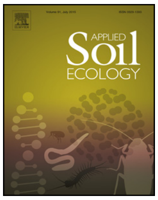
Applied Soil Ecology xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil



Impacts of conversion from secondary forests to larch plantations on the structure and function of microbial communities

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ARTICLE INFO

Article history:
Received 3 March 2016
Received in revised form 26 November 2016
Accepted 30 November 2016
Available online xxx

Keywords:
Forest conversion
Secondary forests
Larch plantations
Microbial community structure
Functional genes

ABSTRACT

In response to increasing timber demands, extensive areas of secondary forests have been converted to larch (*Larix gmelinii*) plantations in northeast China. It has been reported that the conversions have led to reduction in soil organic matter and nutrient availability. Soil microbes play crucial roles in nutrient cycling. However, the effects of forest conversion on soil microbes are not yet well understood in temperate forest ecosystems. In this study, the structure and function of bacterial and fungal communities were compared between larch plantations and adjacent secondary forests relative to surface litter and two soil layers (0–10 cm and 10–20 cm) using Illumina MiSeq sequencing. We found that the impacts of the forest conversion on soil microbes mainly occurred in the top (0–10 cm) soil layer. Soils in secondary forests were associated with a higher proportion of copiotrophic bacteria (Proteobacteria and Actinobacteria). In contrast, larch plantation soil was enriched with Acidobacteria, which are oligotrophs that appear to be well suited to acidic conditions. These differences in soil bacterial communities confirm that the forest conversion resulted in soil acidification and a large decline in available soil nutrient in larch plantations. Furthermore, the results of bacterial functional genes, inferred by PICRUSt, and the results of extracellular enzyme assays indicate that fungi likely dominated soil organic carbon decomposition in forest soils. Sordariomycetes was the most abundant fungal class in soils of secondary forests. The abundance of Sordariomycetes fungi was related to higher levels of almost all enzymes measured, except for cellobiohydrolase and β-1,4-*N*-acetyl-glucosamidase. These two enzymes were positively associated with Agaricomycetes fungi in soils of secondary forests. The fungal community in the soils of larch plantations was dominated by the class Agaricomycetes, which was positively associated with activities of both hydrolytic and oxidative enzymes. These results indicate that fungal classes, Sordariomycetes and Agaricomycetes, are most likely responsible for the decomposition of soil organic matter in secondary forests, while Agaricomycetes fungi might be more important in controlling decomposition in larch plantations.

1. Introduction

Secondary forest is the major forest resource in China, accounting for approximately 62% of all forest cover (Zhu and Liu, 2007). However, the forests are unable to meet the increasing demands for timber. Thus, extensive areas of secondary forests in northeast China have been converted into larch (*Larix gmelinii*) plantations since the 1950s (Mason and Zhu, 2014). With the development of the pure larch plantations, unexpected problems have arisen in these forest ecosystems, including soil acidification and large declines in soil carbon (C) and nitrogen (N) concentration (Liu et al., 1998; Yang et al., 2013). Previous studies show that some possible reasons for soil degradation, after conversion, are the slower decomposition rate of the litter and an imbalance between the input and output of the nutrients (Liu et al., 1998; Yang et al., 2013).

Soil microbes are considered to dominate organic matter decomposition and nutrient cycling in soil (Harris, 2009). However, the contributions of bacteria and fungi to specific ecosystem processes differ. For instance, fungi are thought to dominate the decomposition of complex and recalcitrant plant

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http://dx.doi.org/10.1016/j.apsoil.2016.11.019
0929-1393/

Please cite this article in press as: W. Zhang, et al., Impacts of conversion from secondary forests to larch plantations on the structure and function of microbial communities, Appl. Soil Ecol. (2016), http://dx.doi.org/10.1016/j.apsoil.2016.11.019

litter, particularly lignified cellulose (Schneider et al., 2012). In contrast, contributions of bacteria to lignin and humus decomposition are insignificant, while bacteria are the main drivers of inorganic nitrogen cycling (Boyle et al., 2008; Schneider et al., 2012). Due to the importance of soil microbes providing crucial roles in ecosystem functioning, integrating microbial communities into studies of forest ecosystems would provide much-needed knowledge about nutrient cycling functions in forests.

From a functional perspective, soil enzymes produced by microbes directly mediate C and N cycling in soils. Despite many studies reporting on links between enzyme activities and microbial biomass (Acosta-Martinez et al., 2007; Bossio et al., 2005), there have been contradictory conclusions concerning the contribution of microbial functional groups to the activities of extracellular enzymes (Baldrian, 2008; Phillips et al., 2014; Talbot et al., 2013). Identifying the relative contribution of specific microbial groups to enzyme activities is an important step toward understanding the potential mechanism involved with soil ecological processes.

To date, several studies have attempted to investigate effects of forest conversion on soil microbes in tropical or subtropical areas (Bastias et al., 2007; Curlevski et al., 2010; Vitali et al., 2016; Yu et al., 2012). They demonstrated that conversions from natural forests to plantations altered soil microbial communities and lowered species diversity. Changes in the soil microbial community observed by phospholipid fatty acid analysis (PLFA) show that forest conversion reduces the abundance of fungi, gram-positive bacteria, and gram-negative bacteria (Yu et al., 2012). However, these studies were based on techniques that offered little detail on microbial community composition at the taxonomic level. In addition, little information is thus far available on the effects of forest conversion on the activities and functions of soil microbial communities. A thorough knowledge of forest conversion on microbial community composition and functions in temperate forest soil is needed if we are to elucidate the potential mechanism of the effects of forest conversion on soil ecological processes in managed forest ecosystems.

The aim of this study was to (1) determine the effects of forest conversion from secondary forests to larch plantations on the soil microbial community structure and function and (2) investigate the relative contribution of various microbial groups to C and N cycling in natural and managed temperate forest ecosystems. The study was performed in three paired sites of larch plantation and adjacent secondary forest stands in northeast China. We hypothesized that the changes in aboveground vegetation after the conversion from secondary forests to larch plantations would be accompanied by the development of distinct soil microbial communities, and lead to alterations in functioning of soil microbes, and thus microbial processes.

2. Materials and methods

2.1. Study site and sample collection

The study was conducted at Qingyuan Forest CERN, Chinese Academy of Sciences, located in a mountainous area, Liaoning Province, Northeast China (41°51′ N, 124°54′ E, 500 ~ 1100 m above sea level). This area is characterized by a continental monsoon climate with a windy spring, a warm and humid summer, and a dry and cold winter. Mean annual temperature is 4.7 °C, with the minimum temperature in January (−37.6 °C) and maximum temperature in July (36.5 °C). The frost-free period fluctuates between 120 and 139 days, with an early frost in October and late frost in April. Annual precipitation ranges from 700 to 850 mm, with over 80% falling between June and August. The growing season lasts from early April to late October (Yan et al., 2013; Yang et al., 2013).

Three independent and paired stands of approximately 70-year-old secondary forests and ~40-year-old adjacent larch plantations were randomly chosen from separate watersheds over an area of 100 ha, all with slopes <15° and elevations ranging from 589 to 836 m above sea level (Yang et al., 2013). All the three plantation stands were in their first rotation (Table 1). The soil was a typical brown forest soil, which was classified as Udalfs according to the USDA soil taxonomy (Yang et al., 2013).

A fixed 30 × 30 m plot was randomly selected in each stand of secondary forest and larch plantation, and therefore, total six plots were established for sample collection. Samples were collected during three different periods of the growing season in 2013, i.e., spring (May), summer (August), and autumn (October). Plant litter and soil material were collected separately. Soil samples were divided into 0–10 cm and 10–20 cm layers and the humus was included in the litter layer. Samples were collected from 15 points at each sampled plot and material from the same soil layer was pooled. After removal of visible plant roots and residues, litter material was cut into <0.25 cm^2 pieces and soil material was sieved through a 2-mm mesh. Aliquots for DNA extraction were stored at −20 °C, and at 4 °C for enzyme assays. The remaining samples were then air-dried to determine the chemical properties.

2.2. Soil chemical analysis

All samples were analyzed for total C, total N, and pH. pH values were measured in deionized water (1:20 for litter material and 1:2.5 for soil material, m/v) using a pH meter (Fioretto et al., 2000; McLean, 1982). The samples were analyzed for total C and N content using dry combustion on an elemental analyzer (Vario EL III, Germany).

Table 1
General attributes of the forest stands under study.

Parameter	Secondary forest stands	Larch plantation stands
Dominant tree species	*Acer mono*, *Juglans mandshurica*, *Quercus mongolica*, *Fraxinus rhynchophylla*, *Acer triflorum*	*Larix gmelinii*
Dominant species in the shrub layer	*Acer mono*, *Acer pseudo-sieboldianum*, *Sambucus williamsii*, *Schisandra chinensis*, *Rhamnus davurica*	*Acer mono*, *Euonymus alatus*, *Schisandra chinensis*, *Rhamnus davurica*
Mean stand age (year)	70	40
Mean tree height (m)	13.2	14.5
Diameter at breast height (cm)	14.9	15.9
Tree density (stem hm^{-2})	1021	1490
Total annual litterfall (t hm^{-2})	4.1	2.8
Total forest floor mass (t hm^{-2})	11.8	17.1

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