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Quercus species control nutrients dynamics by determining the composition and activity of the forest floor fungal community

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A B S T R A C T

In forest ecosystems, microbial community structure and activity play an important role in C and nutrient dynamics and are strongly influenced by litter composition. Moreover, litter decomposition rates also depend on microbial activity. Fungi are a key component of the microbial community as they produce extracellular hydrolytic and oxidative enzymes that degrade organic polymers and mobilize inorganic nutrients. In this study, we examined how litter composition affects microbial activity and fungal community structure by comparing decomposing litter derived from sympatric *Quercus castanea* (*Qc*) and *Quercus deserticola* (*Qd*) in a deciduous forest in Mexico. Microbial N and P biomass were higher in the *Qd* litter than in the *Qc* litter. The differences in N and P were seasonal and were not observed at the end of the rainy season (October). The specific enzyme activity was higher in the *Qc* than in the *Qd* litter, mainly at the onset of senescence (May). At this time, phenol oxidase and β-glucosidase activities were significantly higher in the *Qc* litter than in the *Qd* litter; thereby the nutrient acquisition strategies of the microbial community differ in the litter derived from each *Quercus* species. Internal transcribed spacer sequence analysis of the fungal community indicated higher richness (24 operational taxonomic units: OTUs) in the *Qc* litter than in the *Qd* litter (18 OTUs). Six taxonomic orders of microbes were common to both types of litter, and the phylum Basidiomycota was most abundant in the *Qc* litter. The lignin and tannin contents were highest in the *Qc* litter, which also contained diverse fungal taxa associated with POX production. The findings of the present study suggest that the *Quercus* species control the organic nutrient mineralization by determining the composition and activity of the forest floor microbial community.

1. Introduction

The composition of litter in forest ecosystems varies according to plant traits, which influence the physicochemical microenvironment and rates of organic matter decomposition and nutrient cycling (Cornwell et al., 2008). In diverse studies in which litter composition is determined from the C:N ratio, lignin concentration or dissolved organic carbon, rich quality litter (litter with high concentration of labile molecules) has been shown to promote microbial activity and thus bring on higher mass loss and/or mineralization (Aponte et al., 2010; Berrier et al., 2014; Bonanomi et al., 2014; Chávez-Vergara et al., 2014; Osono et al., 2014). Differences in the composition of litter derived from diverse plant species, or even from different genotypes within the same species, contribute to explaining the variable effectiveness of microbial communities in acquire energy and nutrients from litter (Berg and

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Laskowski, 2005; Cornwell et al., 2008; Madritch and Lindroth, 2011; Rinkes et al., 2011; Genung et al., 2013; Berrier et al., 2014).

At local levels, litter decomposition rates are determined by the interaction between the molecular composition of organic residues and the saprophytic microbial community in the forest floor (Cornwell et al., 2008; Duboc et al., 2012; Freschet et al., 2012), as well as the interaction of microbe-microbivore (Bardgett and Wardle, 2010). Microbial activity and the composition of microbial community are both important in the decomposition process (i.e. Aponte et al., 2010; Freschet et al., 2012; Wickings et al., 2012; Koranda et al., 2014). When the composition of plant litter determines the structure and functions of the microbial decomposer community, nutrient cycling is reinforced by plant-trait control at ecosystem level, via a litter-mediated plant-soil feedback mechanism (i.e. Strickland et al., 2009; Miki, 2012). By contrast, in the microbe-mediated plant-soil feedback mechanism, the microbial community can neutralize the plant-trait control over nutrient cycling at ecosystem level (Binkley and Giardina, 1998; Knops et al., 2002; Miki, 2012). Although, both mechanisms are strongly interdependent, the relative importance of which type of plant-soil feedback mechanism dominated is associated with the comparative importance of plant- or microbial-community control in ecosystem functioning, which defines the main drivers of ecosystem resilience.

Fungi constitute a key component of the microbial communities involved in the forest ecosystems functioning, playing a vital role ecosystem dynamics and stability via their participation in the biogeochemical cycles (Morris and Robertson, 2005). Fungi have been recognized as major litter decomposers (Romaní et al., 2006; Jiang et al., 2014; Koranda et al., 2014), because of their ability to produce a wide variety of extracellular hydrolytic and oxidative enzymes that degrade polymers in plant cell walls and nitrogen-rich compounds (Chávez-Vergara et al., 2014; Farrell et al., 2014) and that also release inorganic phosphorous (P) from organic-bounded P (phosphatases) (Berg and McClaugherty, 2008; Sinsabaugh and Follstad, 2011; Hill et al., 2014; Jiang et al., 2014). Additional to the environmental conditions (as pH, temperature, etc.), changes in litter composition during decomposition contribute to modifying the structure and activity of the fungal community (Berg, 2000). Succession of microbial groups on the basis of resources availability is not always clear (Berrier et al., 2014). This can be explained by the continuous depolymerization of recalcitrant polymers to produce low-weight molecular organic compounds (Romaní et al., 2006), which can be used by many microorganisms.

Studies addressing the effect of litter composition on fungal community structure and its metabolic activities have been performed by comparing plant species taxonomically distant and/or functionally different plant species (i.e. Andersson et al., 2004; Šturšová and Baldrian, 2010; Aponte et al., 2014). However, closely related taxonomic and functional plant species can coexist in some forest ecosystems, as already take place in *Quercus* species forests in North America (Cavender-Bares et al., 2004). Several studies have demonstrated that microbial activity is controlled by plant traits (Strickland et al., 2009; Miki, 2012). Moreover, the results of recent molecular analyses have led to an improved description of the soil microbial community (Baldrian et al., 2011a; Saleh-Lakha et al., 2005); however, further studies are required to clarify the relationship between the composition of plant derived organic matter and microbial activity and fungal community composition in forest litter.

The main objective of the present study was to determinate the effect of litter composition on microbial activity and fungal community composition in decomposing forest floor litter in a deciduous oak forest in central Mexico. Our working hypothesis is that the poor quality litter will promote lower microbial C:N and C:P ratios, and a fungal community dominated by highly specialized decomposers of recalcitrant compounds. As a consequence, the nutrient dynamics will mainly be controlled by plant traits at ecosystem levels in a litter-mediated plant-soil feedback mechanism. To test this hypothesis, we examined the relationship between chemical litter composition described in a previous study (Chávez-Vergara et al., 2014) with microbial activity, and also analyzed the molecular composition of fungal communities in different types of forest litter.

2. Methods

2.1. Study site

The study was conducted in the Cuitzeo basin, 11 km south of the city of Morelia (State of Michoacán, Mexico). The semi-natural forest stand under study, affected by a low level of anthropogenic perturbation is located on the slopes of the Remolino Mountain (19° 37′ 01″N; 101° 20′ 07″W). The climate is temperate sub-humid (Cw), with annual mean temperature of 17.6 °C and an annual mean precipitation of 805 mm, concentrated in the summer months. In 2012, the year in which the litter samples were collected, the annual rainfall was 850 mm and the average temperature was 16.4 °C. The dominant soil is *Chromic Luvisol* developed over Quaternary basalts (Chávez-Vergara et al., 2014). The native oaks species present in the study stand are *Quercus castanea* Née (*Qc*; section *Lobatae*) and *Quercus deserticola* Trel. (*Qd*; section *Quercus s.s.*); both are deciduous during the dry season (January to May) and flush leaves early on the rainy season (June). Each oak species dominated at opposite sides of the forest stand under study. The soil under *Q. deserticola* had higher nutrients availability than under *Q. castanea* (Chavéz-Vergara et al., 2015), but the soil water content was similar between both soil conditions (Chávez-Vergara, 2015). Taking this distribution in account, a study plot of 100 m × 150 m was delimited to include both species. Six trees of each species growing along the slope and separated by a distance of 20 m were chosen for sampling. The mean DBH of the selected trees did not differ between the species (*Qc* 52.9 ± 11.7 cm and *Qd* 63.9 ± 11.4 cm; Student's t test, $p = 0.27$). The forest floor litter was not obviously stratified into old and recently materials and the mass of litter at the start of rainy season was calculated to be around 1.8 for *Qc* and 1.4 kg m^{-2} for *Qd* (Chávez-Vergara et al., 2014).

Q. deserticola (*Quercus s.s.* section) litterfall had lower concentrations of recalcitrant and thermostable compounds than the *Q. castanea* (*Lobatae* section) litterfall (Chávez-Vergara et al., 2014). Decomposition of both types of litter followed a similar decomposition trend between May and October, with an increase of around of 20% in the most labile compounds and a decrease of almost 17% in the recalcitrant compounds. The N and P concentrations were higher in the *Q. deserticola* litter than in the *Q. castanea* litter; the C:N and C:P ratios were therefore lower in the *Q. deserticola* litter on both sampling dates. Similarly, the concentrations of dissolved organic forms of carbon (DOC), nitrogen (DON) and phosphorus (DOP), including N and P inorganic forms, were higher in *Q. deserticola* litter than in *Q. castanea* litter. The *Q. castanea* litter appeared to be of poorer quality and to contain fewer nutrients and provide less energy to the microbial community (Chávez-Vergara et al., 2014).

2.2. Forest floor sampling

The sampling area was defined by projecting the canopy of each tree on to the soil. Under each individual canopy, five forest floor