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Response of soil nematode communities to tree girdling in a subtropical evergreen broad-leaved forest of southwest China

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ABSTRACT

The impact of canopy photosynthates on soil microbial biomass and nematode trophic groups was studied in a subtropical evergreen broad-leaved forest by performing a large-scale tree girdling experiment. Total fungal biomass was unaffected by tree girdling. Bacterial biomass differed significantly between the girdled and control plots in the mineral soil, but was not affected by girdling treatment in the humus layer. Girdling reduced total nematode density in the humus layer. The reduced fungivorous nematode density in girdled plots in the humus layer suggested a modified energy flow through the fungal based pathways. There were no differences in the abundance of bacterial-feeding, herbivorous and omnivorous-predatory nematodes between the girdled and control plots in both humus and mineral soil layers. This study provides direct evidence that the termination of belowground photosynthate-C allocation achieved by tree girdling affects soil nematodes, and that different trophic groups vary in their responses to the reduction of C efflux into the soil.

1. Introduction

Terrestrial ecosystems are sustained by photosynthetic fixation of carbon above-ground. Over the past decades, studies on the importance of carbon input from above- and below-ground to soil communities have received great attention (Hättenschwiler et al., 2005). Recent studies showed that plant carbon can flow through soil food-webs at a rapid rate (Albers et al., 2006; Ostle et al., 2007; Pollierer et al., 2007). Plants transfer photosynthate-C to rhizosphere soil via living roots as exudates, mucilages and sloughed off cells, jointly called rhizodeposition (Johansson, 1992). This rhizodeposited C has been suggested as another important driver of soil decomposer communities in addition to the much slower fluxes of carbon arising from the decomposition of shoots and root-derived litter (Högberg and Read, 2006). However, neither the magnitude nor the mechanisms of the supply of canopy photosynthate to soil biota has been fully appreciated, particularly in forest ecosystems, because of the size of the plants and the great spatial heterogeneity of the soils (Mikola and Kytöviita, 2002; Högberg and Read, 2006; Göttlicher et al., 2006).

Tracking the incorporation of current assimilated C into soil organisms through plant roots is difficult under natural soil conditions. In grassland ecosystems, defoliation and herbivores grazing were found to affect the amount of rhizodeposition and subsequently altered soil biota dynamics (Mikola and Kytöviita, 2002; Christensen et al., 2007). However, the effects of defoliation and herbivory on plant C allocation may differ among plant species by either increasing or decreasing the allocation of current assimilates to roots and root exudation (Holland et al., 1996; Wilsey et al., 1997). Carbon-based isotopic labeling techniques have been applied effectively to characterize the pathway of photosynthetically fixed C (Johnson et al., 2002; Leake et al., 2006; Ostle et al., 2007), but these techniques are generally applied in artificial growing environments or grassland/agro-ecosystems (Pollierer et al., 2007). Root exclusion by trenching is a commonly used method in forest ecosystems to suppress the energy link between trees and the soil systems and has been used to assess the photosynthesis controls on soil microbial and faunal communities (Simard et al., 1997; Siira-Pietikäinen et al., 2001; Brant et al., 2006). However, this method destructively disturbs soils and terminates the process of plant uptake of water and nutrients.

In recent years, a number of studies have investigated the effects of eliminating photosynthate translocation to belowground on soil processes by physical girdling of trees. Tree girdling instantaneously terminates the flux of photosynthates from tree canopy through the phloem to tree roots, while there is minimal immediate disturbance to the soil and roots (Högberg et al., 2001). Studies from Åheden and Flakaliden in Sweden (e.g. Högberg et al.,

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2001; Bhupinderpal-Singh et al., 2003; Giesler et al., 2007), Wetzstein of Germany (Subke et al., 2004; Hahn et al., 2006; Ekberg et al., 2007), Bahia of Brazil (Binkley et al., 2006), Pura of Switzerland (Frey et al., 2006), North Carolina of USA (Johnsen et al., 2007) have clearly shown that as much as half of the soil respiration was reduced after large-scale tree girdling, which is interpreted as a disruptive effect of girdling on root respiration and ectomycorrhizal activities. However, whether and how tree girdling affects the composition of soil organisms at multiple trophic levels of soil biota remains mostly unexplored. Schulze et al. (2005) reported a post-girdling reduction in the numbers of proteins by 50% based on indirect proteomic fingerprint evidence, which implied that the current photosynthates allocated belowground may influence different soil taxonomic groups (Högberg and Read, 2006).

Among soil biota, nematodes possess attributes that are useful to reflect the responses of multi-trophic level soil organisms on tree girdling. Nematodes are one of the most abundant groups of soil inhabitants and react quickly to environmental changes (Bongers and Ferris, 1999). Furthermore, nematodes appear in a wide array of trophic groups (herbivores, bacterivores, fungivores, omnivore-predators) reflecting the current or recent availability of their C sources, and their abundance is assumed to mirror that of other important consumers in soil (De Deyn et al., 2004). Hence nematodes may be expected to respond both directly to changes in plant carbon allocation to the belowground environment, and indirectly to changes in microbial communities that respond directly to plant carbon inputs (Neher et al., 2004).

In this study, we examined the impact of photosynthates on soil nematodes at different trophic levels of an evergreen broad-leaved forest of southwest China. We performed a large-scale tree girdling experiment and analyzed the changes of soil microbial biomass and nematode community structure. We hypothesized that the decreased C allocation to belowground induced by tree-girdling will affect soil microbial biomass and nematode trophic groups: (i) as primary consumers, the bacterial biomass will decrease after girdling due to the decreased root exudates in soils, the biomass of fungi will decrease after girdling because of the direct elimination of the root-mycorrhizal network, and the abundance of herbivorous nematodes are expected to decrease because they also strongly depend on current assimilates belowground; (ii) as secondary consumers, bacterivores and fungivores will decrease in abundance when the plants respond to girdling by decreasing exudation of labile substrates and the microbial activities are suppressed after girdling; (iii) as tertiary (and higher) consumers, omnivorous and predacious nematodes are expected to be the least responsive to girdling due to their high hierarchical position in the food web, but their abundance will also decrease if the abundance of lower trophic level groups decreases. The above hypotheses are based on the fact that girdling can prevent the translocation of photosynthate-C from tree canopy to the roots and decrease the input of root exudation to the soil (Högberg et al., 2001), though several researchers have suggested that the roots in the girdled plots eventually die being an input of resources for decomposers (Högberg et al., 2001; Högberg and Högberg, 2002; Binkley et al., 2006).

2. Materials and methods

2.1. Site description and experimental design

The study was conducted in a subtropical evergreen broad-leaved forest in Xujiaba (24°32′ N, 101°01′ E; altitude 2476 m above sea level) which is located at the Ailao Mountains in southwestern China. The soil is acidic yellow-brown loam (pH 4.2–4.5) with a humus layer of 7–12 cm in thickness (Chan et al., 2006). The organic carbon content, nutrient content and exchangeable cations are higher in the humus layer than in the mineral soil (Chan et al., 2006). The mean annual temperature and precipitation are 11.3 °C and 1840 mm, respectively. Precipitation shows a strong seasonal variation with a rainy season from May to October and a dry season from November to April. The trees in the study site have an average diameter of 12 cm at breast height, an average height of 25 m and a density of 2728 trees/hm^2 (Chen et al., 2006). Major overstory species include *Lithocarpus chintungensis*, *Rhododendron leptothirium*, *Vaccinium duclouxii*, *L. xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis*, *Manglietia insignis*, *Machilus viridis*, *Eriobtrya bengalensis*, *L. hipoviridex*, *Illiccium macranthum*, and *Ilex* sp., etc. Understory vegetation is dominated by a bamboo *Sinarundinaria nitida*.

Eight quadrate plots (20 × 20 m) were established in early February 2004. To prevent ingrowth of external roots, each plot was trenched along the four sides to a depth of 40 cm and plastic sheets were buried into the soil. For randomly selected four plots, all the trees (>2 cm in diameter) were girdled by removing a 5–10 cm length of bark and phloem around the circumferences of the stems at a height of 1.5 m above the ground on the 10th and 11th of February. Other four plots were left ungirdled as controls.

2.2. Soil sampling and analyses

Within each of the eight plots, one subplot of 2 × 3 m in size was designed for soil sampling. Soil samples were collected on 15 February, 15 April, 20 June, 18 August and 7 December of 2004, and 3 March of 2005, corresponding to 4, 63, 129, 188, 299 and 388 days after girdling treatment. In each subplot, one humus sample and one mineral soil sample were collected. We collected humus samples using a wooden frame (20 × 20 cm). Mineral soils were collected to a depth of 10 cm using a core sampler of 5 cm in diameter. Each humus or mineral soil sample was then divided into three subsamples. One subsample (ca. 5 g) was used for soil microbial analysis, the second one (ca. 20 g) for measuring soil water content, and the third (ca. 50–100 g) for nematode community analysis. Total fungal biomass was estimated by measuring the length and diameter of hyphae using the agar film technique (Lodge and Ingham, 1991). The Fungal biovolume was converted to biomass C by assuming a hyphal density of 0.33 g (dry weight)/cm^3 and 47% C content (Van Veen and Paul, 1979). Total bacterial biomass was determined by counting the numbers and measuring the diameters of bacteria stained with fluroscein isothiocyanate (FITC) (Babiuk and Paul, 1970). The conversion of bacterial cell counts to biomass C was made by a cell density of 0.3 g (dry weight)/cm^3, and 45% C content (Van Veen and Paul, 1979). Nematodes were extracted by flotation in Ludox™ (Griffiths et al., 1990). Nematodes were counted under a dissecting microscope and their densities were expressed as number of individuals per 10 g dry soil. After counting the total number of individuals, nematode specimens were slowly dehydrated in glycerol and prepared on slides. About 100 specimens per sample were randomly selected and identified to genus, and classified into four functional groups representing three trophic levels in the soil food web (Yeates et al., 1993): primary consumers (herbivores), secondary consumers (fungivores and bacterivores) and tertiary consumers (omnivore-predators). Daily averages of soil temperature and volumetric water content at 10-cm soil depth were automatically monitored with data loggers during the experimental period.

For soil temperature, soil water content, microbial and nematode variables (including biomass and abundance data), repeated measure analysis of variance was used to test for the effects of girdling treatment and sampling time. When the effects were significant, multiple comparisons were made based on least square means. Significance levels were set at alpha < 0.05. To meet assumptions of normality and homogeneity of variance, the