



Root exudation patterns in a beech forest: Dependence on soil depth, root morphology, and environment



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ABSTRACT

Forest subsoils may represent an important C sink in a warming world, but rhizodeposition as the key biogeochemical process determining the C sink strength of mature forests has not yet been quantified in subsoils. According to studies conducted in topsoil or laboratory experiments, soil C inputs by root exudation are increasing with increasing temperature and decreasing nutrient availability. We examined whether these relationships apply to forest subsoil by analyzing the response of root exudation to increasing soil depth up to 130 cm in a mature European beech (*Fagus sylvatica* L.) forest. In two subsequent growing seasons differing in temperature and precipitation, we investigated *in situ* root exudation with a cuvette-based method and analyzed root morphology, microbial biomass, and soil nutrient availability. We proved that root exudation greatly decreases with soil depth as a consequence of a significant decrease in root-mass specific exudation activity to nearly a fifth of topsoil activity. The decrease in specific metabolic activity from 312 mg C g⁻¹ yr⁻¹ in the topsoil to 80 mg C g⁻¹ yr⁻¹ at 130 cm depth was amplified by an exponential decrease in root biomass per soil volume, leading to a relative decrease in root exudation per volume in the deep subsoil to 2% of topsoil root exudation (1 g C 10 cm⁻¹ m⁻² yr⁻¹ at 130 cm depth). Specific root area decreased and mean fine root diameter and root tissue density increased with soil depth, indicating a shift in primary root functionality from fibrous roots in the topsoil to pioneer roots in the subsoil. The decrease in root exudation was accompanied by decreases in soil microbial biomass, extractable organic C (EOC), and N and P availability and increases in the aromatic C portion in SOM, but it did not relate to seasonal differences in climatic conditions. More specifically, it responded positively to an increase in EOC and ETN in the topsoil, but remained at its minimum rate in the SOC-poor subsoil, probably due to a lower organic N and higher mineral N content. The vertical pattern of beech root exudation is in accordance with a strategy to maximize whole-tree carbon-use efficiency, as it reduces C loss by exudation in soil spots where positive priming effects are unlikely, but enhances C exudation where microbes can mine less bioavailable SOM. The exudation patterns further suggest that increased C allocation to root systems as a likely tree response to elevated atmospheric [CO₂] may not lead to enhanced soil C input by root exudation to subsoils poor in SOM.

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1. Introduction

Trees can increase the potential of soils as key global C sink under global warming. Forest soils store up to 70% of all soil organic C (SOC; [Jobbágy and Jackson, 2000](#)) and a considerable part of it in subsoils (in excess of 50%; [Jobbágy and Jackson, 2000](#); [Salomé et al., 2010](#); [Rumpel and Kögel-Knabner, 2011](#)). Yet even though the stability and control of subsoil organic C in forests has received increasing attention in recent years (e.g., [Fontaine et al., 2007](#)),

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quantitative information on plant C inputs to forest subsoils is still scarce. While it is well established that roots exert significant control on the rate at which C cycles between plants, soil, and the atmosphere (Norby and Jackson, 2000; Lal, 2004), how these relationships change from topsoil to subsoil is largely unknown. In particular the process of rhizodeposition which determines the C amount and C sink strength of forest subsoils has remained unstudied in mature forest stands due to methodical constraints.

In the topsoil, roots supply microbes with easily degradable C-rich substrates that drive microbial decomposition processes (Lynch and Whipps, 1990; Kong and Six, 2010; Phillips et al., 2012; Meier et al., 2015, 2017). As a consequence, biogeochemical cycles are much faster in the rhizosphere than in the surrounding bulk soil (Herman et al., 2006; Finzi et al., 2015). Greater soil C inputs by roots, e.g. as a consequence of elevated CO₂, do not necessarily lead to increased C sequestration (Langley et al., 2009; Van Kessel et al., 2006; Marhan et al., 2010) since the exudation of labile, plant-derived C and root turnover can stimulate microbes to decompose less bioavailable SOC (Hoosbeek et al., 2004; Joslin et al., 2006; Phillips et al., 2011, 2012) via a priming effect (Kuzakov et al., 2000). Priming effects can be positive (increase in SOC decomposition) or negative (slow-down of SOC decomposition) and can vary in magnitude (Cheng et al., 2003; Hamer and Marschner, 2005; Blagodatskaya et al., 2007; De Graaff et al., 2010, 2014). Both the direction and magnitude probably depend on the quantity and quality of the deposited root substrate, the microbial community composition and activity, and the quality and availability of soil C (Fierer et al., 2003; Fontaine et al., 2003; Hamer and Marschner, 2004; De Graaff et al., 2010; Salomé et al., 2010), all of which change with increasing soil depth.

Soil organic matter in deep soil is highly processed and several studies suggest that it is enriched in microbial-derived C compounds and depleted in energy-rich plant material in comparison to topsoil SOM (Rumpel and Kögel-Knabner, 2011). The main pathways by which new organic C inputs to subsoils occur are from leaf and root litter and root exudation (Rumpel and Kögel-Knabner, 2011; Angst et al., 2016a). As a consequence, rooting patterns control the vertical distribution of organic matter and nutrients in the soil (Iversen, 2010) and their occurrence in subsoils is highly heterogeneous and mainly confined to hotspots. Spatial separation of SOM, microorganisms, and their extracellular enzyme activities possibly related to the heterogeneity of the root C input is discussed as one of the most important factors leading to the protection of SOM in subsoils (Von Lütow et al., 2006; Salomé et al., 2010; Rumpel and Kögel-Knabner, 2011; Preusser et al., 2017).

Root morphology has a strong control on the C flux from roots to soil: increased root branching can increase root exudation rates (Groleau-Renaud et al., 1998) and promote fine root turnover and decomposition in the topsoil (Wells and Eissenstat, 2001; Guo et al., 2008; Fan and Guo, 2010; De Graaff et al., 2013), but it is unknown if the same relationships also exist in the subsoil with vastly different environmental conditions. While the complex architecture of root systems traditionally has been categorized according to root diameter into fine and coarse roots, this classification may not reflect the functionality of roots. More recently, fine roots were classified according to a stream-based ordering system (Pregitzer et al., 2002) and primary roots were classified into short and thin fibrous roots and longer and thicker pioneer roots (Polverigiani et al., 2011; Zadworny and Eissenstat, 2011). These two root classes differ in their life expectancies and in their uptake and transport capacities (Zadworny and Eissenstat, 2011; Bagniewska-Zadworna et al., 2012), but it remains unknown if this classification also has consequences for root exudation rates in different soil layers.

Despite narratives of decreasing root exudation with increasing soil depth, quantitative information on *in situ* root exudation in the

subsoils of mature forest stands is essentially absent. In our study we investigated fine root morphology and fine root exudation in a mature European beech forest to a soil depth of up to 130 cm in two growing seasons. The aim of the study was to detect adaptive responses of root exudation of beech to changing environmental conditions with increasing soil depth. We predicted that root exudation decreases with increasing root diameter and decreasing temperature, but increases with decreasing nutrient availability in subsoils, which could result in higher or lower root exudation at depth due to partly opposing effects of the environment.

2. Material and methods

2.1. Study site

Root exudates were collected at the Grindewald site (52°14'19" N, 9°20'32" E; 100 m a.s.l.), northwest of Hannover, Germany, in four sampling campaigns between May 2014 and October 2015. At this site, a European beech (*Fagus sylvatica* L.) forest stand was established in 1916 (Forstamt Nienburg, 2010) in the center of the distribution range of European beech in the lowlands of NW Germany. At the time of the study, beech trees in the forest plantation had a basal area of 27 m² ha⁻¹, a closed canopy, and were of mature age (i.e., 100 years old). The parent materials for soil development were Pleistocene fluvioglacial sandy deposits from the penultimate (Saalian) ice age. The medium-to coarse-grained sandy deposits with low silt and clay content had a comparably low water storage capacity. The predominant soil type in the study area was an acidic (pH 3.4–4.5), sandy Dystric Cambisol (IUSS Working Group WRB, 2014) with a small AE horizon (2 cm; represents the topsoil). Subsoil was defined as the soil that is located below the A and E horizons (cf. IPCC, 2000), i.e. below 2 cm soil depth where the Bsw horizon started. The dominating humus form was a mormoder (classification according to Green et al., 1993).

Climate data were obtained from the German Meteorological Service (DWD) for a nearby climate station located in Nienburg (52°38'17" N, 9°12'30" E). Mean annual precipitation and temperature for the period 1947–2015 were 713 mm and 9.4 °C (Table S1). Both study years had higher temperatures than the long-term average, with the warmer year 2014 surpassing the long-term mean by 1.7 °C and the long-term growing season mean by 0.9 °C. Growing season precipitation was above average in 2014 (422 mm) and close to average in 2015 (371 mm).

2.2. Root exudate collection

In four sampling campaigns during the growing seasons 2014 and 2015 (i.e., May 2014, August 2014, June 2015, and October 2015) three soil pits of 1.5 m depth were excavated. The pits had a distance of at least 3 m to the nearest mature beech tree. After excavation, root exudates were collected in three different depths, in the topsoil, the upper subsoil, and the lower subsoil. Since roots were not evenly distributed across the pit walls, we defined depth classes from which root exudates were collected. Specifically, the subsoil₄₀-depth class covered a depth range of 20–50 cm and the subsoil₁₀₀-depth class a depth range of 60–130 cm. In each soil pit, root exudates were collected from three root strands (i.e., from the head wall of the soil pit and the two side walls) per soil depth class.

For the collection of root exudates in cuvettes filled with 2-mm diameter glass beads (cf. Phillips et al., 2008), root strands still attached to a mature tree were carefully extracted from the soil surface of the pit walls and all soil adhering to the root system was carefully removed with deionized water and fine forceps to maintain the integrity of the root. Living root systems were then placed into root cuvettes filled with sterile glass beads moistened with C-

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