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Allelochemical-mediated soil microbial community in long-term monospecific Chinese fir forest plantations

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ABSTRACT

Productivity decline of monospecific forest plantations has remained a serious problem. Despite increasing knowledge of the problem involved in the build-up of soil-borne pathogens and allelopathy, relatively little is known about tree-derived allelochemicals and their impacts on the soil microbial community and root growth. Therefore, the objective of this study was to examine a novel allelochemical cyclic dipeptide in relation to the soil microbial community and phytotoxicity to tree roots in 25-year-old monospecific Chinese fir (*Cunninghamia lanceolata*) forest plantations. We sampled soils and fine roots in situ and quantified soil cyclic dipeptide, microbial and root characteristics along with their correlation analyses. When compared with soil from a plantation established following removal of natural forest vegetation, soil from a replanted plantation contained a greater amount of cyclic dipeptide. Furthermore, increased soil potentially pathogenic fungi and reduced root biomass, root surface area and root length density were observed in the replanted plantations. There were negative relationships among cyclic dipeptide concentration, microbial community composition and root biomass in given plantations. Phospholipid fatty acid profiling showed that the signature lipid biomarkers of soil bacteria and fungi, and soil microbial community structure were affected under cyclic dipeptide application. Soil degradation dynamics indicated that cyclic dipeptide declined rapidly. The results demonstrated that allelochemical cyclic dipeptide not only had direct phytotoxicity to tree roots but also indirectly altered soil microbial community compositions, suggesting that productivity decline of continuous Chinese fir monocultures may be a negative feedback interaction between allelochemical-mediated soil microbial community and root phytotoxicity.

1. Introduction

Regeneration failure and productivity decline frequently occur in natural and managed tree ecosystems. In particular, forest plantations usually involve monocultures that cause replant problem or soil disease (Alias et al., 2006; Cavieres et al., 2007; Fernandez et al., 2008). Although the reasons for this problem are still being elucidated, an increasing number of studies have shown that autotoxicity is a major reason for productivity decline of monospecific forest plantations (Zhang, 1997; Alias et al., 2006; Fernandez et al., 2008; Chen et al., 2014). Autotoxicity is a type of intraspecific allelopathy that a plant exhibits to inhibit the growth of other plants of its own species (Singh et al., 1999). This process involves the release of allelochemicals or phytotoxins through litter decomposition and root exudation (Von Kiparski et al., 2007; Badri and Vivanc, 2009; Bonanomi et al., 2011). Once allelochemicals are released into the soil environment, a series of interactions among allelochemicals with soil abiotic and biotic factors take place. Of these interactions, microbial degradation and persistence of allelochemicals are crucially important factors for the action of allelochemicals in soil (Macias et al., 2004; Teasdale et al., 2012; Li et al., 2013). In particular, allelochemical-induced specific alteration in the soil microbial community may result in a positive or negative feedback effect on plant growth and reproduction (Bonanomi et al., 2005; Bezemer et al., 2006; Sun et al., 2014). However, relatively little is known about tree-derived allelochemicals and their impacts on the soil microbial community and root growth in long-term monospecific forest plantations.

Chinese fir (*Cunninghamia lanceolata*) is a native tree species that has been widely planted in China for more than 1000 years, and its planting area covers about 6.5% of all forest plantations in the world (West, 2006). However, the establishment and productivity decline of monospecific Chinese fir forest plantations have remained a serious problem since 1980s in China (Chen et al.,

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2000). Many studies have shown that autotoxicity or intraspecific allelopathy may be responsible for the replant problem (Zhang, 1993; Bi et al., 2007; Chen and Wang, 2013). Recent studies have shown that Chinese fir trees produce and release a novel allelochemical cyclic dipeptide (6-hydroxy-1,3-dimethyl-8-nonadecyl-[1,4]-diazocane-2,5-diketone) into the soil environment, resulting in an autototoxicity (Kong et al., 2008; Chen et al., 2014). Actually, soil nutrient depletion, the build-up of soil-borne pathogens and allelopathy have been advanced as mechanisms for negative soil feedback on plant growth and productivity (Bonanomi et al., 2005; Eppinga et al., 2006). In continuous Chinese fir monocultures, productivity decline defined as negative soil feedback is not diminished by nutrient input (Chen et al., 2000), implying that the negative feedback is more related to allelopathy and soil microorganisms than to soil nutrients.

Roots can respond to changes in their environment, exhibiting alteration in their growth and distribution (Semchenko et al., 2007; Padilla et al., 2013). In particular, the extreme sensitivity of roots to their environment is mediated by the roots' own allelochemicals (Falik et al., 2005). It is thought that the presence of allelochemical cyclic dipeptide in monospecific Chinese fir forest plantations not only has direct phytotoxicity to tree roots but also indirectly alters soil microbial community compositions. Productivity decline of continuous Chinese fir monocultures would likely to be a negative soil feedback interaction between allelochemical-mediated soil microbial community and root phytotoxicity. Accordingly, in the present study, we test specific hypothesis that allelochemical context alters the soil microbial community and root growth in relation to the productivity decline of monospecifc Chinese fir forest plantations. To address this hypothesis, we sampled soils and fine roots in 25-year-old monospecific Chinese fir forest plantations, and then quantified soil cyclic dipeptide, microbial and root characteristics along with their correlation analyses. Furthermore, the changes in the soil microbial community compositions in an incubation experiment involving the addition of the allelochamical at a soil concentration determined in Chinese fir forest plantations were evaluated. Thus, we aimed at further enhancing the understanding of the role of tree-derived allelochemicals in long-term monospecific forest plantations.

2. Materials and methods

2.1. Experimental site and design

This study was conducted at the Huitong Experimental Station of Forest Ecology, Chinese Academy of Sciences, Hunan Province, China (latitude 26°40′–27°09′N and longitude 109°26′–110°08′E). The experimental site has soil (Typic Dystrudept) and typical climate of Southern China. The climate is mid-subtropical with a mean annual air temperature of 16.5 °C and a mean annual precipitation of 1250 mm. The evergreen broadleaf forest native to this region has the main tree species of *Castanopsis fargesii*, *Cyclobalanopsis glauca*, *Juglans cathayensis, Liquidambar formosana*, and *Machilus pauhoi* with shrub layer species of *Camellia oleosa*, *Eurya chinensis*, *Indocalamus tessellates*,*Loropetalum chinensis* and *Rhus semialata*. Herbaceous species are rarely found in this forest system. In 1954 the experimental station was first planted with Chinese fir after clear-cutting and slash-burning practices of the natural forest vegetation.

The experiment had a completely randomized block design with four replications and two treatments imposed in 1986: (1) removal of all natural vegetation of local species followed by a monoculture planting of Chinese fir (1st rotation plantation); and (2) removal of the first-generation Chinese fir trees planted in 1954 followed by a continuous Chinese fir monoculture (2nd rotation plantation). Each of the treatment plot size was about 2.5 ha with a planting density of 2000 stem ha^{-1}. Finally, four 1st rotation plantations and four 2nd rotation plantations were used in this study. Their soils and Chinese fir fine roots were respectively sampled during the 2011 growing season as described below.

2.2. Sampling

Soils were sampled using a soil coring method. Ten soil cores (diameter 4.5 cm) far apart 50 m were collected from each of 8 plantations at 0–20 cm layer with a hand auger. These ten soil cores in each plantation were homogenized and passed through a 2 mm sieve, resulting in a composite soil sample. A total of 8 soil samples from the 1st rotation plantations and the 2nd rotation plantations

Table 1
The chemical and microbial properties of soils from monospecific Chinese fir forest plantations.

Soil parameters	1st rotation plantation	2nd rotation plantation
Total N ($g\,kg^{-1}$)	1.57 ± 0.01	1.42 ± 0.04
NH_4^+-N ($mg\,kg^{-1}$)	16.41 ± 0.66	20.75 ± 4.05
NO_3^--N ($mg\,kg^{-1}$)	4.06 ± 0.35	3.76 ± 0.41
Total P ($mg\,kg^{-1}$)	162.31 ± 3.95*	125.97 ± 6.52
Available P ($mg\,kg^{-1}$)	1.67 ± 0.46	1.68 ± 0.46
Total K ($g\,kg^{-1}$)	9.37 ± 1.94	11.52 ± 1.70
Available K ($mg\,kg^{-1}$)	56.38 ± 6.68	62.82 ± 10.01
Organic matter content ($g\,kg^{-1}$)	29.81 ± 1.34	26.61 ± 1.08
Total phenolics ($mg\,g^{-1}$)	32.39 ± 1.73	34.86 ± 2.36
Allelochemical cyclic dipeptide ($\mu g\,g^{-1}$)	2.66 ± 0.41	5.06 ± 0.84*
Microbial biomass C ($mg\,kg^{-1}$)	193.61 ± 15.04	180.96 ± 10.81
Cultivable microbes ($CFU\,g^{-1}$)		
Bacteria ($\times 10^6$)	2.99 ± 0.20*	1.77 ± 0.64
Fungi ($\times 10^4$)	1.39 ± 0.05	1.93 ± 0.24*
Actinobacteria ($\times 10^4$)	4.15 ± 0.19	4.43 ± 0.14
PLFA concentration ($nmol\,g^{-1}$)		
Total PLFAs	14.42 ± 2.11*	9.40 ± 1.36
Bacteria	6.74 ± 0.59*	4.19 ± 0.21
Gram (+)	2.42 ± 0.17*	1.80 ± 0.08
Gram (−)	3.68 ± 0.65*	2.35 ± 0.37
Fungi	2.95 ± 0.54*	1.45 ± 0.22
Actinobacteria	2.35 ± 0.68	1.95 ± 0.14

* Indicates significantly different at $P < 0.05$.