

The carbon we do not see—the impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: a review

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Received 22 August 2003; received in revised form 28 May 2004; accepted 15 June 2004

Abstract

Dissolved organic matter (DOM), typically quantified as dissolved organic carbon (DOC), has been hypothesized to play many roles in pedogenesis and soil biogeochemical cycles, however, most research to date concerning forest soils has focussed on the high molecular weight (HMW) components of this DOM. This review aims to assess the role of low molecular weight (LMW) DOM compounds in the C dynamics of temperate and boreal forest soils focussing in particular on organic acids, amino acids and sugars. The current knowledge of concentrations, mineralization kinetics and production rates and sources in soil are summarised. We conclude that although these LMW compounds are typically maintained at very low concentrations in the soil solution ($<50\ \mu\text{M}$), the flux through this pool is extremely rapid (mean residence time 1–10 h) due to continued microbial removal. Due to this rapid flux through the soil solution pool and mineralization to CO_2 , we calculate that the turnover of these LMW compounds may contribute substantially to the total CO_2 efflux from the soil. Moreover, the production rates of these soluble transitory compounds could exceed HMW DOM production. The possible impact of climate change on the behaviour of LMW compounds in soil is also discussed.

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Keywords: Amino acids; Carbon cycling; Dissolved organic carbon; Low molecular weight organic acids; Monosaccharides; Soil respiration

1. Background

In ongoing efforts to balance the earth's carbon budget much attention has been paid to quantifying terrestrial C sources and sinks and the potential of soil and vegetation to sequester or emit atmospheric C. In particular, attention has largely focussed on attempting to quantify the role of soil respiration in the terrestrial flux across a diverse range of ecosystems. The total soil organic C pool has been estimated to $1550 \times 10^{15}\ \text{g C}$ with a further $750 \times 10^{15}\ \text{g C}$ present as inorganic C (Lal, 2003). Among the ecosystems studied, boreal and temperate forests have been highlighted as being of particular importance because of their large intrinsic

carbon pool, a large proportion of which ($440\text{--}620 \times 10^{15}\ \text{g C}$) is contained within the soil (Lal, 2003). Within these forests a fine balance is believed to exist between net primary production and respiration losses (Valentini et al., 2000). The rate of soil respiration is consequently a critical factor in the total carbon exchange of these ecosystems, and may together with changes in productivity determine whether a forest becomes a source or sink for carbon. Gaining a mechanistic understanding of soil respiration and its potential responses to climate and land use change is therefore critical to predicting anthropogenically mediated changes in terrestrial C pools.

Soil respiration can be functionally divided into autotrophic (plant) and heterotrophic (microbial) respiration (Table 1). However, partitioning of autotrophic and heterotrophic soil respiration is experimentally difficult to achieve and the term rhizosphere respiration (Table 1) is

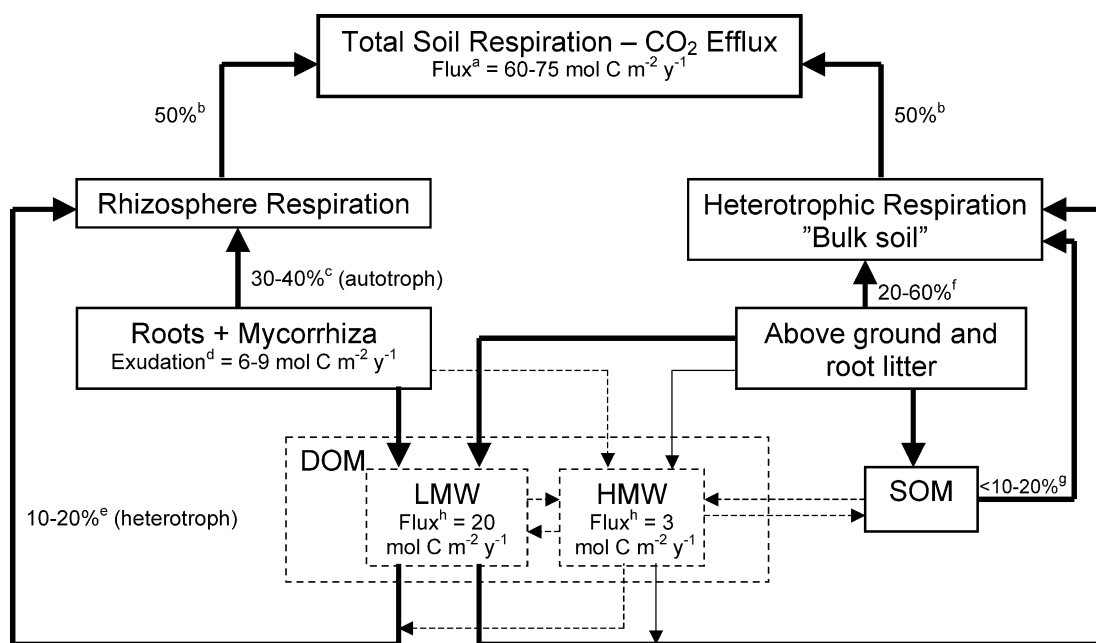
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Table 1
Explanations of the different respiration terms used in the text

Term	Explanation
Autotrophic respiration	Carbon assimilated through photosynthesis by trees and ground vegetation and released by respiration of above ground biomass, roots and associated mycorrhiza
Heterotrophic respiration	CO ₂ released from microbial biomass and animals during decomposition of carbon substrates
Rhizosphere respiration	Operationally defined term, which includes underground autotrophic respiration and heterotrophic respiration of carbon substrates originating from newly assimilated C, e.g. root exudates and recent dead root biomass (so called rhizodeposition) mainly in the rhizosphere. Decomposition of extramatrical hyphal exudates and biomass may or may not be included depending upon the method employed
Total soil respiration	Sum of autotrophic and heterotrophic respiration. Sometimes reported as sum of rhizosphere respiration and bulk soil heterotrophic respiration

also frequently used. Total soil respiration (autotrophic + heterotrophic) is typically in the range $60\text{--}75 \text{ mol C m}^{-2} \text{ y}^{-1}$ (Matteucci et al., 2000; Janssens et al., 2001; Fig. 1), which in the cited studies corresponded to about 70% of the total ecosystem respiration and is equivalent to 0.5–1% of the C stored in the soil profile ($3000\text{--}10000 \text{ mol C m}^{-2}$ from a depth of 0–100 cm). One of the main problems with predicting soil respiration is that it is influenced by a multitude of interacting factors including soil temperature, moisture, soil carbon (or litter) quality, root density, microbial community structure and size, physical and chemical soil properties and vegetation type, nutrient status and growth rate (Raich and Tufekcioglu, 2000). Consequently, in most ecosystems the rate of soil respiration is highly temporally and spatially variable.

Labile or active carbon pools, typically including recent leaf, needle and root litter and microbial biomass, have been emphasised as an important source for heterotrophic respiration. This has also been demonstrated in field studies using isotopic techniques (Gaudinski et al., 2000; Harrison et al., 2000). In this context, dissolved organic matter (DOM) represents a small and very labile C pool ($<10\text{--}20 \text{ g C m}^{-2}$ down to 1 m depth; Ellert and Gregorich, 1995). In turn, a small part of the DOM ($<10\%$) consists of identifiable compounds of low molecular weight (LMW) such as organic acids, amino acids and simple sugars. These compounds are quickly assimilated by the soil microbial biomass, and are recognised to fuel microbial activity in the mycorrhizosphere due to their presence in root exudates (Dakora and Philips, 2002; Jones,



^aMatteucci et al. (2000), Janssens et al. (2001), Gaudinski et al. (2000), ^bHanson et al. (2000), Höglberg et al. (2001), Kelting et al. (1998), ^cBy difference, ^dsee text, ^eKelting et al. (1998), Kuzyakov et al. (2001), ^fGaudinski et al. (2000), Harrison et al. (2000), Lin et al. (2001), ^gGaudinski et al. (2000), Lin et al. (2001), ^hTable 3

Fig. 1. Schematic diagram of soil CO₂ fluxes and relative contributions from different sources (see Table 1) with values taken from cited references in the text and calculations in Table 3. All percentage values refer to total soil respiration. Solid bold arrows represent major carbon fluxes, thin solid arrows small carbon fluxes and dashed arrows minor carbon fluxes. Solid boxes represent major carbon pools and dashed boxes minor carbon pools.

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