dfd 分别表示分子和分母的自由度。 粗体的 *p* 值表示有效项。

However, when only above-ground positions (surface and suspended) were considered in the four-way repeated-measures ANOVA, UV radiation did not have a

main effect on woody litter mass loss and the interaction between UV and position was marginally significant (Table 4.3). UV radiation significantly affected mass loss of surface woody litters, but it did not change mass loss of suspended woody litters (Table 4.4).

Table 4.3 Four-way repeated-measures ANOVA on woody litter mass losses in response to species, diameter class, position, UV radiation treatment, and all their interactions. Harvest time is the within-subjects factor. Dfn and Dfd denotes numerator and denominator degrees of freedom, respectivly. The *P* values in bold denote significant terms.

表 4.3 针对物种，直径等级，位置，UV 辐射处理及其所有相互作用的木质垫料质量损失的四次重复测量方差分析。 收获时间是受试者内的因素。 Dfn 和 Dfd 分别表示分子和分母的自由度。 *P* 值以粗体表示有效项。

	Variation	Dfn, Dfd	F	*P*
Between-subjects effects	Species (S)	3, 320	86.41	< **0.001**
	Diameter classes (D)	4, 320	391.03	< **0.001**
	Position (P)	1, 320	89.31	< **0.001**
	UV radiation (UV)	1, 320	1.74	0.188
	S ×D	12, 320	13.49	< **0.001**
	S × P	3, 320	6.94	**0.002**
	S × UV	3, 320	0.67	0.571
	D × P	4, 320	13.33	< **0.001**
	D ×UV	4, 320	0.84	0.498
	P ×UV	1, 320	3.59	0.059
	S × D × P	12, 320	2.04	**0.021**
	S × D × UV	12, 320	0.45	0.942
	S × P × UV	3, 320	1.02	0.383
	D × P × UV	4, 320	1.07	0.372
	S × D × P × UV	12, 320	0.58	0.859
Within-subjects effects	Time (T)	4, 1268	816.69	< **0.001**
	T × S	12, 1268	7.54	< **0.001**
	T× D	16, 1268	25.83	< **0.001**
	T × P	4, 1268	10.99	< **0.001**
	T × UV	4, 1268	1.78	0.130
	T × S × D	48, 1268	1.16	0.211
	T × S × P	12, 1268	0.95	0.493
	T × S × UV	12, 1268	0.46	0.940
	T × D × P	16, 1268	1.08	0.366
	T × D × UV	16, 1268	1.43	0.120
	T × P × UV	4, 1268	0.59	0.669
	T× S × D × P	48, 1268	0.67	0.958
	T × S × D × UV	48, 1268	0.98	0.517
	T × S × P × UV	12, 1268	1.27	0.231
	T × D × P × UV	16, 1268	0.77	0.722
	T × S × D × P × UV	48, 1268	1.05	0.375

As we expected, after 12, 24 and 34 months of incubation, the mass losses of buried woody litters were higher than those in the above-ground treatments; they ranged 12.7%–47.3%, 25.7%–61.5% and 31.9%–73.9% with averages of 25.7 ± 2.1%, 43.0 ± 2.6% and 53.5 ± 2.7%, respectively (Figure 4.2). By contrast, after 12, 24 and 34 months of incubation, the mass losses under surface and suspended conditions were 2%–15%, 6%–23%, 7%–27% and 5%–13%, 11%–23%, 12%–27%, respectively (Figure 4.2; Table 4.5). During the whole incubation, litter mass loss of suspended woody litter was significantly higher than that on the surface (17.0 ± 1.0% vs. 14.4 ± 1.2%, respectively; Table 4.3). Overall, the mass loss of buried woody litters was three times faster than those of suspended and surface woody litters (Figure 4.2).

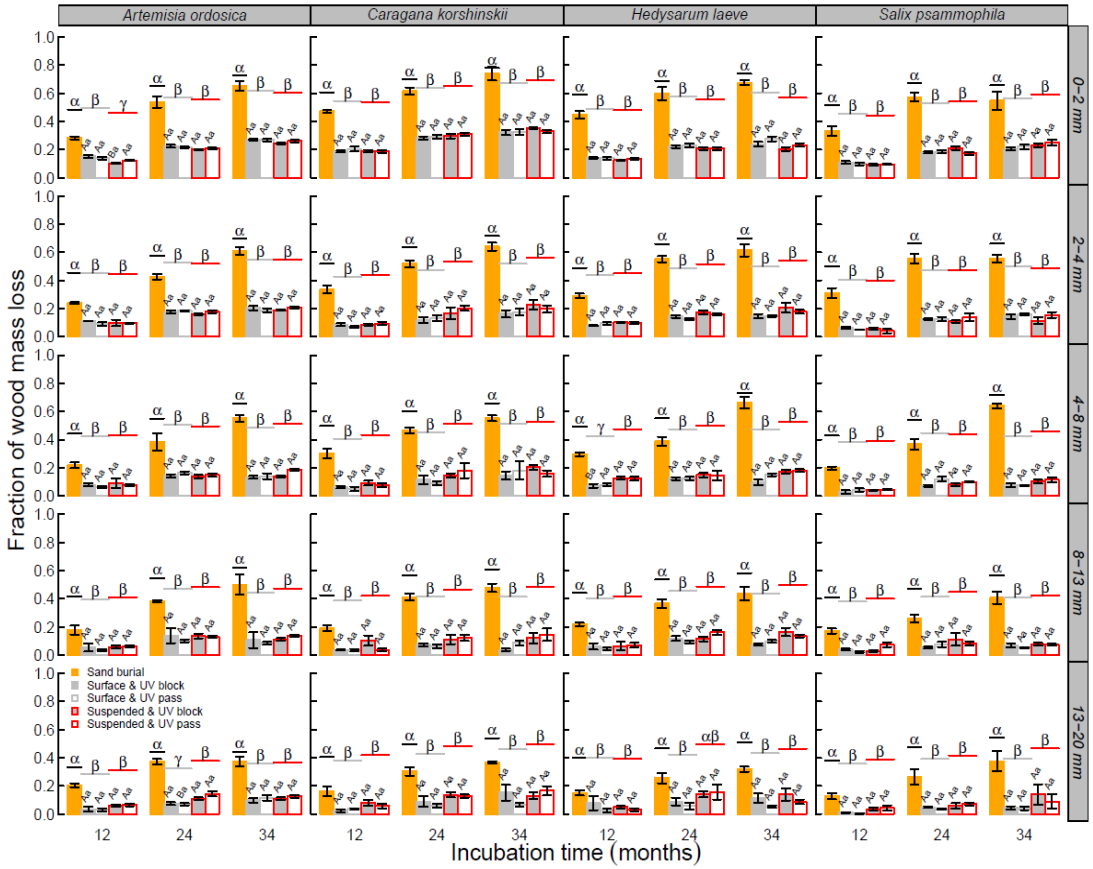


Figure 4.2 Effects of treatment, species and diameter on wood mass losses over 34 months in the semi-arid dune ecosystem. The bars represents mean ± SE (n = 5)

图 4.2 在半干旱沙丘生态系统中，处理，物种和直径对 34 个月内木材质量损失的影响。条形表示平均值±SE（n = 5）

The same Greek symbol denotes no significant difference among three positions including sand burial, soil surface and suspended locations at $p < 0.05$. The same lowercase denotes no

significant difference between UV treatments for soil surface and suspended position, respectively, and the same uppercase denotes no significant difference between the surface and suspended positions for each of the UV treatments at $p < 0.05$.

相同的希腊文符号表示在三个位置之间没有显着差异，包括埋沙，土壤表面和悬浮位置 p <0.05。 相同的小写字母分别表示在土壤表面和悬浮位置的 UV 处理之间无显着差异，相同的大写字母表示在 p <0.05 时，每种 UV 处理的表面和悬浮位置之间无显着差异。

Table 4.4 Three-way repeated measures ANOVA on woody litter mass losses for each of two litter positions in response to species, diameter class, UV radiation treatment, and all their interactions. Harvest time is the within-subjects factor. Dfn and Dfd denote numerator and denominator degrees of freedom, respectively. The *P* values in bold denote significant terms.

表 4.4 关于物种，直径等级，紫外线辐射及其所有相互作用的两种方法，对两个垫料位置中每个垫料的木质垫料质量损失进行三向重复测量方差分析。 收获时间是受试者内的因素。 Dfn 和 Dfd 分别表示分子和分母的自由度。 *P* 值以粗体表示有效项。

			Suspended location		Soil surface location	
	Variation	Dfn, Dfd	F	*P* value	F	*P* value
Between-subjects effects	Species (S)	3, 160	53.17	**<0.001**	38.25	**<0.001**
	Diameter class (DC)	4, 160	115.15	**<0.001**	315.44	**<0.001**
	UV radiation (UV)	1, 160	0.15	0.699	5.98	**0.016**
	S × DC	12, 160	7.29	**<0.001**	8.33	**<0.001**
	S × UV	3, 160	1.37	0.254	0.17	0.917
	DC × UV	4, 160	0.14	0.968	2.01	0.095
	S × DC × UV	12, 160	0.28	0.992	0.84	0.610
Within-subjects effects	Time (T)	4, 631	425.02	**<0.001**	398.39	**<0.001**
	T × S	12, 631	4.26	**<0.001**	4.27	**<0.001**
	T× DC	16, 631	9.28	**<0.001**	18.97	**<0.001**
	T × UV	4, 631	0.68	0.609	1.86	0.116
	T × S × DC	48, 631	0.95	0.566	0.87	0.725
	T × S × UV	12, 631	0.66	0.791	1.14	0.321
	T × DC × UV	16, 631	0.54	0.929	1.82	**0.025**
	T × S × DC × UV	48, 631	1.01	0.453	1.02	0.445

4.2.3 Correlations between bark and woody traits and decomposition rates

The k value for woody litter decomposition was higher towards smaller diameter classes, particularly in the sand burial treatment (Figure 4.3). Pearson's correlation

analyses indicated that *k* values were strongly negatively correlated with initial bark thickness, wood dry matter content (wood DMC), wood C:N ratio and diameter class in all treatments; the *k* values were significantly negatively correlated with initial wood density on the surface and in the sand burial treatment but not in the suspended treatment (all $p < 0.05$; Table 4.6). The *k* values were significantly positively correlated with initial N concentration in all treatments (all $p < 0.05$; Table 4.6). The bark DMC did not exhibit significant correlation with decomposition rate for any of the treatments (Table 4.6).

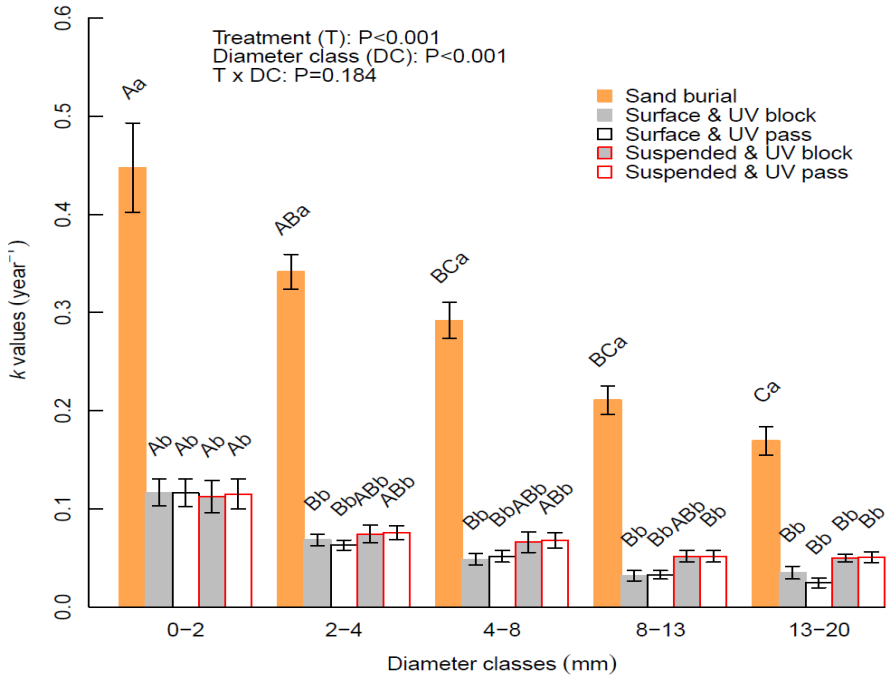


Figure 4.3 Effects of treatment and diameter on k values for wood decomposition in the semi-arid dune ecosystem. The bars represent means ± SE (n = 4 species). The same lowercase denotes no significant difference in k values among species within each of the diameter classes and the same uppercase denotes no significant difference in k values among diameter classes within each of the litter treatments at $p < 0.05$

图 4.3 处理和直径对半干旱沙丘生态系统中木材分解的 k 值的影响。 条形代表平均值±SE（n = 4 种）。 相同的小写字母表示在每个直径类别内的物种之间的 k 值无显着差异，相同的大写字母表示在 p <0.05 时，每个垫料处理中的各个直径处理之间的 k 值均无显着差异。

The structural equation modelling showed that diameter, initial wood DMC and N had direct effects on *k* values, among which diameter had the stronger influence on decomposition rates of buried wood (Figure 4.4). Diameter also had a strong indirect

effect on k values by affecting initial wood DMC directly or indirectly via wood density in the surface treatment. There was a marginally significant positive trend of diameter on *k* values via wood N in all the treatments (p = 0.069; Figure 4.4). The full model analyses showed higher importance of initial N concentration (or C: N ratio) and diameter class in explaining variation in the *k* values for most treatments; for the surface litter under UV blocking, the higher importance was owed to initial wood DMC and N concentration (or C: N ratio; Table 4.7). Generally, the density of decomposed wood litter was negatively correlated with wood mass loss, in which the stronger relationships were observed in sand burial than in the other two positions (Figure 4.5).

Table 4.6 Pearson's correlation coefficients for the relationships between wood decomposition rates (*k*, year^{-1}) and initial bark and woody litter traits. Diameter classes were transformed into a continuous predictive variable (see Table 4.1). The values in bold denote significant correlation at $p < 0.05$.

表 4.6 皮尔逊相关系数用于木材分解速率（*k*，年$^{-1}$）与初始树皮和木质凋落物性状之间的关系。 将直径类别转换为连续的预测变量（请参见表4.1）。 粗体值表示p <0.05时具有显着相关性。

Traits	Suspended				Surface				Sand burial	
	UV block		UV pass		UV block		UV pass			
	r	*P*	r	*P*	r	*P*	r	*P*	r	*P*
Initial bark thickness (mm)	**-0.513**	**0.021**	**-0.504**	**0.024**	**-0.557**	**0.011**	**-0.569**	**0.009**	**-0.643**	**0.002**
Initial bark dry mass content (mg g^{-1})	-0.248	0.292	-0.327	0.160	-0.414	0.070	-0.343	0.139	-0.131	0.581
Initial woody dry mass content (mg g^{-1})	**-0.455**	**0.044**	**-0.533**	**0.016**	**-0.729**	**<0.001**	**-0.689**	**0.001**	**-0.657**	**0.002**
Initial woody density (g cm^{2})	-0.231	0.328	-0.325	0.162	**-0.520**	**0.019**	**-0.489**	**0.029**	**-0.511**	**0.021**
Initial woody N (%)	**0.737**	**<0.001**	**0.671**	**0.001**	**0.485**	**0.030**	**0.508**	**0.022**	**0.558**	**0.011**
Initial woody C (%)	0.018	0.941	0.030	0.900	0.092	0.700	0.108	0.650	0.103	0.665
Initial woody C: N ratio	**-0.670**	**0.001**	**-0.613**	**0.004**	-0.443	0.051	**-0.452**	**0.046**	-0.423	0.063
Woody diameter (mm)	**-0.658**	**0.002**	**-0.693**	**0.001**	**-0.738**	**<0.001**	**-0.790**	**<0.001**	**-0.864**	**<0.001**

Woody diameters were transformed into a continuous predictor variable (also see Abbott and Crossley, 1982). The values in bold denote significant correlation at $P < 0.05$.

茎直径转化为连续预测变量（参见Abbott和Crossley, 1982）。 粗体值表示$P < 0.05$时的

显著相关关系。

Table 4.7 Effects of initial traits on wood decomposition rates *via* model averaging in the semi-arid dune ecosystem

表 4.7 通过半干旱沙丘生态系统中模型平均的初始性状对木材分解速率的影响

Treatment	Source	Estimate	SE	z Value	*p* Value	RVI
Suspended and UV block	Intercept	-1.181	0.017	66.11	**<0.001**	-
	Diameter	-0.170	0.035	4.48	**<0.001**	1.00
	Initial wood C: N ration	-0.110	0.108	1.01	0.311	0.52
	Initial wood N	0.100	0.107	0.93	0.355	0.48
Suspended and UV pass	Intercept	-1.172	0.018	59.64	**<0.001**	-
	Diameter	-0.159	0.081	1.95	0.052	0.83
	Initial wood C: N ration	-0.097	0.095	1.01	0.314	0.54
	Initial wood N	0.084	0.095	0.88	0.379	0.46
	Initial wood dry matter content (DMC)	-0.030	0.068	0.44	0.659	0.17
Surface and UV block	Intercept	-1.288	0.029	41.45	**<0.001**	-
	Initial wood DMC	-0.366	0.059	5.74	**<0.001**	1.00
	Initial wood N	0.119	0.122	0.97	0.334	0.52
	Initial wood C: N ratio	-0.109	0.121	0.90	0.371	0.48
Surface and UV pass	Intercept	-1.317	0.027	44.65	**<0.001**	-
	Diameter	-0.441	0.059	6.95	**<0.001**	1.00
	Initial wood C: N ratio	-0.062	0.078	0.77	0.440	0.45
	Initial wood N	0.058	0.077	0.74	0.459	0.43
Sand burial	Intercept	-0.564	0.013	40.43	**<0.001**	-
	Diameter	-0.281	0.028	9.47	**<0.001**	1.00
	Initial wood C: N ratio	-0.041	0.043	0.92	0.356	0.53
	Initial wood N	0.036	0.043	0.84	0.403	0.47

Model-averaged coefficients and important values for explanatory variables predicting wood decomposition rates (*k* values) are shown for models based on all treatments in terms of litter position and UV exposure. RVI denotes relative variable importance. Diameter classes were transformed into a continuous predictive variable. The *p* values in bold denote significant terms.

对于基于所有垫料位置和紫外线暴露的处理，显示了模型的平均系数和预测变量的重要值，这些变量预测木材的分解速率（k 值）。 RVI 表示相对变量重要性。 直径类别转换为连续的预测变量。 粗体的 *p* 值表示有效项。

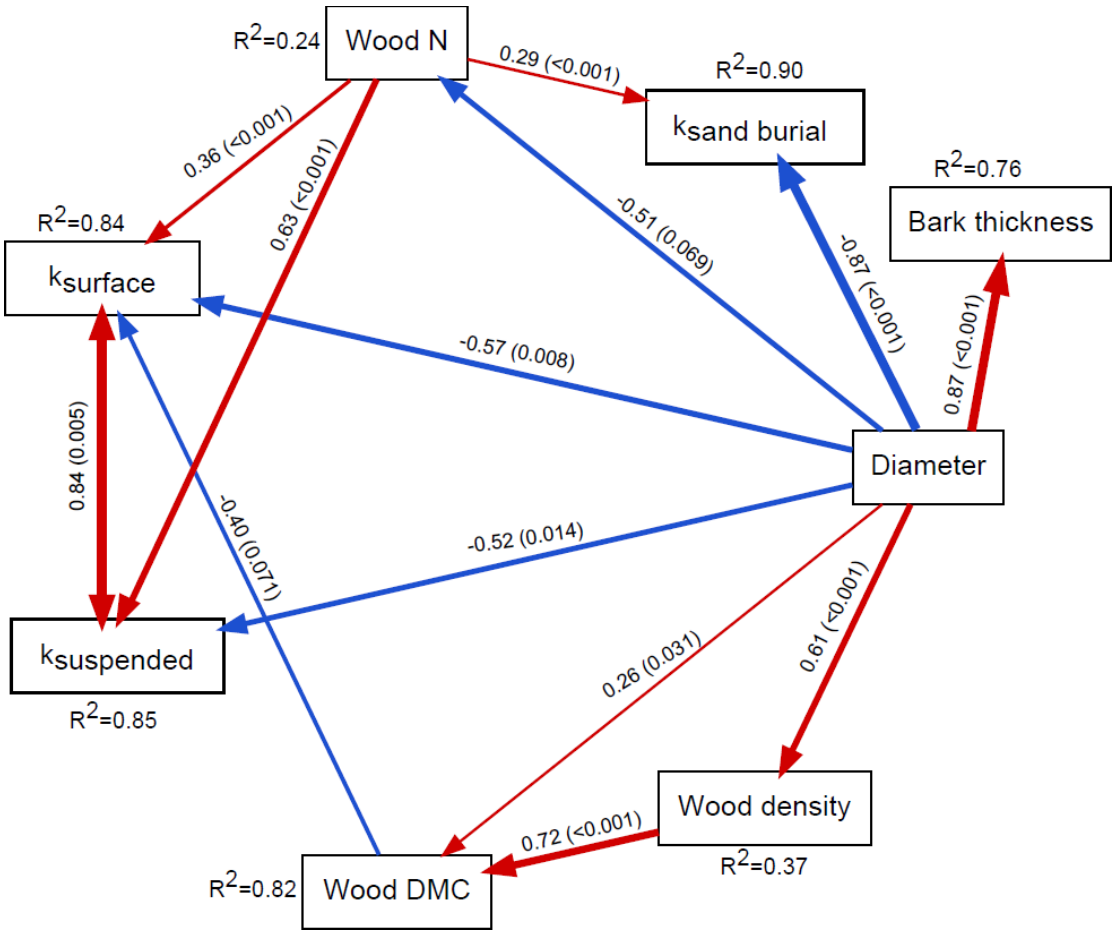


Figure 4.4 The structural equation model (SEM) depicting pathways by which wood traits may influence k values in the semi-arid dune ecosystem.

图 4.4 结构方程模型（SEM）描述了木材特性可能影响半干旱沙丘生态系统中 k 值的途径。

The model parameters in the SEM were $\chi^2_{df=3}$ = 1.013, p = 0.798, GFI = 0.987, RMSEA < 0.001. The red and blue arrows represent positive and negative relationships, respectively. The widths of the arrows are proportional to the strengths of the path coefficients. The double headed arrows between $k_{suspended}$ and $k_{surface}$ indicate there were no causal relationships of wood decomposition rates between these two positions; just a correlation because both were driven by the same traits. The value in parentheses denotes the p value.

SEM 中的模型参数为 $\chi^2_{df=3}$ = 1.013，p = 0.798，GFI = 0.987，RMSEA <0.001。 红色和蓝色箭头分别表示正向和负向关系。 箭头的宽度与路径系数的强度成正比。 $k_{suspended}$ 和 $k_{surface}$ 之间的双箭头表示这两个位置之间没有木材分解速率的因果关系。 只是相关性，因为两者都是由相同的特征驱动的。 括号中的值表示 p 值。

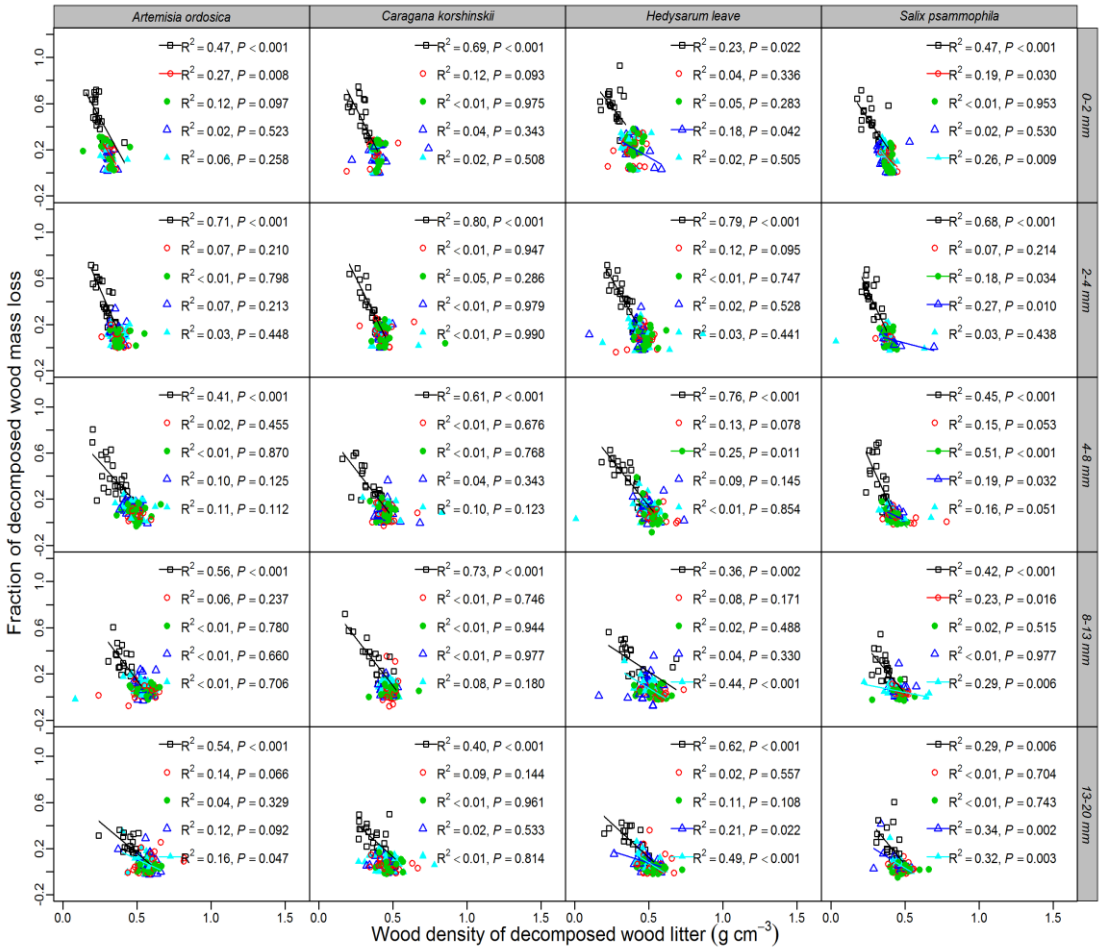


Figure 4.5 The relationship between wood density and mass losses of decomposed woody litters of four shrub species under five diameter classes and each of five treatments

图 4.5 四种灌木的五个径级在五种处理下分解后的茎秆的密度和质量损失之间的关系

Solid lines denote significant relationships at $P < 0.05$. Legends from top to bottom denote sand burial, surface *and* UV block, surface *and* UV pass, suspended *and* UV block, suspended *and* UV pass.

实线表示 P <0.05 时的显著关系。 从上到下表示沙埋，地表和紫外线阻挡，地表和紫外线通过，模拟立枯和紫外线阻挡，模拟立枯和紫外线通过。

4.3. Discussion

Here, we assessed the interactive effects of woody litter diameter, position (sand burial vs. surface vs. suspended) and UV exposure on decomposition rate in a semi-arid inland dune ecosystem across four shrub species over almost 3 years. Among the various abiotic and biotic drivers addressed here, we found that woody litter position (suspended, surface and buried), stem diameter and wood traits and the interactions

between these factors, all had substantial effects on decomposition rates, while differences in exposure to UV radiation did not affect decomposition rates significantly. A key finding was that stem diameter not only had direct effects on decomposition rate, presumably *via* surface area to volume ratio, but also indirect effects via differences in wood traits, especially wood dry matter content and wood N. Below we will discuss these findings in more detail in the context of previous literature.

4.3.1 Environmental rivers of woody litter decomposition

In terrestrial ecosystems, differences in litter decomposition during different periods of incubation are associated with the seasonal changes in solar radiation, temperature and moisture (Lin and King, 2015; Wang et al., 2015). We found that relatively fast rates of wood decomposition occurred in the subsequent summers (Figure 4.2; Table 4.5), when environments conditions benefitted wood decomposition (Figure 4.6). As hypothesized (1), buried woody litter decomposition was faster in the entire decomposition period due to relatively stable and higher moisture as compared with those above-ground (Figure 4.2; Table 4.5). As expected, we found that the mass losses of buried woody litters during 34 months of incubation were three times faster than those of suspended and surface woody litters (Figure 4.2). This supports the reported pattern that the difference between the rate of buried and surface wood decomposition increased with decreasing precipitation (Smyth et al., 2016). The accelerating effect of sand burial on wood decomposition is even stronger compared with previous studies in similar dry habitats, in which litter burial less than doubled the rate of litter decomposition compared to that on the soil surface (Austin et al., 2009; Liu et al., 2015; Santos and Whitford, 1984; Vivanco and Austin, 2006). Also, this finding contrasts with the fact that buried wood had slower decomposition rate than that on the soil surface in diverse forest ecosytems (Fasth and White, 2011; Romero and Fourqurean, 2005). The likely reason is that the sand burial exposes dead wood to an abundant microbial community and to relatively beneficial humidity to microbially driven decomposition. The previous work on soil enzymatic activity in the Mu Us inland dunes showed larger values for polyphenoloxidase, peroxidase and polyphenol oxidase at 0–5 cm of soil depth than those at 5–10 cm of soil depth in the *S. psammophila* community (45.00 ± 3.07 vs. 24.24 ± 0.68 μg g^{-1} hr^{-1}, 730.85 ± 24.95 vs. 354.42 ± 69.35 μg g^{-1} hr^{-1}, 318.14 ± 35.2 vs. 153.01 ± 11.3 μg g^{-1} hr^{-1},

respectively; Wang, 2018). Indeed, the fungal/bacterial biomass ratios based on the phospholipid fatty acid (PLFA) technique nearby the incubation site were 0.378 ± 0.015, 0.381 ± 0.018, 0.398 ± 0.019 and 0.382 ± 0.018 at 0–5, 5–10, 10–15 and 15–20 cm of soil depth, respectively (G. F. Liu, unpubl. data), which indicates that this dry region hosts relatively high fungal abundance (Chen et al., 2015). According to High Throughput DNA Sequencing methodology, the dominant fungal species in the top soil (0–10 cm) of Artemisia ordosia vegetation on Ordos plateau were Ascomycota (64.6%), Mortierellomycota (12.3%) and Basidiomycota (8.4%), accounting for 85.3% of total number of OTUs (G. F. Liu, unpubl. data). Since especially Ascomycota are predominantly saprophytic, these complementary observations imply that relatively faster buried wood decompositon could be owed to fungal activity. There was no visible evidence of termites in our study (observations inside and outside litterbags by the authors), contrasting to strong termite effects on wood decomposition in hot drylands (Buxton, 1981). In forests, slow decomposition of dead wood burial has been associated with exposure to low temperatures in peat or after being overgrown by mosses. These differences emphasize the different driving mechanisms of litter decomposition in different biomes.

In contrast with the fast rate of buried wood decomposition, above-ground decomposition rates were very low in the soil surface and suspended position with exposure to solar radiation; most mass loss in these treatments occurred during the first 2 years (Table 4.5). This relatively slow decomposition is consistent with previous studies (Abbott and Crossley, 1982; Buxton, 1981; Milton and Dean, 1996) and can explain why almost 20% of organic carbon is owed to standing and surface litters in inland dune ecosystems (Li, 2006). We acknowledge that the litter bags could intercept a small portion of solar radiation, so in our experiment we may have slightly underestimated the effect of photodegradation on wood mass loss. Longer-term studies are needed to investigate the trajectory of above-ground wood decomposition more comprehensively (Cornelissen et al., 2012; Prescott, 2005). Many studies have shown that woody plant encroachment increases fluxes of soil C and N (Hibbard et al., 2001; McCulley et al., 2004). This present study highlights that relatively fast decomposition of buried woody litter may be an important contributor to this phenomenon.

Table 4.5 The mass losses of woody litters (Mean ± SE; n = 4) with different diameter classes and incubation times under different treatments.

表 4.5 在不同处理条件下，不同直径类别和孵化时间的木质垫料的质量损失（平均值±标准误差； n = 4）。

Incubation time (month)	Diameter classes				
	0-2 mm	2-4 mm	4-8 mm	8-13 mm	13-20 mm
Sand burial					
6	0.22±0.03	0.16±0.02	0.12±0.03	0.09±0.01	0.04±0.01
12	0.38±0.05	0.29±0.02	0.25±0.03	0.19±0.01	0.16±0.02
18	0.52±0.04	0.39±0.02	0.35±0.03	0.26±0.01	0.25±0.04
24	0.58±0.02	0.51±0.03	0.40±0.02	0.35±0.03	0.30±0.03
34	0.65±0.04	0.61±0.02	0.60±0.03	0.45±0.02	0.36±0.01
Surface *and* UV block					
6	0.04±0.01	0.02±0.01	0.02±0.01	0.00±0.01	0.02±0.00
12	0.15±0.02	0.09±0.01	0.06±0.01	0.05±0.01	0.04±0.01
18	0.15±0.02	0.09±0.01	0.06±0.01	0.02±0.00	0.02±0.01
24	0.23±0.02	0.14±0.01	0.11±0.01	0.09±0.02	0.08±0.01
34	0.26±0.02	0.17±0.01	0.11±0.02	0.07±0.01	0.10±0.02
Surface *and* UV pass					
6	0.03±0.01	0.01±0.00	0.01±0.00	0.01±0.01	0.00±0.00
12	0.14±0.02	0.08±0.01	0.06±0.01	0.03±0.00	0.02±0.01
18	0.12±0.02	0.04±0.01	0.04±0.01	0.04±0.01	0.02±0.01
24	0.23±0.02	0.14±0.01	0.13±0.01	0.08±0.01	0.06±0.01
34	0.27±0.02	0.17±0.01	0.14±0.02	0.08±0.01	0.07±0.02
Suspended *and* UV block					
6	0.02±0.01	0.02±0.01	0.02±0.01	0.01±0.00	0.01±0.00
12	0.13±0.02	0.09±0.01	0.09±0.02	0.06±0.01	0.06±0.01
18	0.14±0.02	0.09±0.01	0.10±0.02	0.08±0.02	0.05±0.01
24	0.23±0.02	0.15±0.02	0.13±0.02	0.12±0.01	0.11±0.02
34	0.26±0.03	0.19±0.02	0.15±0.02	0.12±0.02	0.13±0.01
Suspended *and* UV pass					
6	0.03±0.01	0.01±0.01	0.01±0.00	0.01±0.01	0.01±0.00
12	0.13±0.02	0.08±0.01	0.08±0.02	0.06±0.01	0.05±0.01
18	0.14±0.03	0.08±0.01	0.10±0.02	0.06±0.01	0.07±0.02
24	0.22±0.03	0.17±0.01	0.14±0.02	0.12±0.02	0.13±0.02
34	0.27±0.02	0.19±0.01	0.16±0.02	0.12±0.02	0.12±0.02

Within the above-ground positions, woody litter decomposition rates were somewhat faster in suspended litter than in surface litter (Figure 4.2; Table 4.5), consistent with previous studies (Erdenebileg et al., 2018; Lin and King, 2014). In dryland, decomposition of suspended litters is likely strongly determined by abiotic factors, such as photodegradation and wind abrasion, but also by a favourable combination of temperature or moisture at night promoting microbial decomposition (Wang et al., 2017). However, this conflicts with the finding that termite-mediated

decomposition rate of ground-placed wood debris was over four times greater than that in suspended condition in tropical rainforest (Law et al., 2019). These findings imply that contrasting influential factors determined the carbon turnover between ecosystems varying in water limitation and soil fanua abundance. As revealed by our UV blocking treatments, UV radiation alone had no significant effect on woody litter decomposition (Table 4.3), which is inconsistent with our hypothesis (2); this hypothesis had been informed by the findings of Erdenebileg et al. (2018), who found that UV radiation had a significant effect on leaf litter decomposition. The discrepancy between leaf litter and woody litter in response to UV light may be due to the contrasting architecture between leaf and wood tissues. UV radiation did not affect suspended wood decomposition but it decreased surface wood decomposition, suggesting that UV radiation possibly decreases the activity of colonizing microbes (Wang et al., 2015). This study reinforces how different plant tissues decay in very different ways and how these differences also depend on their vertical position.

Soil-litter mixing and photodegradation are mechanisms that may explain why higher than expected non-woody litter decomposition occurred in drylands (Austin *and* Vivanco, 2006; Hewins and Throop, 2016; Liu et al., 2018). In addition, Liu et al. (2018) found that relative exposure of the leaf surface to sunlight per unit leaf mass (i.e. specific leaf area) could be a predominant factor in explaining variation in leaf litter decomposition. As noted above, together these suggest that sand burial is a main environmental factor in driving woody litter decomposition in shrub-dominated drylands.

4.3.2 Controls of initial litter quality on woody litter decomposition

Litter decomposition rates depend on both incubation environment and the afterlife legacy of functional traits of different species through litter substrate quality (Cornwell et al., 2009; Harmon et al., 1986; Swift et al., 1979). We found that the rates of woody litter decomposition increased with increasing initial wood N concentration or decreasing initial C:N ratio in all treatments; initial wood N concentration and C:N ratio were highly correlated due to their log-transformation and to the stable C concentration. Our observations confirm previous reports that litter with higher nutritional quality (e.g. higher N concentration and lower C:N ratio) can decompose relatively fast (Liu et al., 2015; van Geffen et al., 2010; Weedon et al., 2009). Wood dry matter content (wood DMC), as a key trait representing internal

litter structure, is known to be a negative predictor of wood decomposition rate (Freschet et al., 2012; Liu et al., 2015) and our findings add to this body of evidence. However, a novel finding of our work, revealed by structural equation modelling, was that variation in wood DMC was one of the two different mechanisms by which stem diameter strongly controlled wood decomposition, with thinner stems having lower initial DMC or higher N and faster decomposition. The other mechanism in our study, consistent with our hypothesis (4) based on previous literature, was that the lower wood surface area to volume ratio for larger diameter stems likely lowered the rate of colonization by microbial decomposer communities (Cornwell et al., 2009), thereby reducing their decomposition rate (Hu et al., 2018; van Geffen et al., 2010). We acknowledge that fungal colonization can be facilitated through cuts and wounds. In wider stems, the possibility of colonizing the stem through the cut ends may be relatively higher than in thinner stems. Thus, the effects of stem diameter on wood decomposition would be expected to be stronger if the cut surfaces would be sealed in order to prevent fungal colonization. However, this is inconsistent with the finding that half-buried stems decomposed relatively faster than buried stems in temperate deciduous forest with 1,030 mm of annual precipitation (Oberle et al., 2018), emphasizing that burial effects on woody litter decomposition are dependent on the precipitation and associated soil moisture of different ecosystems. The relationships between wood density and the rate of decomposition are contrasting between different studies. For instance, Liu et al. (2015) showed a negative relationship in a rainforest ecosystem. By contrast, wood density could not explain variation in rates of decomposition at local or global scales in some other studies (van Geffen et al., 2010; Weedon et al., 2009). Probably the negative relationship only features in those cases where wood density is strongly correlated with DMC, as the volume basis at which mass is expressed in wood density can at best only be indirectly involved in dry matter decomposition. The model averaging procedure and structural equation modelling demonstrated that initial wood N (or wood C:N ratio) and diameter class were predominant and mostly independent controls on wood decomposition rates. This result at a local scale is consistent with the finding at global scale reported by Hu et al. (2018). These findings together confirm the importance of initial wood N (or wood C:N ratio) and diameter as key wood traits in predicting wood decomposition rates. Different from previous literature, however, we revealed a strong indirect effect

of stem diameter on wood decomposition via wood DMC and N, an effect that strongly depended on litter position. Indeed, the dual role of stem diameter on decomposition of woody litter was particularly strong under buried condition and incorporating this role may help to improve the accuracy and confidence of modelling global carbon cycling in drylands. The bark is of considerable importance as an environment filter for community assembly through habitat access and provision during the early stage of wood decomposition (Zuo et al., 2016). Previous studies showed mixed effects of bark thickness on the abundance of decomposers, for instance negative effects on bark beetles in spruce (Wainhouse and Howell, 1990) and positive effects, probably via bark fissuredness on wide-ranging macroinvertebrate populations across 11 temperate tree species (Zuo et al., 2016). In our study, with very small stem diameters, invertebrates did not play any significant role in decomposition. In SEM, bark thickness did not regulate woody litter decomposition although it was significantly negatively correlated with rates of wood decomposition due to its tight relationship with diameter (Table 4.6; Figure 4.4). By contrast, any direct effect of bark on wood decomposition above-ground was not apparent. Together our findings, which were inconsistent with our hypothesis (3), suggest that the effects of bark on wood decomposition rates are distinct between mesic and dry ecosystems due to contrasting moisture regimes. Additionally, the recalcitrant outer bark might shelter the softer inner bark and wood below from mainly abiotic UV degradation in drylands. Future studies on the effects of bark on wood organic turnover should therefore focus on how such effects vary in importance and mechanisms across diverse terrestrial ecosystems with contrasting precipitation and irradiance regimes. For instance, bark removal experiments are needed to disentangle the effects of bark protection on wood decomposition on the soil surface or suspended above it.

4.4. Conclusion

Over 34 months of incubation, the decomposition rates of buried woody litters were three times faster than those of above-ground woody litters of the same four shrub species in an inland dune ecosystem. UV had no significant influence on the rates of wood decomposition, suggesting that the importance of UV radiation for wood decomposition is negligible compared to that for leaf litters. Among several litter traits previously linked to litter quality, initial wood N concentration (or C:N ratio) and diameter class were predominant factors driving wood decomposition. A

key finding (see hypothesis 4) was that stem diameter played a dual role in determining wood decomposition: directly via surface area to volume ratio and indirectly via its link with wood dry matter content and wood N. This dual role of diameter on wood decomposition and, thereby, as a promotor of below-ground organic fluxes, may be of particular importance in grasslands subject to shrub encroachment and other shrub-dominated semi-arid and arid ecosystems. The accuracy and confidence of global carbon cycling model would be improved by incorporating the different effects of stem diameter on woody litter decomposition and below-ground wood decomposition processes in drylands.

Erdenebileg E, Wang C, Ye X, Cui Q, Du J, Huang Zh, Liu G. and Cornelissen JHC. 2020. Multiple abiotic and biotic drivers of long-term wood decomposition within and among species in the semi-arid inland dunes: A dual role for stem diameter. Functional Ecology. 34: 1466–1478. https://doi.org/10.1111/1365-2435.13559

Chapter 5. Effects of litter position and litter quality on the decomposition of leaf and fine roots

5.1 Introduction

A key part of the C cycle is the link between vegetation and carbon pools in the soil. This link can be further divided into the aboveground and belowground components of the vegetation (Aulen et al., 2012). Fine roots and green leaves are among the most nutrient-rich of plant tissues with relatively higher surface area to volume ratio (Berg and McClaugherty, 2008). Therefore, their fast decomposition processes play crucial roles in carbon and nutrient cycles. Generally, climate, decomposing organisms and litter chemical or morphological traits are important drivers of the decay rate of litters (Hobbie et al., 2010; Adair et al., 2008; Meentemeyer, 1978). Climate is considered as a main influential factor in controlling litter decomposition during past decades. However, litter quality has become a predominant factor during the recent decade (Bradford et al., 2016; Cornwell et al., 2008). Initial morphological traits and litter chemistry, including N, C and lignin concentrations, the lignin: N and C: N ratios that affect litter decomposition rates differ among species and as well as plant organs such as leaves, stem, and roots (Freschet et al., 2012b; Mclaren and Turkington, 2010; Scott and Binkley, 1997). Luo et al. (2017) found that substrate quality and soil microbial communities key determinants affecting leaf litter and fine root decomposition. However, Birouste et al. (2012) found that leaf and fine root decomposition was influenced by initial chemical traits rather than morphological traits.

Plant traits relevant to carbon, water, and nutrient are coordinated between leaf and fine roots (Liu et al., 2010; Tjoelker et al., 2005), which is called as fast-slow plant economics spectrum theory (Freschet et al., 2010; Reich, 2014). As the same litter traits largely determine the decomposition of different plant organs and these support the notion that natural selection facilitates plants with coordinated nutrient and carbon investment approaches both aboveground and belowground (Freschet et al., 2013). In the past decade, the decomposition of leaf litter and fine roots have been studied substantially in forest ecosystems (Luo et al., 2017; Fujii and Takeda, 2012; 2010; Wang et al., 2010; Harmon et al., 2009). Many previous studies suggested that the faster decomposition rates observed in leaf litter than in fine roots in the different

ecosystems (Sun et al., 2018; Luo et al., 2017; Birouste et al., 2012; Vivanco and Austin, 2006). In addition, the relationships between leaf and root decomposition rates are inconsistent in different researches. The decomposition rate of leaves was coordinated with those of roots (Freschet et al., 2013; Birouste et al., 2012; Wang et al., 2010), while some researchers did not find the coordination of litter turnover between aboveground and belowground (Sun et al., 2018; Hobbie et al., 1999). Litter position (above versus below ground) had a stronger influence on leaf decomposition rates compared with little effect on root decomposition (Fujii and Takeda, 2010). However, understanding of controlling the variation of leaf litter and fine root decomposition is scarce in the water-limited ecosystem, such as arid and semiarid ecosystems. Plant growth form regulates the litter initial chemical composition (Castro et al., 2010; Cornwell et al., 2008; Dorrepaal et al., 2005; Coûteaux et al., 1995). Generally, herbaceous species have a higher relative growth rate associated with higher specific leaf area, leaf N concentration than shrubs (Liu et al., 2015b; Wright et al., 2001). Therefore, the contrasting initial chemical composition between plant growth forms can affect litter decomposition (Seeber et al., 2008; Cornwell et al., 2008; Aerts et al., 2003).

Therefore, I examined how litter quality and incubation environment would impact litter decomposition of leaves and fine roots in a semiarid ecosystem. To answer this question, I carried out a long-term (two years) *in situ* decomposition experiment covering leaf litter and the fine root of 25 herbaceous and shrub species, which leaf litter was incubated under sand burial and on the surface positions and fine root was incubated under sand burial in Ordos, Inner Mongolia. I tested the following hypotheses that (i) leaf litter would decompose faster on the soil surface and much faster under sand burial than buried fine roots; (ii) leaf litter and fine roots of herbs would decompose faster than these of shrub litters due to their higher initial N concentrations and lower C: N ratios; (iii) there would be coordination between decomposition rates of leaf litter and fine roots.

5.2 Results

5.2.1 Relationship between green leaf, leaf litter, and fine root traits

A total of 28 green leaf, initial leaf litter, and fine root traits were used for candidate predictors of litter decomposition (Figure 5.1). Principal component

analysis (PCA) showed that for leaf traits significant relationships for multiple pairs of traits, i.e. specific leaf area- leaf C, leaf dry matter content (LDMC)- leaf C: N ratio, LDMC-leaf Ca, etc. (Figure 5.1 upper panel); for fine root traits, significant relationships for three pairs of traits (root dry mass content – root carbon content, specific root length – root carbon content, root nitrogen content – root C: N ratio) were exhibited (Figure 5.1 bottom panel). These results imply that there exist leaf and fine root economics spectrum relevant to carbon, water, and nutrient resources. Moreover, there were multiple significant correlations between leaf-root trait pairs, i.e. green leaf or leaf litter N, Ca, Mg - root N, Ca, Mg, respectively and leaf litter N, C: N ratio, P, K - root N, C: N ratio, P, K, respectively (Table 5.1). The strong negative relationships between N and C: N ratio for green leaves, initial leaf litter, and fine roots were shown likely due to relatively stable carbon concentration (Figure 5.1).

Table 5.1 Correlations between the fine root and green leaf or initial leaf litter traits. The terms in bold denote significant relationships at $P < 0.05$

图 5.1 细根和鲜叶或初始叶凋落物性状间的相关性。粗体表示相关关系显著（$P < 0.05$）

Leaf versus fine root	r	*P*
SLA- SRL	0.295	0.152
leaf DMC-root DMC	0.284	0.169
leaf C - root C	0.322	0.116
leaf N - root N	**0.495**	**0.012**
leaf C: N ratio - root C: N ratio	0.332	0.105
leaf P - root P	0.334	0.103
leaf K - root K	0.093	0.658
leaf Ca - root Ca	**0.496**	**0.012**
leaf Mg - root Mg	**0.433**	**0.030**
leaf Mn - root Mn	-0.163	0.436
leaf litter C - root C	0.252	0.224
leaf litter N - root N	**0.689**	**<0.001**
leaf litter C: N ratio - root C: N ratio	**0.523**	**0.007**
leaf litter P - root P	**0.515**	**0.008**
Leaf litter K - root K	**0.595**	**0.002**
leaf litter Ca - root Ca	**0.523**	**0.007**
leaf litter Mg - root Mg	**0.461**	**0.020**
leaf litter Mn - root Mn	-0.253	0.222

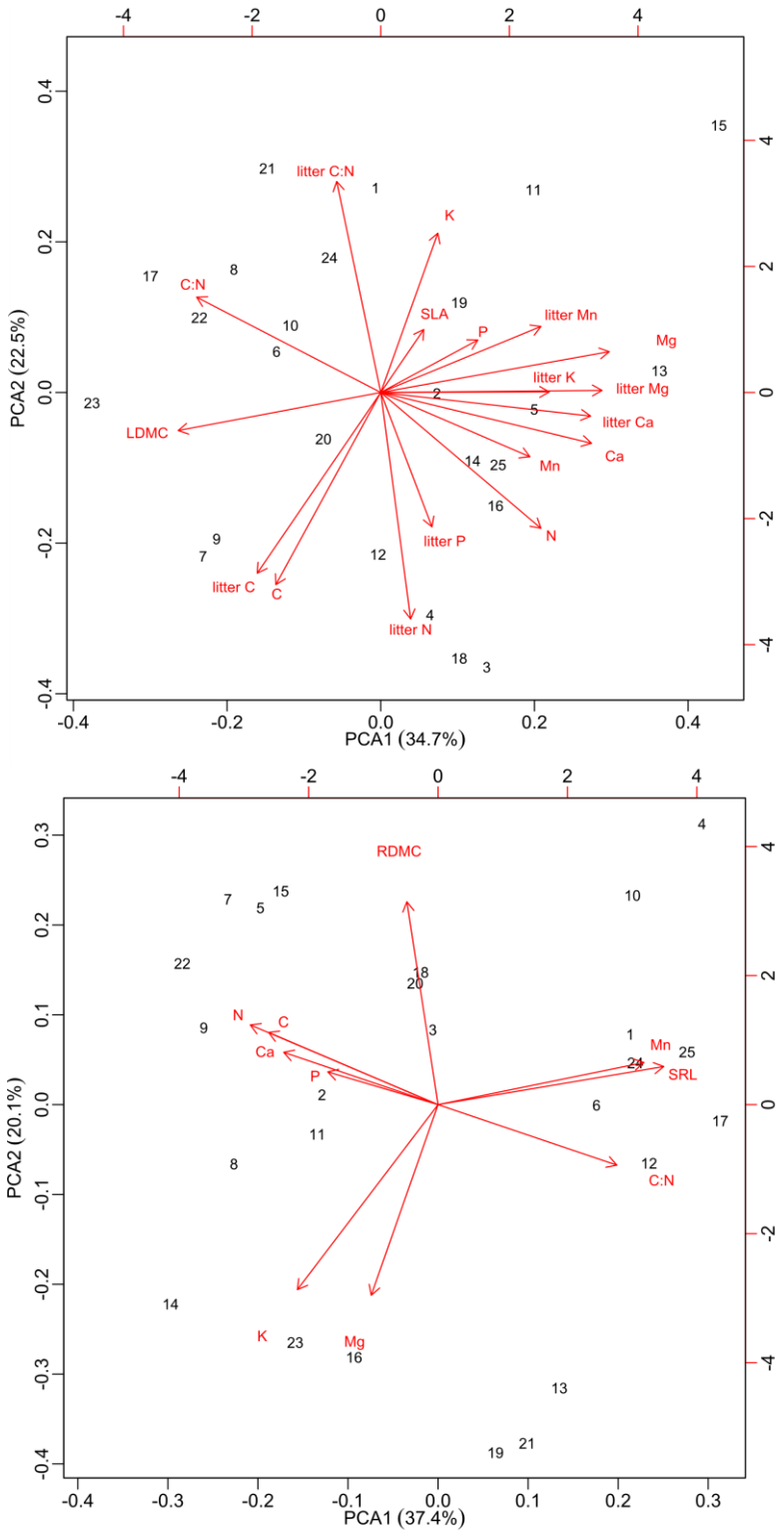


Figure 5.1 Principal Component Analysis (PCA) of 18 traits of green leaves or initial leaf litter (upper panel) and 10 fine root traits (bottom penal) for 25 species. The numbers denote species code which can be seen in Table 2.1

图 5.1 18 个鲜叶或初始叶凋落物性状（上图）和 10 个细根性状（下图）的主成分分析图（n = 25）。数字表示物种代码（详见表 2.1）

5.2.2 Leaf litter and fine root decomposition dynamics

Two-way ANOVA with repeated measurements showed that incubation time ($F = 5466.32$, $P < 0.001$), litter treatment ($F = 1171.51$, $P < 0.001$), species ($F = 186.50$, $P < 0.001$), and their interactions significantly affected loss rates of litter mass (Table 5.2). After one year of *in situ* decomposition, the average loss rate of leaf litter on the soil surface and buried positions were 45.9 ± 1.2% and 54.0 ± 1.1%, respectively, while the rate of mass loss of buried fine root was 41.4 ± 1.3%. After 2 years of incubation, the average loss rate of leaf litter on the soil surface and buried positions became 64.0 ± 1.2%, 73.4 ± 1.4%, respectively, while buried fine root loss rate was 56.8 ± 1.3% (Figure 5.2). When leaf litter and fine roots were incubated in a unified underground sand burial environment, the greater difference in decomposition rates was observed between leaves and fine roots. The decomposition rates of surface leaves and sand burial roots were similar; in the same sand burial environment, the decomposition rate of fine roots was slower than that of leaves (Figure 5.2).

During the litter decomposition, the carbon loss rate in leaf litter under sand burial position was significantly higher than that in the surface leaf litters. After a half year of the field *in situ* decomposition, the C loss rates of litters in the surface leaves and sand buried roots showed a similar pattern. When the decomposition time progresses, the litter C loss rate was as follows: buried leaf > surface leaf > buried root (Figure 5.2). Under surface and sand burial treatments, nitrogen accumulation in leaf litters was showed during the first three months of incubation, which may be related to the low loss rate of litters and microbial nitrogen immobilization. The N loss of litters increased with increasing incubation time, but much lower than the C loss of litters (Figure 5.2).

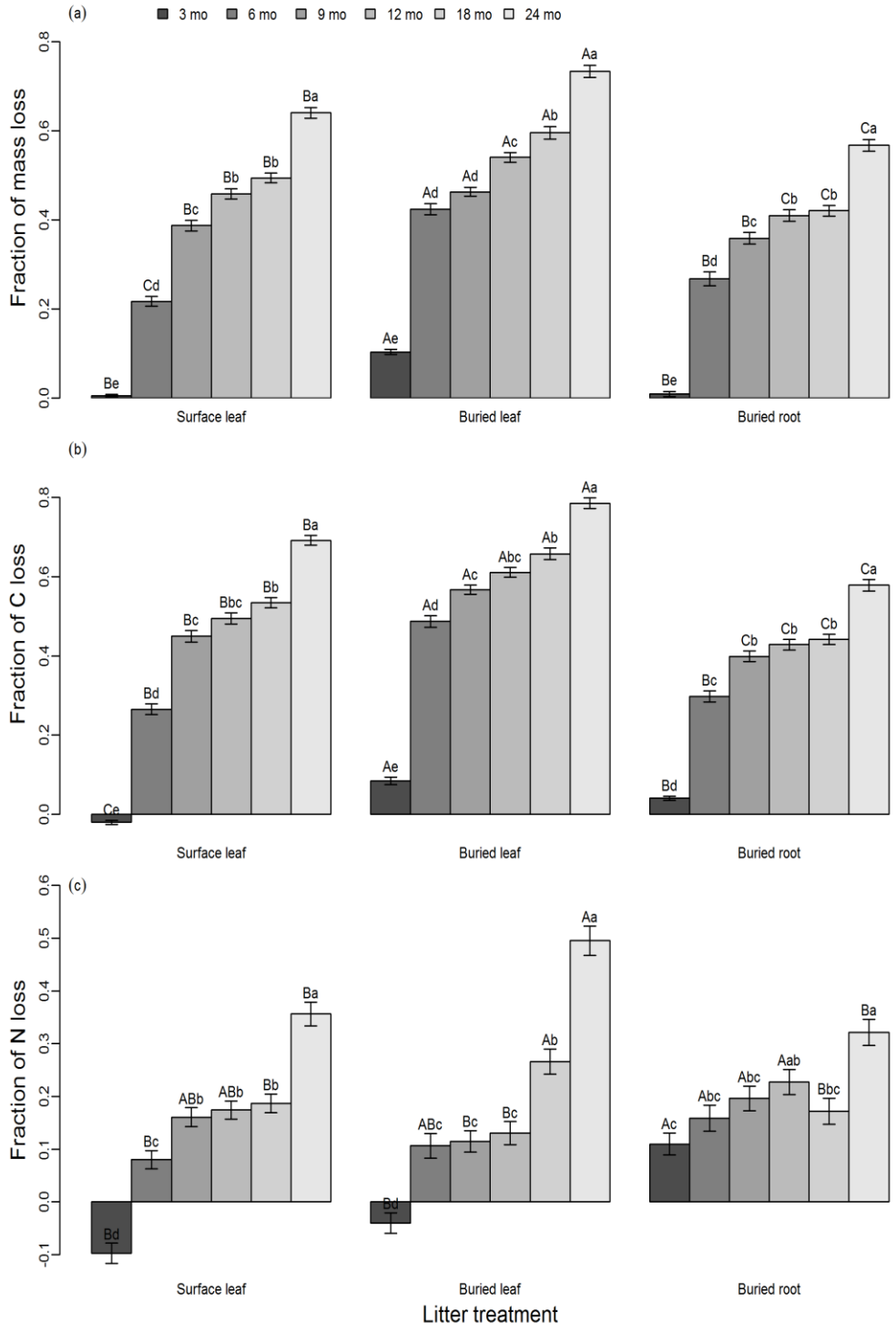


Figure 5.2 Loss rates of litter mass, carbon, and nitrogen at different decomposition times for different litter treatments

图 5.2 不同处理条件不同分解时间上的凋落物和碳、氮损失率

Table 5.2 Repeated-measures analysis of variance on the effects of different treatments and species on litter decomposition rates

表 5.2 不同处理和物种对凋落物分解速率影响的可重复性方差分析

Source	numDF	denDF	F-value	*P*-value
Between subject effect				
Litter treatment (LT)	2	318	1171.51	**<0.001**
Species (S)	24	318	186.50	**<0.001**
LT × S	48	318	48.01	**<0.001**
Within-subject effect				
Harvest (H)	5	1474	5466.32	**<0.001**
LT × H	10	1474	40.94	**<0.001**
S × H	120	1474	12.97	**<0.001**
LT ×S × H	240	1474	5.41	**<0.001**

The exponential decay model was used to calculate the decomposition rate constant *k* value. There was a significant positive correlation of the decomposition rate of the leaves between surface and sand burial position overall and across either of growth forms considered (all $r^2 \geq 0.50$), and mainly laid above the 1:1 line (Figure 5.3a). These imply that for most species, the decomposition rate of the leaves was higher under sand burial position than on the surface. In addition, the decomposition rates of leaf litter on the soil surface were coordinated with these of fine roots overall ($r^2 = 0.24$, $P = 0.013$) with lower explained variance. When the dataset was separated based on growth form, the significant relationships disappeared (Figure 5.3c). However, when leaf and fine roots were incubated into same sand burial environment, there was no significant relationship between leaf and fine root decomposition rates (Figure 5.3b). Since the litter decomposition is mainly affected by the incubation environment and litter quality, these indicate that the litter traits were more important than the environment. There is a phenotypic integration between leaf and fine root organs for the utilization of water, nutrient and light resources. This study showed there exist coupling/decoupling relationships between fine root and leaf litter turnover when they were incubated specific environments. These indicate that there exists limitation when plant economic spectrum can be extended to litter turnover. In addition, the results indicate that the decomposition rate of herbaceous plants is higher than that of shrubs (Figure 5.4), which is related to the rapid growth strategy of herbaceous plants, and the decomposition of litter rapid growth plants is faster.

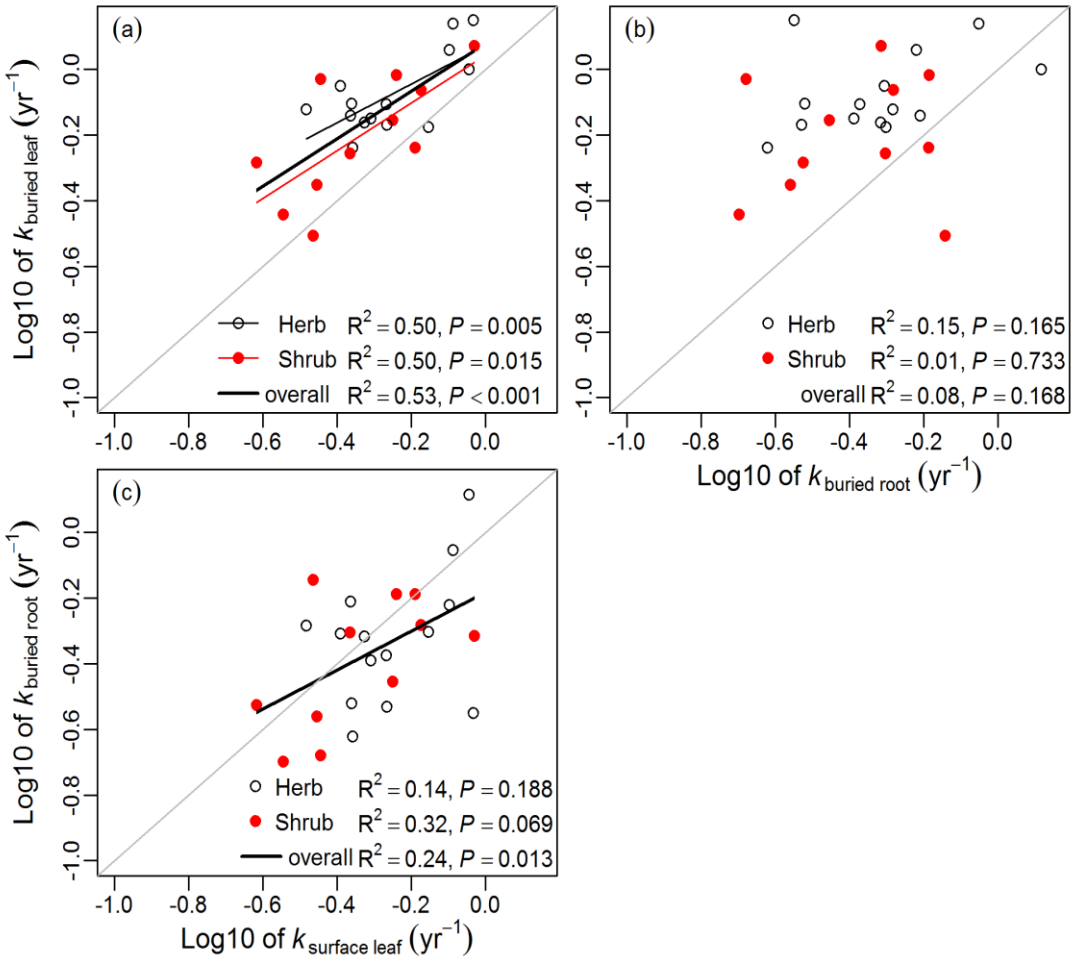


Figure 5.3 The relationship between the decomposition rates of leaf litter and fine roots overall and across different growth forms in different treatments. The solid line denotes a significant relationship at $P < 0.05$

图 5.3 总体上和不同生长型间不同处理叶凋落物和细根分解速率的关系。实线表示回归关系显著（P <0.05）

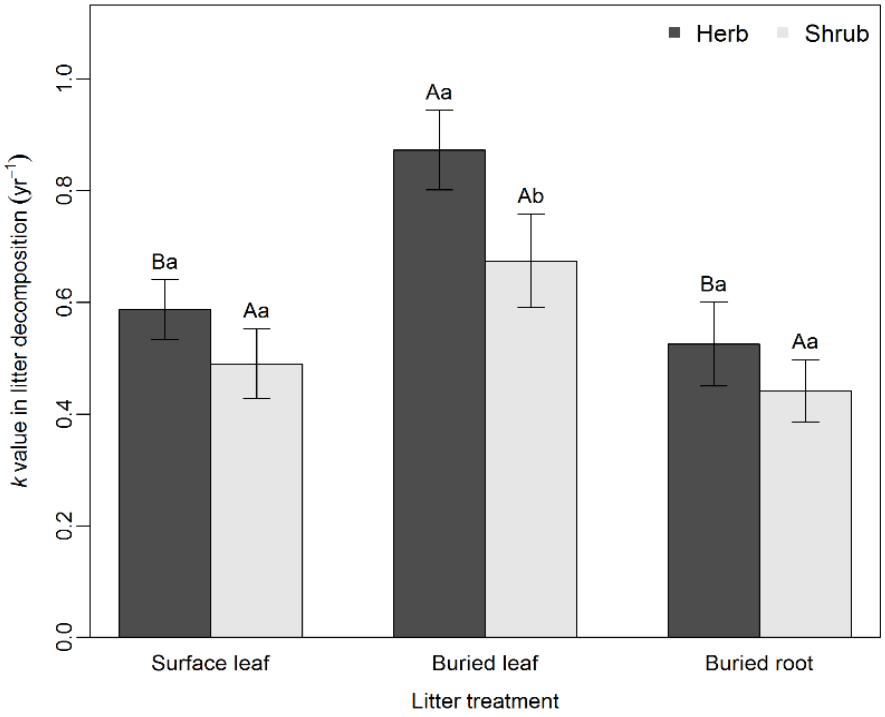


Figure 5.4 Differences in litter decomposition rates of two growth forms under different litter treatments

图 5.4 不同凋落物处理下两种生长型植物凋落物分解速率差异

The same lowercase letter denotes no significant difference in *k* values for litter decomposition between growth forms under each of litter treatments and the same uppercase letter denotes significant difference between litter treatments for each of two growth forms at $P < 0.05$.

相同小写字母表示每一处理条件下生长型间分解速率 *k* 值没有显著差异， 相同大写字母表示每一个生长型下不同处理间分解速率 *k* 值没有显著差异（$P < 0.05$）。

5.2.3 Leaf litter and fine roots carbon, nitrogen and C: N ratio

The N concentrations of litter increased with increasing incubation time in all treatments (Figure 5.5), which may be due to the soluble matter in the litter with relatively faster turnover. At the same time, the nitrogen immobilization of the microorganism causes increasing the N concentration of the litter during the incubation time. As the decomposition time increases, the C concentration in leaf litter under the surface and sand burial positions decreased, while the buried roots did not show a trend (Figure 5.5). During the decomposition process, the carbon and nitrogen ratios of litter decreased under the three treatment conditions (Figure 5.5).

While during the decomposition, the C and C: N ratio of fine roots were significantly higher than those of surface and buried leaves, which means that the decomposition rate of fine roots is slower than that of leaf litters. For the 25 species, the relationship between C, N concentrations or C: N ratios and the decomposition time were analyzed using ordinary linear regressions, respectively (Figures 5.6; 5.7; 5.8). The results showed that the C concentrations of leaf litters in some species were significantly negatively correlated with the incubation time, while the C concentrations of roots in some species were significantly positively or negatively correlated with the incubation time (Figure 5.6). Under the three treatment conditions, the litter N concentrations of most species were significantly increased with the incubation time, while C: N ratios significantly decreased with the incubation time (Figures 5.7; 5.8). Moreover, during the decomposition process, the litter C: N exhibits a convergence reaction with the incubation time.

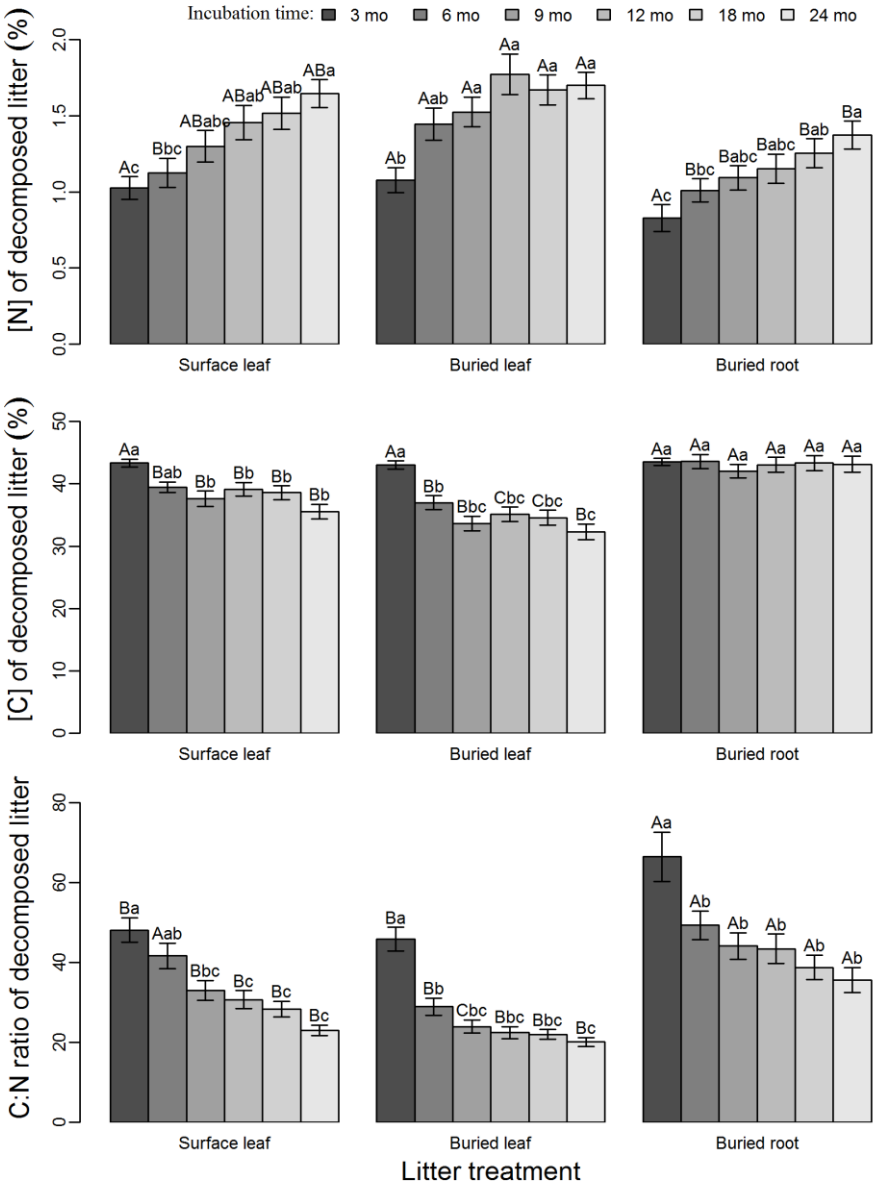


Figure 5.5 Changes in carbon, nitrogen concentration and carbon to nitrogen ratio under different treatment conditions

图 5.5 不同处理条件下碳、氮浓度和碳氮比变化

The same lowercase letter denotes a significant difference in carbon, nitrogen concentrations, and C: N ratios of decomposed litters between growth forms under each of litter treatments and the same uppercase letter denotes significant difference between litter treatments for each of two growth forms at $P < 0.05$.

相同小写字母表示每一处理条件下生长型间 C、N 浓度和 C: N 比没有显著差异， 相同大写字母表示每一个生长型下不同处理间 C、N 浓度和 C: N 比没有显著差异（$P < 0.05$）。

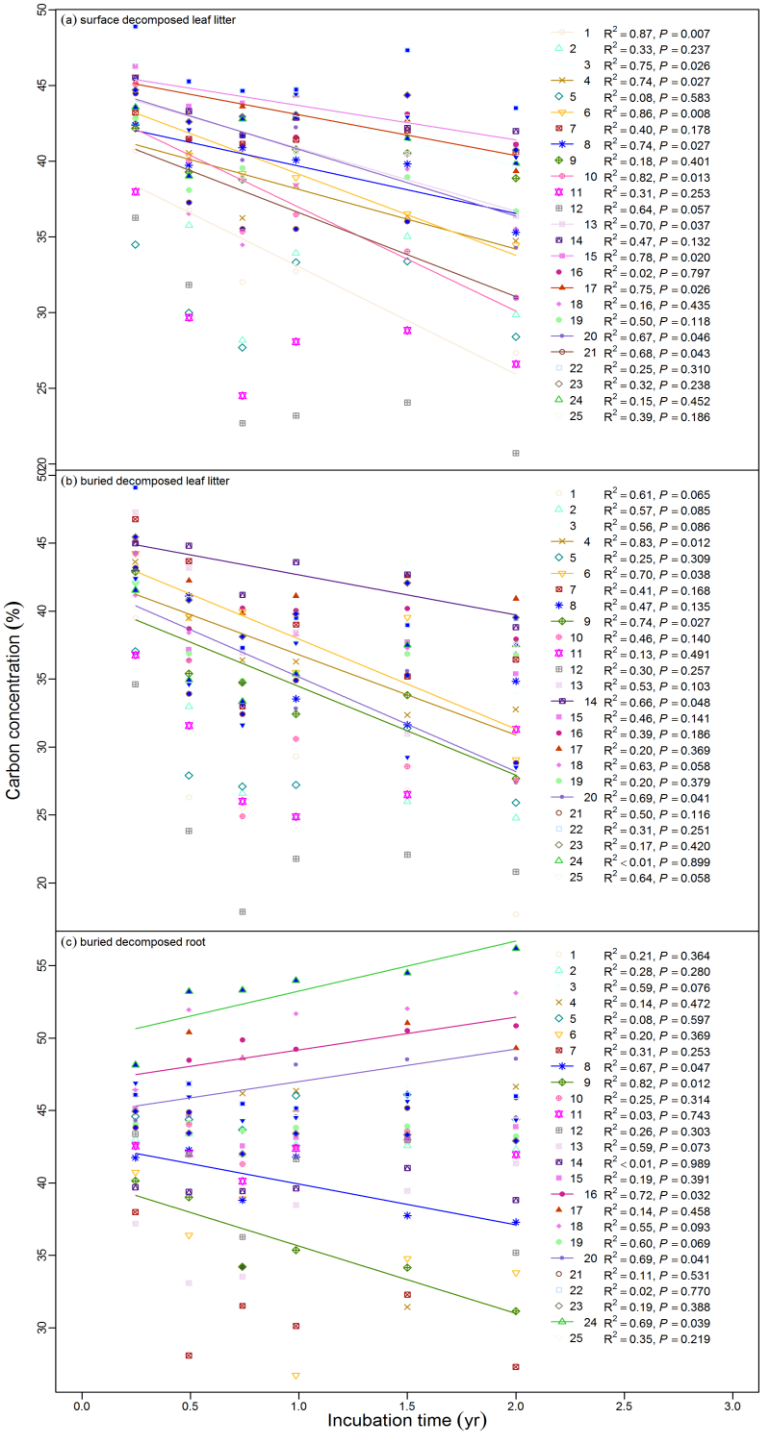


Figure 5.6 The relationship between the C concentration of decomposed litters and decomposition time under different treatments. The solid line denotes a significant regression relationship between an incubation time and C concentration of decomposed litters under different treatments at *P* < 0.05. The numbers denote species codes and can be seen in Table 2.1

图 5.6 不同处理下凋落物碳浓度和分解时间的关系。实线表示分解时间与分解过程中凋落物 C 浓度的回归关系显著（*P* <0.05）。数字表示物种代码，见表 2.1

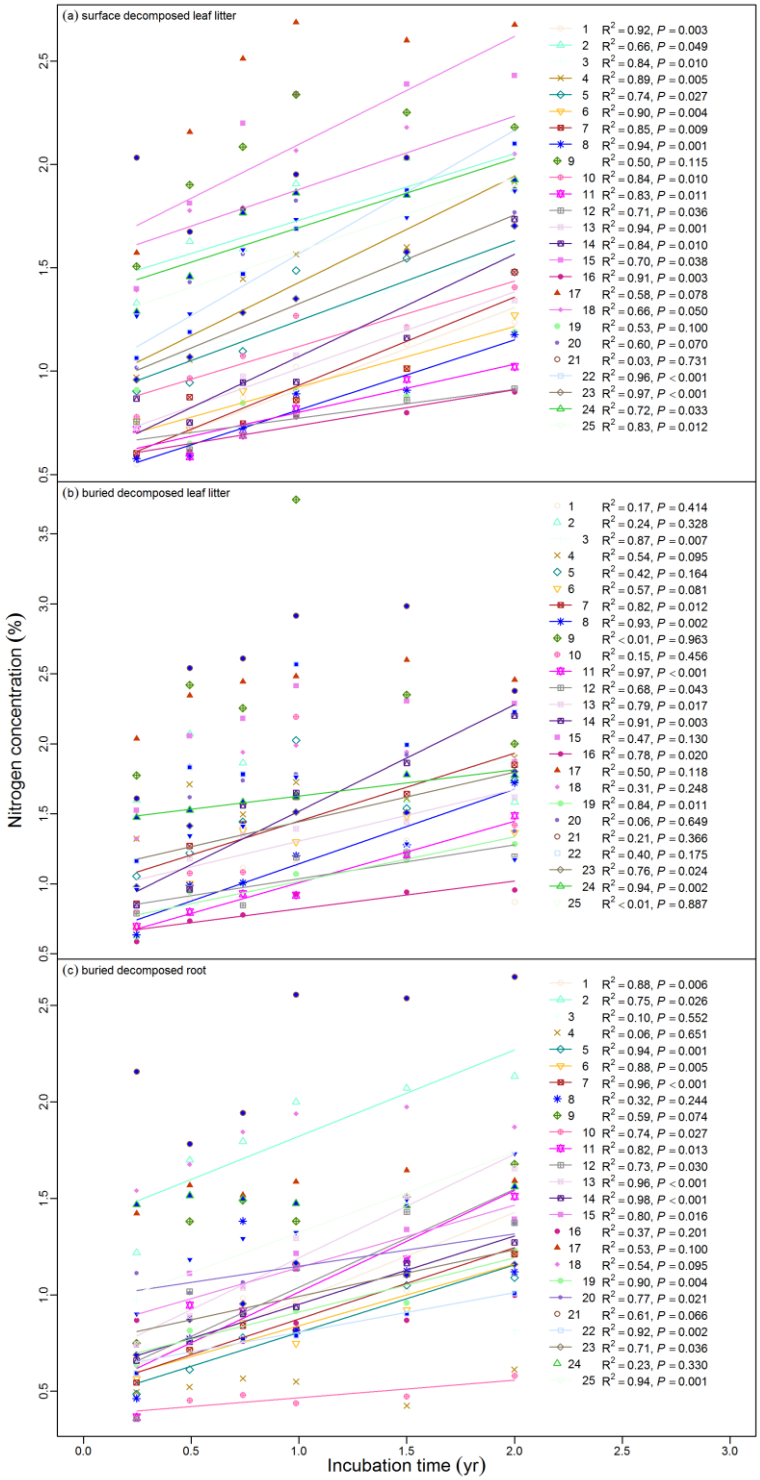


Figure 5.7 The relationship between N concentration of litters and decomposition time under different treatments. The solid line denotes a significant regression relationship between an incubation time and N concentration of decomposed litters under different treatments at *P* < 0.05. The numbers denote species codes and can be seen in Table 2.1

图 5.7 不同处理下凋落物氮浓度和分解时间的关系。实线表示分解时间与分解过程中凋落物 N 浓度的回归关系显著（*P* <0.05）。数字表示物种代码，见表 2.1

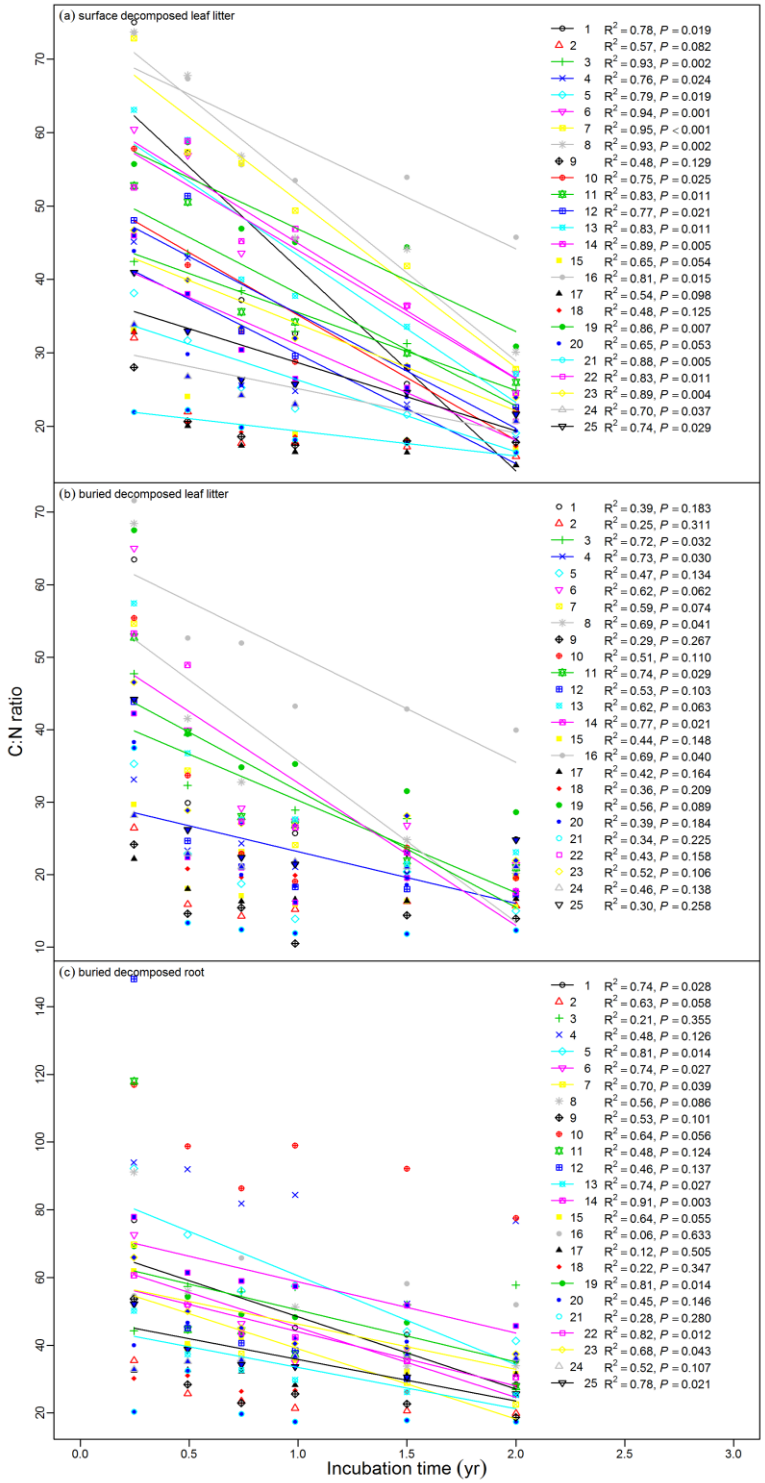


Figure 5.8 The relationship between C: N ratio of litters and decomposition time in different treatments. The solid line denotes a significant regression relationship between an incubation time and C: N ratio of decomposed litters under different treatments at *P* < 0.05. The numbers denote species codes and can be seen in Table 2.1

图 5.8 不同处理凋落物 C: N 比和分解时间的关系。实线表示分解时间与分解过程中凋落物 C: N 比的回归关系显著（*P* <0.05）。数字表示物种代码，见表 2.1

5.2.4 Relationship between the decomposition rate of leaf litter and fine roots and functional traits

Litter decomposition is affected by the initial litter quality. Multiple species experiments represent different litter qualities, which helps to answer the regulation effect of the litter itself on the decomposition rate. Linear regression showed that the leaf litter decomposition rate (*k* value) under soil surface was significantly negatively correlated with LDMC, C: N ratio, but it was significantly positively correlated with specific leaf area (SLA), leaf Mn and Mg (Table 5.3). Leaf litter decomposition under sand burial rates was significantly negatively correlated with LDMC but significantly positively correlated with leaf litter P (Table 5.3). The fine root decomposition rates under sand burial were significantly negatively correlated with root C: N ratio, but significantly positively correlated with root N concentration (Table 5.3). These results indicate that both environmental factors and litter quality can change the regulation of plant functional traits on litter decomposition, and the driving mechanisms of litter decomposition in different decomposition environments.

Table 5.3 Relationships between functional traits and litter decomposition rate under different treatments. The values in bold represent a significant correlation at $P < 0.05$

表 5.3 功能性状与不同处理条件凋落物分解速率的关系。黑体代表显著的相关关系

trait-*k*	Surface leaf		buried leaf		trait-*k*	buried fine root	
	r	*P*	r	*P*		r	*P*
SLA-*k*	**0.440**	**0.028**	0.292	0.157	SRL-*k*	0.011	0.958
Leaf DMC-*k*	**-0.706**	**<0.001**	**-0.455**	**0.022**	Root DMC-*k*	-0.230	0.268
Leaf N-*k*	0.344	0.092	-0.044	0.836	**Root N-*k***	**0.428**	**0.033**
Leaf C-*k*	-0.269	0.194	-0.259	0.212	Root C-k	-0.216	0.300
Leaf C: N-*k*	**-0.434**	**0.030**	0.002	0.992	**Root C: N-*k***	**-0.464**	**0.019**
Leaf Ca-*k*	0.336	0.100	0.052	0.804	Root Ca-*k*	-0.235	0.259
Leaf K-*k*	0.187	0.370	0.207	0.320	Root K-*k*	0.212	0.308
Leaf Mg-*k*	**0.445**	**0.026**	0.186	0.374	Root Mg-*k*	0.268	0.195
Leaf Mn-*k*	**0.401**	**0.047**	0.002	0.991	Root Mn-*k*	-0.228	0.273
Leaf P-*k*	0.330	0.107	0.312	0.129	Root P-*k*	0.127	0.546
Leaf litter N-*k*	0.121	0.566	-0.073	0.730			
Leaf litter C-*k*	-0.159	0.447	-0.139	0.509			
Leaf Litter C: N-*k*	-0.173	0.407	0.052	0.805			
Leaf litter Ca-*k*	0.264	0.203	-0.026	0.902			
Leaf litter K-*k*	0.272	0.189	0.324	0.114			
Leaf litter Mg-*k*	0.284	0.169	0.116	0.581			
Leaf litter Mn-*k*	0.218	0.294	0.013	0.950			
Leaf litter P-*k*	0.340	0.096	**0.410**	**0.042**			

5.3 Discussion

5.3.1 Changes in leaf litter and fine root decomposition rates

In this study, I disentangled the effects of litter position and litter quality on leaf litter and fine root decomposition across 25 species with herb and shrub growth forms. I found that leaves decomposed faster under sand burial and on soil surface (73.2 ± 2.9 % and 63.8 ± 2.6 %, respectively) than buried roots (56.8 ± 2.7 %) (Figure 5.2). In addition, for most of species, buried leaf litter decomposed relatively faster than leaf litter placed at the surface (Table 5.2; Figure 5.3), suggesting that sand burial is a suitable condition for decomposition than the surface. The accelerating effect of sand burial on leaf litter decomposition is consistent with the previous finding conducted in mesofauna habitat that burial significantly increased the rate of the leaf litter (Fujii and Takeda, 2012). However, few studies showed an opposite trend (Zhao et al., 2014; Ostertag and Hobbie, 1999). These results support our first hypothesis that leaf litter decomposition is faster than fine roots and coincides with previous studies that lower initial concentration of lignin and C: N ratios in leaves results in a faster decay than fine roots (Sun et al., 2018; Hobbie et al., 2010; Vivanco and Austin, 2006).

Austin and Vivanco (2006) demonstrated that photodegradation is a dominant control on above-ground litter decomposition in a semiarid ecosystem. In this ecosystem soils are in most case poorly developed and low in organic matter and nutrients in contrast with other ecosystems (Wang et al., 2010; Fisher et al., 1988; Parker et al., 1984) and photodegradation have indirect negative effect on microorganisms and direct positive effect on surface litter decomposition (Wang et al., 2017b; Huang et al., 2017; Smith et al., 2010). Most of the previous studies showed that buried plant litters had faster decomposition rates than in surface due to favorable moisture condition and microbial activity (Luo et al., 2017; Liu et al., 2018; 2015b; Wang et al., 2010; Smith and Lake, 1993). However, our results confirmed this pattern as surface leaf litter decomposed faster than the sand buried fine root. Those indicate that litter decomposition process depends strongly on the plant organs and even varied among species due to their different morphological and chemical trait values (Djukic et al., 2018; Freschet et al., 2012a; Berg and McClaugherty, 2008).

Our results revealed that multiple herb and shrub species could affect the decomposition dynamics of both leaf litter and fine root based on the different litter

qualities. Leaf litter and fine root *k* values in herb species ranged from 0.33 to 0.92 yr^{-1}, 0.57 to 1.41 yr^{-1} and 0.23 to 0.88 yr^{-1} under the surface and sand burial positions, respectively. For shrub species, leaf litter and fine root *k* values ranged from 0.24 to 0.93 yr^{-1}; 0.31 to 1.18 yr^{-1} and 0.20 to 0.72 yr^{-1} under the surface and sand burial positions, respectively (Figure 5.4). Similarly, Zhao et al. (2014) found that the decomposition rates of ephemeral herbs were faster than that of perennial in desert habitat after 2 years of incubation, implying that decomposition of desert litters depended on plant growth form. The faster decay of litter from herbaceous plants than these from shrub and woody species has been reported (Cornwell et al., 2008). Thus, these inherent differences between plant growth forms seem to be related strongly to their contrasting chemistry traits affecting litter decomposition in diverse ecosystems, which is called afterlife effects of plant traits (Cornelissen et al., 1996). These findings support our second hypothesis. In addition, these are dependent on the strong coherence between plant traits of plant types (Freschet et al., 2010). The relative growth rate (RGR) strongly depends on the growth form, from the higher values in herbs to lower in woody perennials. The slow-growing species, i.e. woody perennial shrubs, had the lowest SLA and the fast-growing perennial herbs, the highest, while woody semi-deciduous shrubs appeared intermediate (Galmés et al., 2005). Liu et al. (2015) found that the decomposition rate of leaf litter increased along the evolutionary trajectories from gymnosperms, via monocots to eudicots. Therefore, their results demonstrate comprehensively that the relative differences in litter decomposition rate among litter positions are consistent across clades and growth forms.

5.3.2 Nutrient dynamics and relationship between leaf litter and fine root decomposition rate and traits

I observed similar patterns of nutrient release for leaf litters and fine roots across treatments which are generally consistent with the global trends (Parton et al., 2007). Nitrogen concentration of decomposed litters generally increases (Aber and Melillo, 1982) because nutrients in mineral forms are immobilized by the decomposers and consequently accumulate in the litter (Marian et al., 2017; Manzoni et al., 2008; Berg and McClaugherty, 2003). Our results are partly consistent with this trend that N concentration of decomposed leaf litters and fine roots increased with increasing incubation time for all treatments, but C: N ratios showed opposite trends due to increasing N concentration of decomposed litters. In addition, C concentration of

decomposed leaf litters was slightly decreased with increasing incubation time due to their higher C release but fine roots were relatively stable in the sand burial position (Figures 5.5). In this study, the pattern of C loss was similar with that of the mass loss of each organ (Figure 5.2) because C is a structural component of plant litter.

Cornwell et al. (2008) considered plant functional traits as a driving factor in controlling the rate of litter decomposition. The previous studies showed that initial litter chemical characteristics, such as the concentration of N (Castro et al., 2010) and P (Vivanco and Austin, 2006) and the C: N ratio (Tripathi et al., 2006) can predict litter decomposition. Zhao et al. (2014) found that the significantly positive relations were found between N or P concentrations and mass loss in aboveground litters, while root turnover did not show the consistent change as aboveground litters. In this study, we found that LDMC had a predominant effect on leaf decomposition rates under surface and burial conditions (Table 5.3). Leaf surface traits such as LDMC or SLA had relatively higher predictive capacity on litter turnover. This supports the importance of leaf surface trait on predicting leaf litter turnover under surface and burial environments (Liu et al., 2018). In addition, C: N ratio was significantly negatively correlated with the decomposition rate of surface leaf litter and buried fine root, respectively (Table 5.3). This may be the reason why there exists coordination between surface leaf litter and buried fine root decomposition rates. Similarly, Freschet et al. (2012) found that all organs including leaves, stem and root decomposition were consistently controlled by the same structure-related traits (lignin, C and DMC) whilst nutrition-related traits (N, P, pH, phenols) had more variable effects, probably due to their contrast function between organs. Surprisingly, there was no significant relationship between initial C: N ratio and buried leaf litter decomposition. The finding that different traits controlled litter decomposition of buried leaf and buried fine roots can be explained that why there was no coordination between buried leaf litter and fine root decomposition. Thus, our results partly support the third hypothesis. Plant economic spectrum theory asserts that there are linkages across organs and coupling among resources, resulting in an integrated whole-plant economics spectrum (Freschet et al., 2010; Reich, 2014). Freschet et al. (2012) extend plant economics spectrum to litter turnover. Our results suggest that there exists limitation when plant economics spectrum theory can be extended to litter turnover.

Our results indicate that both environmental factors and litter quality can change the regulation of plant functional traits on litter decomposition.

5.4 Conclusion

In conclusion, the decomposition rate of leaf litter was faster under sand burial and on the soil surface position than belowground fine roots. Additionally, herbs were faster than that of shrubs at each treatment, respectively. Litter traits, as a proxy of litter quality, could correlate with the rates of leaf litter and fine root decomposition, LDMC was a predominant factor of leaf litter in each treatment. The litter C: N ratio was also driving decomposition of surface leaf litter and buried fine roots. Different plant traits control litter decomposition of leaf and fine root, respectively. The coupling of decomposition of surface leaf litter and buried fine roots and decoupling of decomposition of buried leaf and roots were observed. According to these findings, the leaf litter and fine root decomposition rates indicate that there exists limitation on the extended plant economic spectrum theory to litter turnover.

Chapter 6. Conclusion and further research directions

6.1 Conclusion

Throughout this thesis, I have examined environmental factors including solar radiation or UV radiation and sand burial on leaf or woody litter and fine root decomposition in a semiarid ecosystem. I conducted experimental research using leaf and woody litters and fine roots from shrub and herbaceous species and looked at the effects of biotic and abiotic factors on litter decomposition. Based on the research of this thesis, the following main conclusions are reached:

1) The importance of interspecific morphological and chemical properties for the effect of UV radiation on leaf litter decomposition and while litter N concentration and C: N ratio was a stronger predictor of decomposition rates in this semiarid dryland. The lack of overall net effect of UV on surface litter decomposition across eight species indicates the complexity of relationships due to dual UV radiation effect on surface litters decomposition via direct UV breakdown of plant litters and indirect changes via microbial processes.

2) For the 34 months of incubation, the decomposition rate of buried woody litter was as triple times like these of aboveground woody litters. Sand burial is a predominant factor in woody litter decomposition in a semiarid Mu Us Sandland. Litter traits, as a proxy of litter quality, could correlate with the rates of wood decomposition, which initial wood N concentration and diameter classes were predominant factors in driving wood decomposition. UV had no significant influences on the rates of wood decomposition, suggesting that the importance of UV radiation on wood decomposition decreased compared with non-woody litters. These findings highlight the importance of belowground organic fluxes in accelerating biogeochemical processes in shrub-encroachment grasslands or shrub-dominated semiarid and arid ecosystems. The accuracy and uncertainty of global carbon cycling model would be improved by incorporating belowground wood decomposition processes in drylands.

3) The decomposition rate of leaf litter was faster under sand burial and on the soil surface position than belowground fine roots. The average loss rate of leaf litter on the soil surface and buried positions became 64.0 ± 1.2%, 73.4 ± 1.4%,

respectively. However, buried fine root loss rate was 56.8 ± 1.3%. When they were incubated in the unified underground sand burial environment, the greater difference in decomposition rates was observed between leaf and fine roots. Herbs were faster than that of shrubs at each treatment, respectively. Multiple trait pairs between leaf and fine roots covaried, i.e. green leaf or leaf litter N, Ca, Mg - root N, Ca, Mg, respectively and leaf litter N, C: N ratio, P, K - root N, C: N ratio, P, K, respectively. In addition, there was coordination between the decomposition rates of surface leaf litter and fine roots. Litter traits, as a proxy of litter quality, could correlate with the rates of leaf litter and fine root decomposition, LDMC was a predominant factor of leaf litter in each treatment. The litter C: N ratio was also driving decomposition of surface leaf litter and buried fine roots. Different plant traits control litter decomposition of leaf and fine root, respectively. The coupling of decomposition of surface leaf litter and buried fine roots and decoupling of decomposition of buried leaf and roots were observed. According to these findings, the leaf litter and fine root decomposition rates indicate that there exists limitation on the extended plant economic spectrum theory to litter turnover. This conclusion expands the theory of the coupling relationship between fine roots and leaf economic traits.

6.2 Further research directions

In this thesis, only solar radiation or UV radiation and sand burial are investigated as environmental factors due to a peculiarity in semiarid Mu Us Sandland. For a more and deeper understanding of the process of litter decomposition in arid and semiarid ecosystems, further studies are required to consider other abiotic and biotic factors such as precipitation pulse (amount and frequency), air moisture and microbial community and their interactions with solar radiation or UV radiation on litter decomposition in sun-lit dryland ecosystems. Additionally, Mu Us Sandland is very poor in soil fertility, thus N deposition mediated changes in plant litters and decomposing organisms would significantly affect litter decomposition. Therefore, further studies on N deposition on litter decomposition should be considered. Another important future direction is that researchers can incubate branch or stem litters with or without bark and thus disentangle the importance and role of bark in woody litter decomposition.

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