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Review

The role of microbial community in the decomposition of leaf litter and deadwood

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ABSTRACT

Leaf litter and deadwood have important roles in the forest ecosystems, providing shelter for several organisms, preventing erosion and microclimate fluctuations. Their decomposition is a key process of biogeochemical cycles in forest. Microorganisms are the primary agents of decomposition. Particularly, fungi are considered the major contributors due to their ability to produce specific enzymes and the possibility to access new substrates through hyphae. In this review, we highlighted the role of fungi in decomposition and reconsider the role of bacteria, neglected in the past, identifying key research needs and knowledge. Particular attention is given to the succession of different taxa with different ecological role that are able to use a substrate that undergoes to chemical and structural modifications. The quality of substrates is a critical factor that influences the microbial community together with environmental variables, such as temperature and moisture. However, the microbial community is also able to influence the substrate characteristics. Litter nitrogen content is influenced by the uptake of exogenous N by decomposers to meet their metabolic requirements. The complex interactions among microbial communities, ecosystem attributes and chemical composition of fine litter and woody debris remain unclear and almost exclusively referred to boreal and temperate forests.

1. Introduction

In forest ecosystems dead organic material consists of a heterogeneous group of residues including coarse and fine deadwood, as well as fallen leaves and needles (Didion et al., 2014). Leaf litter may account for 22–81% of the annual production of plant litter (Mason, 1977; Scarascia-Mugnozza et al., 2000); other type of litter are twigs, branches, bark, flowers, and sometimes cones (Berg and McClaugherty, 2008). It has been estimated that leaf litter (hereafter referred to as "litter") produced every year by deciduous trees is in the range of 3–5 tons per hectare in cold and warm temperate forests (Bray and Gorham, 1964). In deciduous forests, during autumn, senescent leaves start to fall down and create the first stratification of the litter. The presence of this litter layer has multiple important functions in the forest floor: Prevents the erosion, decreases and/or prevents the destruction of the aggregates of the soil by raindrops, provides protection against microclimate fluctuations and soil compaction (Sayer, 2006).

The other key component of forest debris is represented by deadwood, consisting of standing dead trees, downed logs, snags, stumps and dead roots. Coarse Woody Debris (CWD) provides food and shelter for a variety of organisms including plants, insects, fungi, lichens, birds and mammals (Heilmann-Clausen and Christensen, 2005). As a result, the reduction of deadwood in managed forests can lead to a loss of habitats and resources for a wide range of species. In ecosystems with a rapid decomposition of litter or frequent fires, CWD plays an important role for the conservation of the organic layer. In dry conditions, CWD acts as a source of humidity that sustains the vegetation during dry periods (Harmon et al., 1986).

The decomposition of litter and deadwood is a key step in carbon (C) and nitrogen (N) cycles, as it contributes to CO_2 release (Van Geffen et al., 2010), and is the main source of mineral N in terrestrial ecosystems (Hobbie, 2015; Manzoni et al., 2008; Parton et al., 2007) (Fig. 1). At global scale, the amount of C released yearly by litter decomposition, 60 Tg C y^{-1}, is 11 times higher than the one released by the combustion of fossil fuels (Schlesinger, 1991). Likewise, deadwood is regarded as an important source of nutrients for forest soils (Fig. 1),

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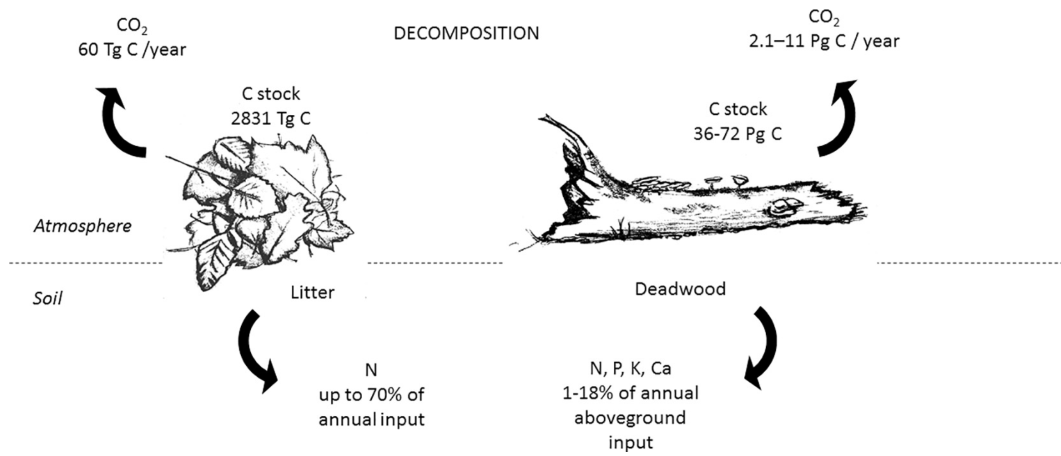

Fig. 1. Relative contribution of leaf litter and deadwood decomposition to C and nutrient flows in forest ecosystems. See supplementary S1 for references.

although to a lesser extent compared to litter. In fact, it contributes to only 1–18% of the annual aboveground input of N, P, K and Ca in forest litter (Laiho and Prescott, 2004). However, N accumulation in deadwood contributes to the reduction of nutrient leaching after a disturbance, therefore, preserving soil fertility and productivity in a long-term perspective (Lombardi et al., 2013; Palviainen et al., 2010 and references therein).

In forest ecosystems, decomposition is a complex process resulting from the interaction of abiotic and biotic drivers that cause physical and chemical changes of the substrate (Freschet et al., 2012). Climatic variables such as temperature and moisture, along with substrate quality and decomposer community attributes, are known to affect the decomposition process and decay rates (Cornwell et al., 2008; Gholz et al., 2000; Purahong et al., 2016b; Santonja et al., 2015; Trofymow et al., 2002). This paper aims to provide a comprehensive review of studies on litter and deadwood decomposition, highlighting the most important findings related to the drivers of this process and identifying key research needs. We will mainly focus on the role of microbial communities and on how they are influenced by the substrate properties and ecosystem attributes, as these were proved to be critical aspects (Baldrian, 2016; Bradford et al., 2016; Cotrufo and Ineson, 2000; Harmon et al., 1986; Prescott, 2010; Trofymow et al., 2002). We will then discuss the different methodological approaches that have been applied for the study of litter and deadwood decomposition in forest ecosystems. Finally, we will present the current knowledge gaps to orient future research on this topic.

2. Decomposition process: Physical and chemical changes

2.1. Physical and structural changes

Carbon contained in the litter is released through the degradation of the cell walls. The cell wall constituents can be divided into three broad groups, according to their recalcitrance: i) The water soluble molecules, ii) the hemicellulose, cellulose and pectin and iii) lignin and other aromatic compounds (Fioretto et al., 2005). The first group is composed by small molecules, such as amino acids and sugars that are easily accessible and degraded by the fast-growing microorganisms of the decomposing community (Adair et al., 2008; Fioretto et al., 2005). Cellulose is the most abundant natural polymer on Earth (30–50% dry mass of a plant) (de Boer et al., 2005). It is a repetition of 1,4-linked D-glucose and forms linear chains that are held together with hydrogen bonds to create a crystalline structure and amorphous regions that give rigidity to cell walls (Rytioja et al., 2014). The hemicellulose supports the crystals of cellulose and has an amorphous structure: its backbone is mainly constituted by xylans, xyloglucans and mannans with branched monomers and short oligomers (Rytioja et al., 2014). Lignin is the most recalcitrant polymer in litter. Lignin is a complex aromatic matrix, which provides strength and rigidity to plant cell wall and function, as a glue between the polysaccharides fibers (Ten Have and Teunissen, 2001).

During decomposition, litter undergoes to a rapid loss of easily soluble compounds, including starch, amino acids and sugar, due to leaching, microbial activity and soil fauna attack. In the second phase, lignin and cellulose become the main compounds found in the litter and are degraded by specific microbial taxa. This phase is characterized by lower decay rates in comparison with the early phase (Preston et al., 2009; Purahong et al., 2014).

Wood goes through different changes during decomposition compared to leaf litter, as reflected in its different chemical composition, structure and biological function (Cornwell et al., 2009). In particular, these changes are related to the reduction of density, the increase of water content and the accumulation of nutrients and lignin compounds and, in some cases, a reduction of pH is also observed (Fukasawa and Matsuoka, 2015; Petrillo et al., 2015; Rayner and Boddy, 1988). The rate of wood density decrease depends on the initial wood density and differs according to the tree species. For example, density decreases more slowly in conifers compared to birch wood that was reported to fully decompose in a rather short time period (around 25–40 years) (Mäkinen et al., 2006).

The concentration of structural compounds in deadwood changes as decomposition proceeds. According to the chemistry of the substrate, it is possible to identify two main steps. The first phase is dominated by the loss of acid-unhydrolyzable residue (AUR), which contains lignin compounds, and by the reduction of holocellulose (Fukasawa et al., 2009; Klotzbücher et al., 2011). In the advanced decay stages, holocellulose is selectively decomposed and AUR accumulates in the remaining woody debris (Fukasawa et al., 2009; Strukelj et al., 2013). Because of the changing chemical conditions within deadwood, decomposition rates are not constant during the process. A first period with high decay rates is generally followed by slower decomposition possibly due to the retention of recalcitrant compounds that are slowly decomposed by microorganisms (Fukasawa et al., 2009). This two-phases pattern reflects the fungal succession of groups with different decaying abilities (see section “Main agents of decomposition” for details) and it has been described for both conifer and deciduous forest types (Fukasawa et al., 2009). As decomposition proceeds, deadwood is gradually incorporated into the organic soil horizons, still maintaining a chemical composition that differs from that originating from foliar litter (Strukelj et al., 2013).

2.2. Carbon and nutrient dynamics

Carbon content and nutrient chemistry and stoichiometry are