Tree girdling affects the soil microbial community by modifying resource availability in two subtropical plantations

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ABSTRACT

We used tree girdling and phospholipid fatty acid (PLFA) analysis to evaluate the effect of nutrient availability and rhizodeposition on soil microbial community composition in two plantations (*Acacia crassicarpa* and *Eucalyptus urophylla*) in subtropical China. The magnitude of the girdling effect was also evaluated as a function of tree species and time after girdling (2 months vs. 9 months). In both plantations, tree girdling reduced the concentration of fungal PLFAs and increased the concentration of bacterial PLFAs with a consequent decrease in the fungi/bacteria ratio, but did not affect the concentration of total PLFAs. Tree girdling affected the concentration of gram-negative PLFAs and the ratio of gram-positive bacteria to gram-negative bacteria at 9 months but not at 2 months after girdling. The ratio of cy17:0 to 16:1ω7*c* was increased by girdling of *A. crassicarpa*, indicating a stressful and nutrient-deficient habitat for soil microorganisms, but was inconsistent for girdling of *E. urophylla*. In the *A. crassicarpa* plantation, responses to girdling for most microbial groups were associated with changes in dissolved organic carbon (DOC), dissolved organic nitrogen (DON), the ratio of carbon to nitrogen, and soil pH. In the *E. urophylla* plantation, responses to girdling were associated with changes in DON, DOC, and NO_3^--N. These results confirm that (i) recent photosynthates allocated belowground affect soil C and N availability and therefore greatly affect microbial community composition in subtropical plantations; (ii) the magnitude of the tree girdling effect increases with time after girdling and differs between plant species; and (iii) soil microbial communities are closely linked to vegetation types and plant C allocation.

1. Introduction

Soil microbial communities greatly affect soil organic matter decomposition and soil structure formation, which in turn control many belowground processes critical to ecosystem function (Allison et al., 2007). Among the many edaphic, climatic, and environmental factors that influence microbial community composition, soil pH, and carbon (C) and nitrogen (N) availability are especially important (Bossio and Scow, 1998; Drenovsky et al., 2004; Fierer and Jackson, 2006). For example, both the relative concentration and diversity of bacteria are positively related to pH (Fierer and Jackson, 2006; Rousk et al., 2010), and fungi use substrates with larger C/N ratios than bacteria (Sterner and Elser, 2002). Identifying the factors that control microbial community composition and dynamics may improve our understanding of biogeochemical processes (Keith-Roach et al., 2002), food web dynamics (Laakso et al., 2000; Schmidt et al., 2000), and overall soil quality (Calderon et al., 2001; Yao et al., 2000). However, the mechanisms responsible for changes in microbial community composition have been difficult to untangle because soil variables are highly correlated.

Photosynthates recently shaped by plants and released by their roots in the form of rhizodeposition are a major source of C for soil microbes and shape the composition of the microbial community in the rhizosphere (Fu and Cheng, 2004; Priha et al., 2001; Rajaniemi and Allison, 2009; Yarwood et al., 2009). Microbial decomposition processes in soil are highly sensitive to the availability of labile C and N (Rasche et al., 2010). The physical, chemical, and biological properties of root-associated soil result in greater microbial activity in the rhizosphere than in the bulk soil (Bardgett et al., 1998; Wardle et al., 2004). Root exudates and decaying plant material provide C that is used by heterotrophic soil organisms as a source of energy and structural material (Barea et al., 2005; Kuzyakov and Cheng, 2001). In turn, microbial activity in the rhizosphere affects root branching patterns and controls the supply of nutrients available to plants, thereby modifying the quality and quantity of root exudates (Bowen and Rovira, 1999).

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Tree girdling is a tool used to stop rhizodeposition and to thereby measure the effect of tree rhizodeposition on the microbial community (Scott-Denton et al., 2006). Tree girdling is also used to control non-commercial trees in tropical forests (Ohlson-Kiehn et al., 2006) and to clear savannas of invasive brush and trees (Czarapata, 2005). Tree girdling, in which the bark and phloem are removed down to the youngest xylem, is useful as a research tool because it stops rhizodeposition without mechanically disturbing the soil–root–microbe system (Bhupinderpal-Singh et al., 2003; Chen et al., 2009, 2010, 2011; Dannenmann et al., 2009; Göttlicher et al., 2006; Högberg et al., 2001; Kaiser et al., 2010; Rasche et al., 2010; Scott-Denton et al., 2006; Subke et al., 2004; Weintraub et al., 2007; Yarwood et al., 2009). In a large-scale study in a boreal forest, tree girdling reduced the number and biomass of fruiting bodies of ectomycorrhizal (ECM) fungi in soil to almost zero after 2 months but did not affect the number or biomass of saprotrophic fungi (Högberg et al., 2001, 2007). In a 4-year tree-girdling experiment in a boreal Scots pine forest, tree girdling significantly altered fungal and bacterial communities (Yarwood et al., 2009). It is thus likely that girdling-related changes in soil chemistry, and especially in labile C and N pools, have considerable effects on the soil microbial community structure (Dannenmann et al., 2009; Högberg et al., 2007; Kaiser et al., 2010; Rasche et al., 2010; Weintraub et al., 2007). Weintraub et al. (2007) measured reduced quantities of dissolved organic C and N as well as an increase over time in nitrate and ammonium in girdled plots of a subalpine forest. Högberg et al. (2007) observed a tendency towards increased inorganic N levels in girdled plots of a boreal forest, whereas Ekberg et al. (2007) detected a decrease in total organic C in girdled plots of a temperate spruce stand.

One possible indicator of change in substrate availability is the ratio of cyclopropyl to cyclopropyl precursor (e.g., cy17:0/16:1ω7c) in microbial cell membranes. An increase in this ratio has been used as an indicator of microbial stress caused by insufficient substrate availability (Bossio and Scow, 1998; Feng and Simpson, 2009), anaerobic conditions (Kieft et al., 1997), and water limitations (Moore-Kucera and Dick, 2008). A lower cy17:0/16:1ω7c ratio has been related to higher substrate availability, an increase in bacterial growth rates, and a decrease in carbon limitation (Bååth et al., 1995; Bossio and Scow, 1998). As indicated above, links between responses of microbial stress indicators and the availability of substrates supporting microbial growth have been examined in only a few studies (Feng and Simpson, 2009).

Although previous studies have used tree girdling to determine how soil microbial communities are influenced by C and N availability resulting from rhizodeposition (Kaiser et al., 2010; Rasche et al., 2010; Yarwood et al., 2009), to the best of our knowledge none of these considered the effects of girdling different tree species or were conducted in subtropical plantations. In the current study, we assessed how tree girdling alters microbial community composition in two plantations in southern China. One plantation was planted with *Acacia crassicarpa* and the other with *Eucalyptus urophylla*. Both are fast-growing and major subtropical tree species that are commonly used for pulpwood production because of their high productivity and short rotations. These two tree species respond differently to tree girdling; most importantly for our purposes, the biomass of living fine roots was reduced by 94% for *A. crassicarpa* but by only 18% for *E. urophylla* 6 months after tree girdling (Chen et al., 2010, 2011). This suggests that for at least 6 months after girdling, rhizodeposition is substantial for *E. urophylla* but not for *A. crassicarpa*. Thus, we hypothesized that the magnitude of the tree girdling effect on microbial community composition would depend on both the tree species and soil properties. The two main objectives of this study were: (i) to quantify the effects of tree girdling on C and N availability and soil microbial community composition for the two plantations at different times after girdling; and (ii) to determine whether changes in soil microbial community composition are correlated with changes in C and N availability and other soil properties induced by tree girdling.

2. Materials and methods

2.1. Site description

The study was conducted in *A. crassicarpa* and *E. urophylla* mono-specific plantations at the Heshan Hilly Land Interdisciplinary Experimental Station (112°50′E, 22°34′N), Chinese Academy of Sciences (CAS). The field station is located in Heshan County, Guangdong Province, which is a hilly region with laterite soils and a subtropical monsoon climate. The mean annual precipitation between 1984 and 2006 was 1295 mm. About 80% of the precipitation falls during the wet season, between March and September. The mean annual temperature at the site is 21.7 °C. The tree plantations used in this study were established in 2005, with *A. crassicarpa* and *E. urophylla* saplings planted at 3 m × 2 m spacing. Each plantation occupies an area of 50 ha. In January 2008, the average height and diameter at breast height were about 6.3 m and 6.4 cm for *A. crassicarpa* and about 11.9 m and 9.1 cm for *E. urophylla*.

2.2. Tree girdling treatment

The girdling treatments are described in detail in Chen et al. (2010), who conducted a study with the same plots. Briefly, in each *A. crassicarpa* and *E. urophylla* plantation, six plots (10 m × 10 m each) were established, and understory vegetation was mowed in January 2007. Three of the six plots were used as girdling plots and the other three were used as controls in a completely randomized design. The girdling treatment was applied to all trees for each girdling plot. Each plot contained about 20 trees. All plots were trenched to 50 cm before girdling to avoid root encroachment from outside. For girdling, 10 cm of bark and cambium were removed over the entire circumference of the stem at about 1 m height on 11 February 2007. The two plant species respond differently to tree girdling: *A. crassicarpa*, which belongs to the Leguminosae, resprouts (the ability of growing new branches under the girdled wound) only weakly after girdling, while *E. urophylla* resprouts vigorously after girdling (Fig. 1). Leaves of *A. crassicarpa* started to fall 3 months after girdling, and no leaves remained on the plants 5 months after girdling; leaf litter was removed periodically so that it did not accumulate on the soil surface. In contrast, *E. urophylla* leaves did not fall until 7 months after girdling, and 70% of the trees were still alive 1 year after girdling.

2.3. Soil sampling and analysis

Soils were sampled on 19 April and 28 November 2007. Four soil cores (3 cm in diameter and 20 cm depth) were taken at an even distance between two neighboring girdled trees, and the soil cores were mixed to obtain a composite soil sample. For each plot, five composite soil samples were collected. We determined soil microbial biomass C (C_{mic}) and soil microbial biomass N (N_{mic}) using chloroform fumigation–extraction (Brookes et al., 1985; Vance et al., 1987). Briefly, a 20-g subsample of field-moist soil was used for the fumigation and non-fumigation treatments. The filtered soil K_2SO_4-extracts of both fumigated and non-fumigated samples were analyzed for dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) using a total organic carbon analyzer (Shimadzu TOC-VCPH). Soil microbial biomass C (C_{mic}) and soil microbial biomass N (N_{mic}) were calculated as follows: C_{mic} (or N_{mic}) = 2.22 × E (Wu et al., 1990), where E is the quantity of carbon (or nitrogen) extracted from fumigated soil minus the quantity of carbon (or nitrogen) extracted from non-fumigated soil. The