

## 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.

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### 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<sup>2</sup> (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*, *Eriobrya bengalensis*, *L. hipoviridex*, *Illicium macranthum*, and *Ilex* sp., etc. Understory vegetation is dominated by a bamboo *Sinarundinaria nitida*.

Eight quadrat 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 un-girdled 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<sup>3</sup> 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 fluorescein 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<sup>3</sup>, 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

biomass and abundance data were arcsine, square root or  $\log_{10}(x + 1)$  transformed if necessary.

### 3. Results

Soil temperature was highest in August and June 2004 and lowest in March 2005 (Fig. 1a). During the experimental period, soil temperature was not significantly affected by girdling (repeated measure ANOVA:  $F = 0.195$ ,  $P = 0.677$ ). Soil water content was highest during the period from April to August 2004 and lowest in winter and early spring (Fig. 1b). Although the soil water content tended to be lower in the plots with girdled trees, it did not differ significantly between the girdled and control plots (repeated measure ANOVA:  $F = 1.304$ ,  $P = 0.305$ ).

Mean fungal biomass ranged between 312.5 and 822.3  $\mu\text{g C/g}$  dry soil in the humus layer (Fig. 2a) and between 163.9 and 420.6  $\mu\text{g C/g}$  dry soil in the mineral soil (Fig. 2b) across all samples. Fungal biomass was not significantly affected by girdling in both humus and mineral soil layers (Table 1). Mean bacterial biomass in the humus layer exhibited a similar temporal fluctuation pattern as that in the mineral soil (Fig. 2c,d), and ranged from 179.0 to 555.1  $\mu\text{g C/g}$  dry soil in the humus layer over the entire experiments and from 157.3 to 339.6  $\mu\text{g C/g}$  dry soil in the mineral soil. In the mineral soil, bacterial biomass differed significantly between the girdled and control plots, but was not significantly affected by girdling treatment in the humus layer (Table 1).

A total of 58 nematode genera were found for all the collected samples (Supplementary Table 1). Total nematode density averaged

751–2285 individuals/10 g dry soil in the humus layer and 266–1500 individuals/10 g dry soil in the mineral soil across all samples (Fig. 3a,b), showing significant time effects in both layers. In the humus layer, girdling caused a significant decrease in total nematode density (Table 1), up to 46% reduction in girdled plots compared to control plots at the end of the experiment (Fig. 3a). In the mineral soil, the reduction of total nematode density resulted from girdling treatment was not significant (repeated measure ANOVA:  $F = 2.867$ ,  $P = 0.141$ ) (Fig. 3b).

Responses of soil nematodes to girdling treatment varied among different trophic groups (Fig. 3). Herbivore density was unaffected by girdling treatment in both mineral and humus layers. The density of fungivores in the humus layer was significantly affected by girdling (repeated measure ANOVA:  $F = 12.706$ ,  $P = 0.012$ ). In the mineral soil, the fungivore density of the girdled plots was lower than that of the control plots, but the difference was modest (repeated measure ANOVA:  $F = 5.188$ ,  $P = 0.063$ ). Density of bacterivores and omnivore-predators were unaffected by girdling in both soil layers.

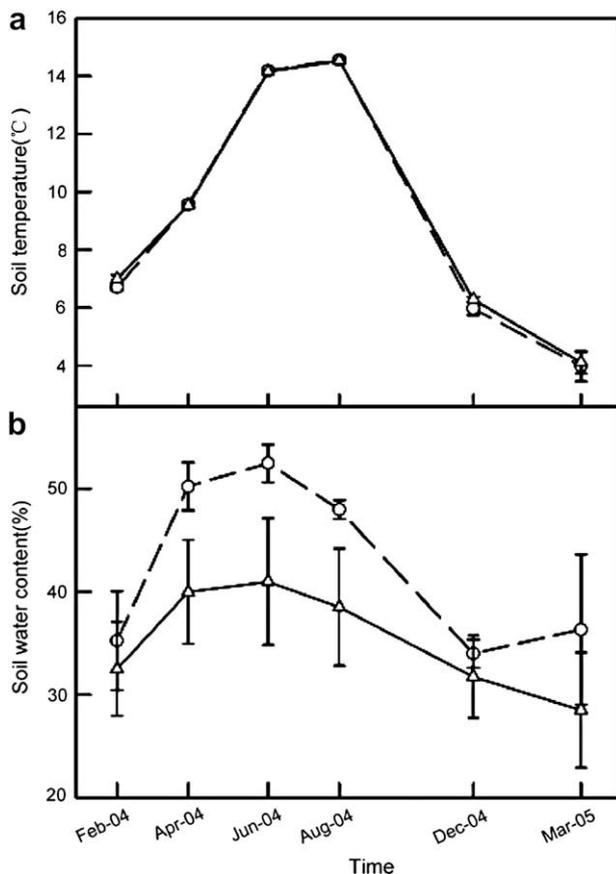
### 4. Discussion

#### 4.1. Influences of tree girdling on fungi and fungivorous nematodes

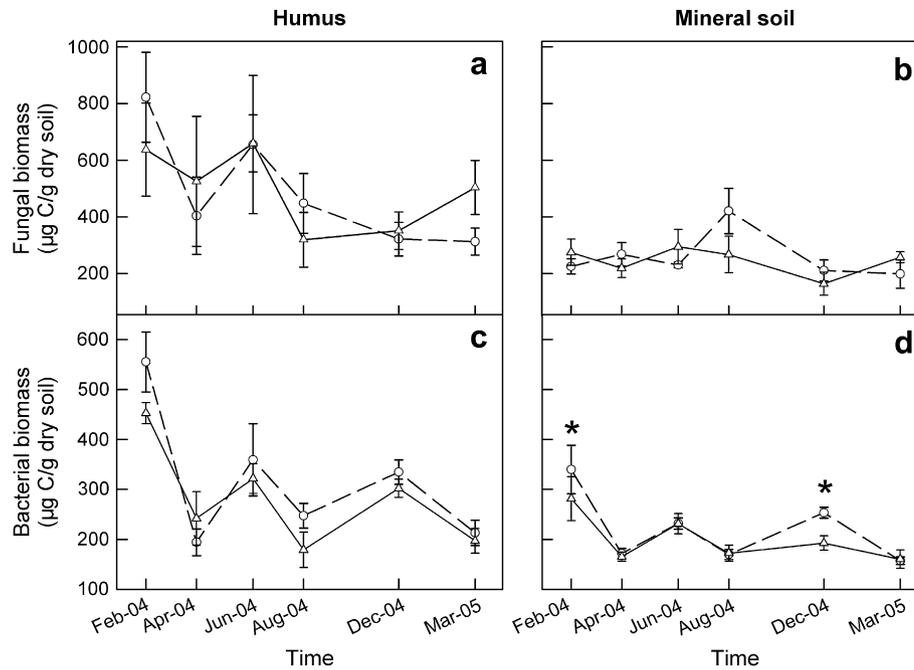
Girdling terminates the direct flow of photosynthate-C to roots and soil systems and should have negative effects on mycorrhizal fungi which receive carbon in the form of photosynthates directly from host plants (Högberg et al., 2001; Högberg and Read, 2006). The girdling-induced reductions in mycorrhizal fungi biomass have been confirmed by many previous studies (Högberg et al., 2001, 2007; Högberg and Högberg, 2002; Högberg, 2006). The reduced mycorrhizal biomass is supposed to result in a subsequent decrease in the total fungal biomass, though the numbers of saprotrophic fungi may remain unchanged in the girdled relative to the control plots (Subke et al., 2004; Högberg et al., 2001, 2007). Such a decline of total fungal biomass in girdled plots was not detected in our study by means of direct measurements; however, decreased numbers of fungivorous nematodes possibly reflected a decreased fungal activity or fungal reproduction especially in the humus layer. Since the biomass of microbivores has been suggested to reflect the variations in rhizodeposition more sensitively than the microorganisms themselves (Christensen et al., 2007), the reduced abundances of fungivorous nematodes in the girdled plots suggest a decreased allocation of C flowing through the fungal-mediated energy pathway.

#### 4.2. Influences of tree girdling on bacteria and bacterivorous nematodes

In the humus layer, the bacterial biomass was found unaffected by tree girdling in our study. This result is consistent with other girdling experiments where bacterial abundance was not responsive to tree girdling (Högberg et al., 2007). Other carbon input manipulation experiments such as root exclusion and aboveground insect herbivory also yielded similar results that bacterial biomass weakly correlates with plant rhizodeposition (Siira-Pietikäinen et al., 2001, 2003; Brant et al., 2006; Christensen et al., 2007). Although changes in bacterial populations were generally not detected, some studies have revealed a tight coupling between the carbon transport belowground and the population size of bacterivorous microfauna such as protozoa or nematodes (Neher et al., 2004; Allen et al., 2005). In this study, however, the abundance of bacterivorous nematodes was unaffected by girdling treatment, though the bacterial biomass in mineral soil of the girdled plots significantly decreased. This unchanged bacterivorous nematode



**Fig. 1.** Soil temperature (a) and moisture (b) in the mineral soil layer of control (circles with dashed line) and girdled plots (triangles with solid line) during the experimental period between February 2004 and March 2005. Bars indicate standard errors of means.



**Fig. 2.** Fungal and bacterial biomass of control (circles with dashed line) and girdled plots (triangles with solid line) in humus and mineral soil layers during the experimental period between February 2004 and March 2005. (a) Fungal biomass in humus; (b) fungal biomass in mineral soil; (c) bacterial biomass in humus; (d) bacterial biomass in mineral soil. Bars indicate standard errors of means. Asterisks indicate significant difference ( $P < 0.05$ ) between treatments.

populations after girdling might suggest a relatively unchanged energy flow through the bacterial-mediated pathway.

#### 4.3. Influences of tree girdling on herbivorous nematodes

Belowground herbivores feed on roots and rely on root carbohydrates. Girdling blocked the phloem flux of photosynthate-C from the tree canopies to the roots and is supposed to reduce the populations of herbivorous nematodes. Contrary to our hypothesis, the abundance of herbivorous nematodes which were dominated by ectoparasitic species such as *Criconema* and *Ogma*, did not significantly differ between girdled and control plots.

#### 4.4. Implications from the tree girdling influences

Application of proteomic analysis revealed a dramatic post-girdling reduction in the numbers of proteins at Wetzstein,

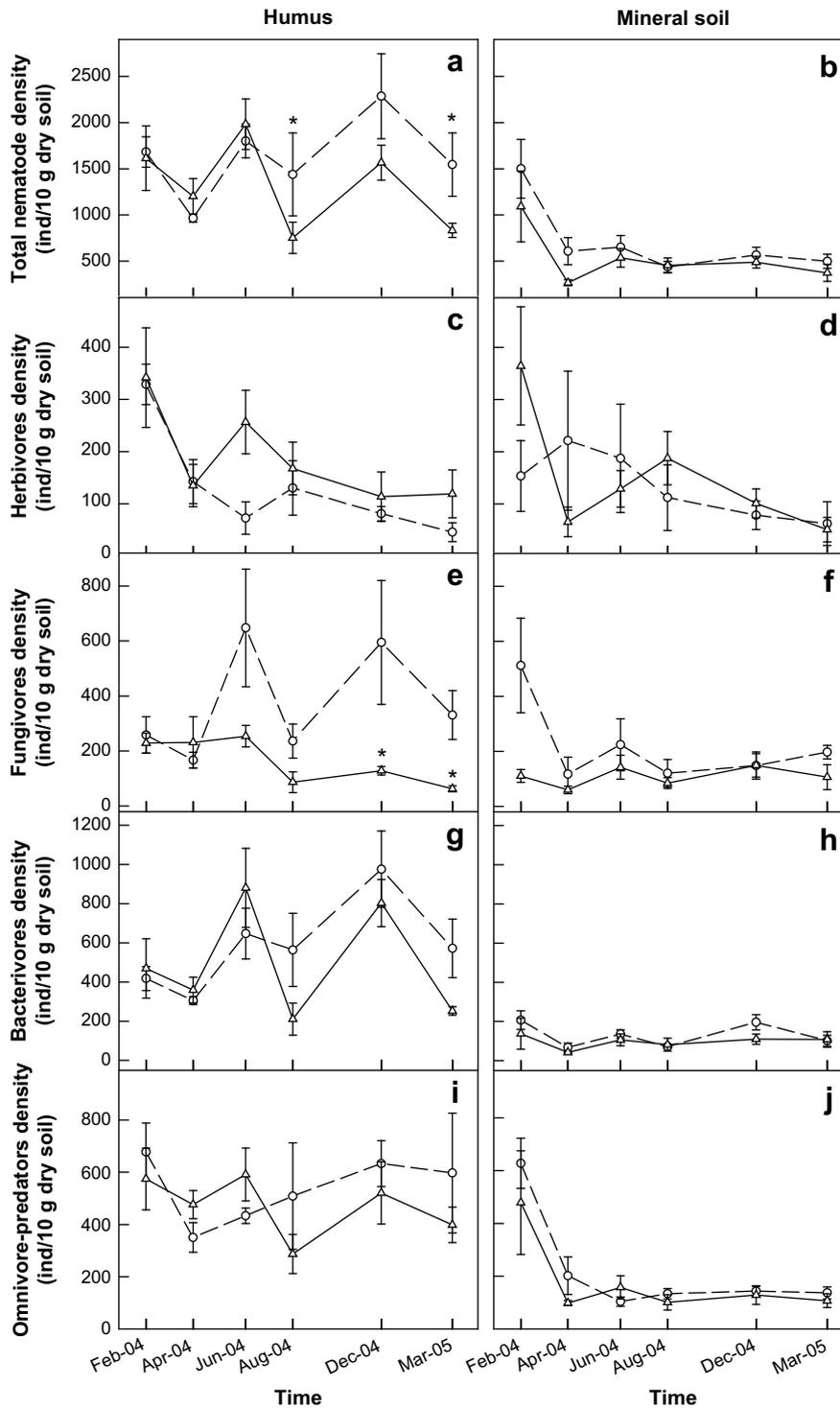
indicating a decreased abundance of most soil organisms in girdled plots (Schulze et al., 2005). Using isotopic labeling methods, Albers et al. (2006), Ostle et al. (2007) and Pollierer et al. (2007) demonstrated that the root-derived C was incorporated into virtually all decomposer animals such as mites, collembolans, earthworms, enchytraeids and isopods in the arable, grassland and forest soils. Consistent with these findings, our study shows that the termination of the belowground C supply by tree girdling leads to a prominent decrease in the abundance of total soil nematodes which is statistically significant in the humus layer. This result supports the recent views that forest soil animals can acquire carbon from belowground via roots (Pollierer et al., 2007).

Tree girdling is generally conducted to separate soil autotrophic (mycorrhizal root) from heterotrophic respirations without physical disturbing soils, because it is considered to stop the autotrophic respiration while the heterotrophic respiration remains unchanged for a short period of time (Högberg et al., 2001; Binkley et al., 2006).

**Table 1**  
Effects of girdling treatment and sampling time on soil microbial biomass and nematode densities tested by repeated ANOVA.

Dependent variable	Error df	Treatment (1 df)	Time (5 df)	Treatment × Time (5 df)
<b>Humus</b>				
Fungal biomass	30	0.017 (0.901)	<b>3.299 (0.017)</b>	0.741 (0.599)
Bacterial biomass	30	0.750 (0.420)	<b>26.995 (&lt;0.001)</b>	1.309 (0.287)
Total nematode density	30	<b>7.352 (0.035)</b>	<b>4.798 (0.002)</b>	1.418 (0.246)
Herbivorous nematodes density	30	3.166 (0.126)	<b>5.899 (&lt;0.001)</b>	1.260 (0.307)
Fungivorous nematodes density	30	<b>12.706 (0.012)</b>	<b>5.083 (0.002)</b>	<b>3.630 (0.011)</b>
Bacterivorous nematodes density	30	2.258 (0.184)	<b>6.687 (&lt;0.001)</b>	1.907 (0.123)
Omnivorous-predatory nematodes density	30	1.034 (0.348)	1.329 (0.279)	0.874 (0.510)
<b>Mineral soil</b>				
Fungal biomass	30	0.088 (0.777)	<b>3.135 (0.022)</b>	2.227 (0.078)
Bacterial biomass	30	<b>6.952 (0.039)</b>	<b>12.388 (&lt;0.001)</b>	0.816 (0.548)
Total nematode density	30	2.867 (0.141)	<b>8.306 (&lt;0.001)</b>	0.900 (0.494)
Herbivorous nematodes density	30	0.227 (0.651)	<b>2.590 (0.046)</b>	1.597 (0.191)
Fungivorous nematodes density	30	5.188 (0.063)	<b>2.634 (0.043)</b>	1.637 (0.181)
Bacterivorous nematodes density	30	1.559 (0.258)	<b>3.673 (0.010)</b>	0.660 (0.656)
Omnivorous-predatory nematodes density	30	1.242 (0.308)	<b>15.738 (&lt;0.001)</b>	0.970 (0.453)

Shown are *F*-values with significance levels in parentheses. Significant effects ( $P < 0.05$ ) are indicated in bold.



**Fig. 3.** Densities of total nematodes and different nematode trophic groups of control (circles with dashed line) and girdled plots (triangles with solid line) in humus and mineral soil layers during the experimental period between February 2004 and March 2005. (a) Total nematode density in humus; (b) total nematode density in mineral soil; (c) herbivores density in humus; (d) herbivores density in mineral soil; (e) fungivores density in humus; (f) fungivores density in mineral soil; (g) bacterivores density in humus; (h) bacterivores density in mineral soil; (i) omnivore-predators density in humus; (j) omnivore-predators density in mineral soil. Bars indicate standard errors of means. Asterisks indicate significant difference ( $P < 0.05$ ) between treatments.

This study provides direct evidence that tree girdling also affected soil faunal groups, and that soil organisms of different trophic groups varied in their responses to tree girdling. Thus, we agree with [Bhupinderpal-Singh et al. \(2003\)](#) and [Subke et al. \(2004\)](#) that the reported values for “soil autotrophic respiration” inferred from forest girdling experiments should be understood as

“root mediated” respiration rather than the contributions of mycorrhizal root only.

The main effects of girdling on soil nematode communities were generally observed in the humus layer rather than the mineral soil layer. This is probably because of the greater biomass of fungal hyphae in the upper soil layers. In a trenching experiment,

Siira-Pietikäinen et al., 2003 also found that the significant responses of microbes only occurred in the humus layer not in the mineral soil layer. This may imply that the photosynthetically active C was mainly distributed to the humus layers.

The treatment induced change in soil nematode communities was detectable during the study period; however, it was generally weaker than expected. It probably reveals only partial effects of girdling treatments in the studied forest because of the large storage of carbohydrates in roots and stems (Qiao, personal communication). Greater differences in certain nematode ecological parameters between treatments were observed at the end of the experiment than those at the early stages of the study. Therefore, longer-term studies would probably show more pronounced girdling effects on soil communities.

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### Appendix. Supplementary information

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.soilbio.2008.07.031.

### References

- Albers, D., Schaefer, M., Scheu, A., 2006. Incorporation of plant carbon into the soil animal food web of an arable system. *Ecology* 87, 235–245.
- Allen, M.F., Klironomos, J.N., Treseder, K.K., Oechel, W.C., 2005. Responses of soil biota to elevated CO<sub>2</sub> in a chaparral ecosystem. *Ecological Applications* 15, 1701–1711.
- Babiuk, L.A., Paul, E.A., 1970. The use of fluorescein isothiocyanate in the determination of the bacterial biomass of grassland soil. *Canadian Journal of Microbiology* 16, 57–62.
- Bhupinderpal-Singh, Nordgren, A., Löfvenius, M.O., Högborg, M.N., Mellander, P.E., Högborg, P., 2003. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant, Cell and Environment* 26, 1287–1296.
- Binkley, D., Stape, J.L., Takahashi, E.N., Ryan, M.G., 2006. Tree-girdling to separate root and heterotrophic respiration in two Eucalyptus stands in Brazil. *Oecologia* 148, 447–454.
- Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology and Evolution* 14, 224–228.
- Brant, J.B., Myrold, D.D., Sulzman, E.W., 2006. Root controls on soil microbial community structure in forest soils. *Oecologia* 148, 650–659.
- Chan, O.C., Yang, X.D., Fu, Y., Feng, Z.L., Sha, L.Q., Casper, P., Zou, X.M., 2006. 16S rRNA gene analyses of bacterial community structures in the soils of evergreen broad-leaved forests in south-west China. *FEMS Microbiology Ecology* 58, 247–259.
- Chen, J.H., Zou, X.M., Yang, X.D., 2006. Retention of plant available P in acid soils of tropical and subtropical evergreen broad-leaved forests. *Acta Ecologica Sinica* 26, 2294–2300.
- Christensen, S., Bjørnlund, L., Vestergård, M., 2007. Decomposer biomass in the rhizosphere to assess rhizodeposition. *Oikos* 116, 65–74.
- De Deyn, G.B., Raaijmakers, C.E., van Ruijven, J., Berendse, F., van der Putten, W.H., 2004. Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. *Oikos* 106, 576–586.
- Ekberg, A., Buchmann, N., Gleixner, G., 2007. Rhizospheric influence on soil respiration and decomposition in a temperate Norway spruce stand. *Soil Biology and Biochemistry* 39, 2103–2110.
- Frey, B., Hagedorn, F., Giudici, F., 2006. Effect of girdling on soil respiration and root composition in a sweet chestnut forest. *Forest Ecology and Management* 225, 271–277.
- Giesler, R., Högborg, M.N., Strobel, B.W., Richter, A., Nordgren, A., Högborg, P., 2007. Production of dissolved organic carbon and low-molecular weight organic acids in soil solution driven by recent tree photosynthate. *Biogeochemistry* 84, 1–12.
- Göttlicher, S.G., Steinmann, K., Betson, N.R., Högborg, P., 2006. The dependence of soil microbial activity on recent photosynthate from trees. *Plant and Soil* 287, 85–94.
- Griffiths, B.S., Boag, B., Neilson, R., Palmer, L., 1990. The use of colloidal silica to extract nematodes from small samples of soil and sediment. *Nematologica* 36, 465–473.
- Hahn, V., Högborg, P., Buchmann, N., 2006. <sup>14</sup>C—a tool for separation of autotrophic and heterotrophic soil respiration. *Global Change Biology* 12, 972–982.
- Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics* 36, 191–218.
- Högborg, M.N., 2006. Discrepancies between ergosterol and the phospholipid fatty acid 18:2ω6,9 as biomarkers for fungi in boreal forest soils. *Soil Biology and Biochemistry* 38, 3431–3435.
- Högborg, M.N., Högborg, P., 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytologist* 154, 791–795.
- Högborg, P., Read, D.J., 2006. Towards a more plant physiological perspective on soil ecology. *Trends in Ecology and Evolution* 41, 789–792.
- Högborg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högborg, M.N., Nyberg, G., Ottosson, M., Read, A.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411, 789–792.
- Högborg, M.N., Högborg, P., Myrold, D.D., 2007. Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three? *Oecologia* 150, 590–601.
- Holland, J.N., Cheng, W., Crossley, D.A.J., 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. *Oecologia* 107, 87–94.
- Johansson, G., 1992. Release of organic C from growing roots of meadow fescue (*Festuca pratensis* L.). *Soil Biology and Biochemistry* 24, 427–433.
- Johnson, D., Leake, J.R., Read, D.J., 2002. Transfer of recent photosynthate into mycorrhizal mycelium of an upland grassland: short-term respiratory losses and accumulation of <sup>14</sup>C. *Soil Biology and Biochemistry* 34, 1521–1524.
- Johnsen, K., Maier, C., Sanchez, F., Anderson, P., Butnor, J., Waring, R., Linder, S., 2007. Physiological girdling of pine trees via phloem chilling: proof of concept. *Plant, Cell and Environment* 30, 128–134.
- Leake, J.R., Ostle, N.J., Ignacio Rangel-Castro, J., Johnson, D., 2006. Carbon fluxes from plants through soil organisms determined by field <sup>13</sup>CO<sub>2</sub> pulse-labelling in an upland grassland. *Applied Soil Ecology* 33, 152–175.
- Lodge, D.J., Ingham, E.R., 1991. A comparison of agar film techniques for estimating fungal biovolumes in litter and soil. *Agriculture, Ecosystems and Environment* 34, 131–144.
- Mikola, J., Kytöviita, M.M., 2002. Defoliation and the availability of currently assimilated carbon in the *Pheum pratense* rhizosphere. *Soil Biology and Biochemistry* 34, 1869–1874.
- Neher, D.A., Weicht, T.R., Moorhead, D.L., Sinsabaugh, R.L., 2004. Elevated CO<sub>2</sub> alter functional attributes of nematode communities in forest soils. *Functional Ecology* 18, 584–591.
- Ostle, N., Briones, M.J.I., Ineson, P., Cole, L., Staddon, P., Sleep, D., 2007. Isotopic detection of recent photosynthate carbon flow into grassland rhizosphere fauna. *Soil Biology and Biochemistry* 39, 768–777.
- Pollierer, M.M., Langel, R., Körner, C., Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology Letters* 10, 729–736.
- Schulze, W.X., Gleixner, G., Kaiser, K., Guggenberger, G., Mann, M., Schulze, E.D., 2005. A proteomic fingerprint of dissolved organic carbon and of soil particles. *Oecologia* 142, 335–343.
- Siira-Pietikäinen, A., Haimi, J., Kanninen, A., Pietikäinen, J., Fritze, H., 2001. Responses of decomposer community to root-isolation and addition of slash. *Soil Biology and Biochemistry* 33, 1993–2004.
- Siira-Pietikäinen, A., Haimi, J., Fritze, H., 2003. Organisms, decomposition, and growth of pine seedlings in boreal forest soil affected by sod cutting and trenching. *Biology and Fertility of Soils* 37, 163–174.
- Simard, S.W., Perry, D.A., Smith, J.E., Molina, R., 1997. Effects of soil trenching on occurrence of ectomycorrhizas on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. *New Phytologist* 136, 327–340.
- Subke, J.A., Hahn, V., Battipaglia, G., Linder, S., Buchmann, N., Cotrufo, M.F., 2004. Feedback interactions between needle litter decomposition and rhizosphere activity. *Oecologia* 139, 551–559.
- Van Veen, J.A., Paul, E.A., 1979. Conversion of biovolume measurements of soil organisms grown under various moisture tensions to biomass and their nutrient content. *Applied and Environmental Microbiology* 37, 686–692.
- Wilsey, B.J., Coleman, J.S., McNaughton, S.J., 1997. Effects of elevated CO<sub>2</sub> and defoliation on grasses: a comparative ecosystem approach. *Ecological Applications* 7, 844–853.
- Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habitats in soil nematode families and genera—an outline for soil ecologists. *Journal of Nematology* 25, 315–331.