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Tree species effects on microbial respiration from decomposing leaf and fine root litter

Naoki Makita [a, b, *], Saori Fujii [a, c]

[a] Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan
[b] Kansai Research Center, Forestry and Forest Products Research Institute, Kyoto 612-0855, Japan
[c] Graduate School of Environment and Information Sciences, Yokohama National University, Yokohama 240-8501, Japan

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ABSTRACT

Tree species have an impact on decomposition processes of woody litter, but the effects of different tree species on microbial heterotrophic respiration derived from decomposing litter are still unclear. Here we used leaf and fine root litter of six tree species differing in chemical and morphological traits in a temperate forest and elucidated the effects of tree species on the relationships between litter-derived microbial respiration rates and decomposition rates and morphological traits, including specific leaf area ($cm^2\ g^{-1}$) and specific root length ($m\ g^{-1}$) of litter at the same site. Litterbags set in forest soil were sequentially collected five times over the course of 18 months. During litter decomposition, microbial respiration from leaf and fine root litter differed among the six tree species. Temporal changes in the remaining mass and morphology (specific leaf area and specific root length) were observed, and the magnitude of these changes differed among species. Positive correlations were observed between respiration and mass loss or morphology across species. These results revealed that litter mass loss and morphological dynamics during decomposition jointly enhanced microbial respiration, and these carbon-based litter traits explained species differences in decomposition of leaves and fine roots. In conclusion, tree species influenced the magnitude and direction of microbial respiration during leaf/fine root litter decomposition. Tree species also affected the relationship between microbial respiration and litter decomposition through direct effects of litter traits and indirect effects mediated by regulation of heterotroph requirements.

1. Introduction

Decomposition of plant litter and soil organic matter (SOM) is an important process that contributes to carbon (C) and nutrient cycling in forest ecosystems, regulating C release to the atmosphere, C accumulation in soil, and supply of inorganic nutrients to plants (Heal et al., 1997; Berg and McClaugherty, 2008). These important roles of decomposition are performed by mineralization of dead organic matter through metabolism by microorganisms (Prescott and Grayston, 2013). Therefore, understanding microbial mechanisms of litter decomposition is crucial for the elucidation of matter flux and C sequestration. Moreover, given the importance of forest soils as the largest C pool in forest ecosystems, even small changes in the C pool of the soil could profoundly influence the increase in atmospheric CO_2, and thus, an accurate estimate of net soil C balance in litter decomposition is needed (Davidson and Janssens, 2006; Harmon et al., 2011).

Microbial heterotrophic respiration (Rm) is a crucial component of soil CO_2 efflux associated with mineralization of dead organic matter via metabolism by fungi and bacteria (Raich and Schlesinger, 1992; Couteaux et al., 1995; Harmon et al., 2011). The Rm from the soil surface has been estimated at 53–57 Pg C yr^{-1} globally and is typically 30–80% of total annual soil respiration (Bond-Lamberty et al., 2004). Generally, the soil C is supplied through leaf litterfall and root-derived C input. In temperate forests, leaf litterfall may represent 20–31% of net primary productivity (NPP) (Curtis et al., 2002). In addition, tree fine roots are dynamic and short-lived, supplying much belowground litter input (Leppälammi-Kujansuua et al., 2014) and accounting for 10–60% of NPP of temperate ecosystems (Gill and Jackson, 2000; Finér et al., 2011). Sulzman et al. (2005) reported that aboveground litter decomposition contributed 19%, and belowground litter decomposition contributed 58% to

* Corresponding author. Kansai Research Center, Forestry and Forest Products Research Institute, Nagai-Kyutarou Momoyama Fushimi, Kyoto 612-0855, Japan. Tel.: +81 75 611 1201; fax: +81 75 611 1207.
E-mail address: makita701@gmail.com (N. Makita).

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total soil respiration in an old-growth coniferous forest in Oregon. The Rm is often regulated by environmental factors, such as temperature and moisture (Harmon et al., 2011). Studies on these regulating factors have facilitated the development of the SOM models, such as CENTURY and RothC, for predicting the Rm and decomposition of SOM under different environment conditions (Falloon et al., 2009). However, when only considering environmental factors, the estimated Rm is not always matched with the observed Rm in the field because biotic factors, including substrate quality of litter, may limit the decomposition process.

Most studies of woody litter decomposition have quantified the rates as either mass loss or density change per unit time, and decomposition is treated as an aggregate process (Berg and McClaugherty, 2008). The litter quality during decomposition varies because of the ingrowth of fungal and bacterial cells in fresh litter and the transfer of mineral nutrients (Gusewell and Gessner, 2009; Aponte et al., 2013). Recent studies have suggested that the temperature sensitivity of Rm during decomposition could vary with the quantity and quality of labile and recalcitrant compartments of SOM (Conant et al., 2011), leaf litter (Fierer et al., 2005), and root litter (Makita and Kawamura, 2015). However, little is known about how specific rates of Rm derived from leaf and root litter are integrated with the decomposition process in forest fields. The analysis of Rm rates during the decomposition process may reveal changes in the abundance and activity of microbial decomposers over time (Anderson and Herherington, 1999; Fanin et al., 2011; De Graaff et al., 2013). Thus, in order to accurately assess the Rm, it is necessary to determine the contributions of biotic factors and elucidate the characteristics in Rm values derived from the litter relative to different substrate qualities and decay periods under field conditions.

Another important factor that is likely to play an important role in explaining specific rates of Rm is tree species. The interspecific decay patterns in litter dynamics are highly diverse, even within leaf or root litter. Moreover, tree species can affect the decomposition process through the quality of species-specific chemical and morphological traits (Hobbie et al., 2006; Cornwell et al., 2008). Each tree species possesses unique functional traits that may have distinctive effects on litter decomposition and hence C and nutrient cycling (Prescott, 2010) in relation to changes in the requirements of the decomposer community (Prescott and Grayston, 2013). Differences among tree species are generally thought to be related to distinct substrate quality, with litter C:N and N:P ratios, lignin content, and Ca and Mn concentrations emerging as the main controlling factors of decomposition rates for leaf litter (Hobbie et al., 2006; Cornwell et al., 2008) and root litter (Silver and Miya, 2001; Goebel et al., 2011). Furthermore, inherent variation in litter morphological traits among tree species is related to the physical quality of plant litter and can potentially affect the accessibility of substrates to decomposers (Angers and Recous, 1997; Cornelissen et al., 1999; Fortunel et al., 2009; Kazakou et al., 2009; Birouste et al., 2012). However, while these data imply that plant species affect the litter decomposition process, the effects of tree species on Rm rates have rarely been explored. Here, we focused on elucidating the relationship between Rm and morphological properties in decomposing litter, including specific leaf area (SLA, ratio of leaf area to mass) and specific root length (SRL, ratio of root length to mass). The morphological dynamics of decomposing leaf and root litter could be thought to influence the specific rates of decomposition and microbial respiration through changes in heat, nutrient, and water exchange between the litter and soil. Given the close coupling of Rm and different substrate qualities of the litter, it is likely that species-driven litter decomposition at the tissue-level scale may affect both soil C sequestration and soil C flux in forest ecosystems.

In this study, we aimed to elucidate the effects of tree species on the potential Rm of leaf and fine root litter decomposition and to determine the association of Rm with litter substrate quality with respect to morphological and chemical traits. Our objectives were to determine whether (1) the Rm from decomposing leaves and fine roots varies during the decomposition process in relation to the decomposition rates and SLA or SRL of litter and (2) the magnitude of the Rm differed among species.

2. Materials and methods

2.1. Study site

The study was conducted in a temperate mixed broad-leaf/conifer forest at the Kamigamo Experimental Forest Station, Kyoto University, Kyoto, Japan (35°04′N, 135°43′E, 200 m above sea level). The mean annual precipitation and temperature are 1582 mm and 14.6 °C, respectively. The forest canopy was mostly composed of *Chamaecyparis obtusa* Endl and *Quercus serrata* Murray. The subcanopy and understory vegetation contained various species, including *Ilex pedunculosa* Miq, *Lyonia ovalifolia* Wall, and *Eurya japonica* Thunb. The soil humus was a moder type with a 5-cm-thick organic layer above a poorly developed A-horizon layer that was 5 cm thick and a BC layer (Fujii and Takeda, 2010). The soil type was dry brown forest soil and Cambisols (IUSS Working Group WRB, 2006) on sandstone and slate. The soil pH and C/N ratio were 4.1 and 23.5, respectively (Kuroiwa et al., 2011).

2.2. Experimental setup and sample measurements

The litterbag method was used to evaluate the mass loss and Rm from decomposing litter of leaves and fine roots. We selected litter material from six tree species based on leaf life span (evergreen versus deciduous) and root mycorrhizal type (ectomycorrhiza [ECM] versus arbuscular mycorrhiza [AM] versus ericoid mycorrhiza [ERM]), as shown in Table 1. The six species chosen in this study, i.e., *Chengiopanax sciadophylloides* Franch. et Sav., *L. ovalifolia* Wall., *Q. serrata* Thunb., *Quercus glauca* Thunb., *I. pedunculosa* Miq., and *C. obtusa* Endl., are dominant species for warm temperate forests in Japan (Table 1). During autumn 2010, at the time of the respective leaf-fall periods, freshly senesced leaves of each species were collected from a large forest near one plot to minimize within-species litter heterogeneity. Simultaneously, fine root segments of each species were collected from the surface organic soil layer (0–5 cm) of the original forest stand. In the laboratory, large root systems were carefully isolated from the soil and organic matter, and washed gently to remove soil. The roots were then sorted by visual inspection into live and dead segments according to the resilience, brittleness, and color of the bark and xylem. Live roots have an intact stele and cortex, are slightly elastic and white or brown in color. Dead roots often have fragmented bark, and are inelastic, brittle, and very dark in color. The living roots (<1.0 mm in diameter) of each species were collected. Finally, the leaves and roots were air dried at room temperature to a constant mass.

Then, 1.0 g of dried leaves from each species was enclosed in 10×10 cm^2 litter mesh bags, and 0.5 g of dried roots was enclosed in 5×10 cm^2 bags. The litter mesh bag was made of 1.0-mm mesh nylon netting, which allowed free access of soil microfauna, mesofauna, and microorganisms (Swift et al., 1979). We established a study plot of 10×15 m^2 and divided this plot into six subplots of 5×5 m^2. On July 7, 2011, the litter bags were placed on the soil surface for leaf bags and vertically at a soil depth of 0–5 cm for root bags in the six subplots. In total, 360 litterbags (two litter types × six species × six subplots × five harvests) were tested. On each occasion, six replicate litterbags for each species for each litter