Soil Biology & Biochemistry xxx (2014) 1–8

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Exploring carbon flow through the root channel in a temperate forest soil food web

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ARTICLE INFO

Article history:
Received 15 January 2014
Received in revised form
25 April 2014
Accepted 3 May 2014
Available online xxx

Keywords:
Ants
Carbon
Earthworms
Energy flow
Invasive species
Salamander

ABSTRACT

Soil food webs play an important role in forest ecosystem functions that may be sensitive to global environmental change. We traced a pulse of ^{13}C from the root systems of young sugar maple stands through the soil food web to explore energy flow from roots to soil heterotrophs. Invasive earthworms (Lumbricidae) were the most highly-enriched taxa sampled, indicating that they were consuming significant quantities of live fine roots and mycorrhizae and assimilating significant amounts of root-derived C. Another invasive invertebrate, a weevil (*Barypeithes pellucidus*) also appeared to consume significant amounts of roots or root-derived C. High isotope enrichment in ants (Formicidae) may reflect their feeding on phloem-sucking coccids in soil. All the predators collected from the litter layer also exhibited high isotope enrichment, including the salamander *Plethodon cinereus*. Moreover, in the absence of invasive earthworms all the taxa of animals collected from surface soil were similarly highly-enriched in root-derived isotopes. The apparent importance of the root channel in supplying energy to the soil food web suggests that forest ecosystem functions could be highly sensitive to global changes that alter proportional tree C allocation belowground.

1. Introduction

In the face of global environmental change, the dynamics of soil food webs need to be better resolved because of their likely importance for terrestrial ecosystem responses to changing climate, pollution loading and invasive species (Wardle et al., 2004). Soil food webs play a major role in soil carbon stabilization (Brussaard et al., 2007) and nutrient recycling (Bonkowski et al., 2009), and invasive species can disrupt these key ecosystem functions (Fahey et al., 2012). Energy is supplied to soil food webs by two principal input channels, aboveground detritus and roots, both of which contribute directly or indirectly to a third energy source, older soil organic matter. Evidence suggests that the living root channel may predominate in energy supply to the soil food web in temperate forests (Pollierer et al., 2007, 2012). This is not surprising because roots supply a high proportion of C inputs to forest soil (Kuzyakov and Domanski, 2000; Matamala et al., 2003), and leaf litter on the soil surface is often biochemically recalcitrant (e.g., high C:N ratio and high lignin concentration) and subject to environmental extremes (e.g., drying, heating, freezing).

The nature of the root-based energy channel of the soil food web has received limited study because it is difficult to observe. Photosynthetic C supplied to roots can reach soil heterotrophs directly via living roots and root hairs (grazing), but also indirectly via root detritus, root exudates and mycorrhizal fungi. The feeding habits of many taxonomic groups of soil animals have been classified in general (e.g., detritivores, fungivores, omnivores, predators), and food web linkages are a topic of great interest (Scheu, 2002). The basal resources supplying the soil food web have been evaluated qualitatively based on fatty acid (FA) signatures that

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http://dx.doi.org/10.1016/j.soilbio.2014.05.005
0038-0717/

distinguish among plant, fungal and bacterial sources (Ruess and Chamberlain, 2010). Recently, Pollierer et al., (2012) utilized FA signatures in combination with stable isotopes of C to demonstrate the details of the soil food web in a beech (*Fagus sylvatica*)-dominated forest. They demonstrated the predominant role of ectomycorrhizal fungi and rhizosphere bacteria as basal resources for the food web in tis forest, as well as the lesser importance of leaf litter sources. They also clarified the feeding relationships among Collembola, mites, native earthworms and predators. Analogous studies have not been reported in forests dominated by trees with arbuscular mycorrhizal associations.

Invasive soil invertebrates can profoundly disrupt the normal functioning of soil food webs. Most prominent in many northern forest ecosystems in this respect are large earthworms (Annelida) (Hale et al., 2005; Eisenhauer et al., 2011; Greiner et al., 2012). For example, earthworm invasion of temperate broadleaf forest reduced the bacterial:fungal ratios in soils (Dempsey et al., 2011, 2013), altered and simplified the oribatid mite (Acari) fauna (Burke et al., 2011), and altered the diet and abundance of forest floor consumers such as salamanders (Maerz et al., 2005, 2009) and birds (Loss and Blair, 2011; Loss et al., 2012). The principal mechanism underlying these earthworm-induced changes was the elimination of surface organic horizons by earthworm feeding and mixing, thereby altering the habitat of other soil-dwelling organisms. Also, Cortez and Bouche (1992) showed conclusively that earthworms graze on live fine roots in a laboratory setting, and recent isotopic studies indicate the likely importance of this process in natural forest settings (Horowitz et al., 2009; Fahey et al., 2013a). Another important group of invasive soil invertebrate taxa is soil-dwelling weevils (Curculionidae); which as larvae may consume significant amounts of live fine roots of trees (Coyle et al., 2008) and when they emerge en masse constitute an import prey resource for other taxa (Maerz et al., 2005).

The objective of the present study was to quantify C flux from fine tree roots through dominant taxa in the surface soil food web of the arbuscular mycorrhizal tree species sugar maple (*Acer saccharum* Marsh.). We labeled sugar maple saplings with a large pulse of ^{13}C and traced this pulse for several years through roots, rhizosphere soil and soil invertebrates, as well as a prominent soil vertebrate, the red-backed salamander (*Plethodon cinereus*). We hypothesized high ^{13}C enrichment of soil food web components, reflecting the prominence of the root channel in energy supply to soil organisms. Further, we expected especially high enrichment of invasive soil invertebrates, earthworms and weevils that are known to feed on live roots. Finally we hypothesized higher enrichment of saprotrophic and fungivorous soil invertebrates (Collembola, Diploda) than predatory taxa (Araneae, Chilopoda, Coleoptera, salamanders), reflecting dilution of the isotope signal along the soil food chain.

2. Methods

2.1. Study site

The research was conducted in a natural northern hardwood forest in the Arnot Forest, central New York, USA (Fain et al., 1994). Annual precipitation at the site averages 90 cm, and average June and December temperatures are 22° and −4 °C, respectively. Soils are acidic (pH 4.5–5.0) Dystrochrepts formed in glacial till locally derived from Devonian shales. We chose a 90-yr-old forest dominated by sugar maple that had been selectively harvested in 2000 leaving about 50 overstory trees per ha. This thinning released a dense sugar maple understory which at the time of isotope labeling in 2006 averaged 2.5 m height.

2.2. Isotope labeling

The sugar maple saplings were labeled with ^{13}C following procedures detailed elsewhere (Horowitz et al., 2009; Fahey et al., 2011). Briefly, seven aluminum-frame chambers (2.5 m tall × 3 m diameter) were positioned around nearly pure groves of sugar maple saplings (ca. 10 stems/m^2) in spring 2006. The soils in each chamber were isolated by trenching around the chambers to 0.5 m depth, lining with 6-mil polyethylene and back-filling with soil. The saplings were labeled with ^{13}C by enclosing the chambers in polyethylene sheeting and injecting 40% atom-enriched $^{13}CO_2$ into the chambers on 13 sunny mornings between 1 September and 20 September 2006. This procedure was successful in enriching foliage to $\delta^{13}C$ over 300‰ (Horowitz et al., 2009). All leaf litterfall was removed from the chambers in October and early November 2006–2008 and replaced with equivalent amounts of unlabeled leaf litter so that ^{13}C isotope enrichment of the soil food web was derived almost entirely from belowground inputs (i.e., ^{13}C translocated to root systems).

2.3. Field sampling

Roots and rhizosphere soil were collected from 0 to 5 cm soil depth in four chambers in October 2006 (after leaf senescence), prior to leaf out in May 2007, and in late summer (15 August) 2007. For these samples root fans were gently excavated by loosening soil, and fine roots (<1 mm diameter) and adhering rhizosphere soil were manually separated (Phillips and Fahey, 2006), dried and stored for isotope analysis. Roots and soil also were sampled in early June and mid-October 2008 and mid-October 2009 by collecting four soil cores (5 cm diameter, 0–10 cm depth) from each chamber. Fine roots (<1 mm) were manually separated from soil, pooled within chambers, dried and stored for isotope analysis. Subsamples of soil from the October 2008 collection were used to measure microbial biomass C and ^{13}C. Roots and soil for isotope natural abundance measurements were collected in fall 2006 from adjacent locations outside the chambers and processed as above. In late October of each year (2006–2008) we added unlabeled fresh sugar maple leaf litter collected from adjacent forest in an amount designed to replace that removed from the chambers (300 g/m^2).

Soil invertebrates were obtained from each chamber by collecting surface organic horizons in two 0.25 m^2 sub-plots on each of four dates: 4 June and 15 October 2008, 1 June and 15 October 2009; also in June 2011 only two chambers were sampled as the others had received an additional ^{13}C labeling. These samples were returned to the laboratory for invertebrate extractions the same day. Earthworms were collected from the chambers on 26 April 2007, 10–25 October 2007, 4 June 2008 and 15 May 2009. Whenever available the earthworms were obtained from beneath two 30 × 15 cm cover boards in each chamber; however, in 2008 and 2009 we applied a mustard suspension (Lawrence and Bowers, 2002) to extract earthworms from the chambers. Finally, we collected 2–4 salamanders (*P. cinereus*) from beneath cover boards in each of the chambers on 9–11 October 2008 and from two chambers on 25 July 2009. Reference collections of earthworms, other soil invertebrates and salamanders were obtained from a nearby study site (Fahey et al., 2013a) for isotope natural abundance measurements.

2.4. Laboratory processing

Fine root samples were finely ground and homogenized for isotope analysis using a ball mill. Soil samples were sieved to 2 mm and finely ground in a ball mill for isotope analysis. The isotopic composition of these samples was measured on a Finnegan IRMS at

Please cite this article in press as: Gilbert, K.J., et al., Exploring carbon flow through the root channel in a temperate forest soil food web, Soil Biology & Biochemistry (2014), http://dx.doi.org/10.1016/j.soilbio.2014.05.005