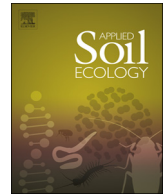




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Applied Soil Ecology

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## Reprint of: Structural and functional differences in the belowground compartment of healthy and declining beech trees<sup>☆</sup>

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### ARTICLE INFO

#### Keywords:

Beech  
Forest decline  
Soil profile  
Roots  
Rhizodeposition  
Mineral deficiency

### ABSTRACT

Functional studies of tree decline have mainly focused on process inside the plant showing possible alterations of carbon transport, storage and hydraulic functions. However, the processes occurring at the plant-soil interface have been seldom investigated. Our objective is to examine carbon functional alterations in the belowground compartment in the case of a long term beech decline. Soil and nutrient content profiles were characterized under five healthy and five declining trees. Seasonal root growth and rhizodeposition were characterized using, ingrowth cores, and microbial biomass combined with soluble carbon organic content, respectively. Podzolisation associated with soil acidification and deficiencies in Ca, Mg and Mn were observed in the soil under declining trees, but not under healthy trees. Spring fine root growth was higher in declining trees than in healthy trees but there were only minor differences concerning rhizodeposition proxies. In our study, we showed that the tree health status is associated to a marked heterogeneity of soil characteristics. Podzolisation close to declining trees leads to a local mineral deficiency which probably stimulates their fine root growth but without altering their flux of carbon exudates.

### 1. Introduction

Tree decline is a complex phenomenon, in which several biotic and abiotic factors often interact with one another (Manion, 1981). Some of these factors, for example drought and/or pest-related damages, might be enhanced in temperate regions as a result of global warming (IPCC, 2014; Lindner et al., 2010), however its effect on the frequency and intensity of future tree decline and mortality events is still uncertain (Allen et al., 2010). To better predict the impact of global change on forests, it is therefore necessary to increase our understanding of the functional mechanisms underlying tree decline and mortality (Bréda and Badeau, 2008). Recent research on the short term or long term ecophysiological responses of trees to moderate or severe drought leading to decline, has shown that carbon (C) and/or water transport and/or storage could be altered during these events (Delaporte et al., 2016; McDowell, 2011; McDowell et al., 2008; Sala et al., 2010). To date, most of the studies have focused on processes occurring in the plant itself. Despite their potential importance in tree functioning (Högberg, 2011), processes occurring at the plant-soil interface have

seldom been investigated.

Both internal and external factors influence root growth and the structure of the root system in trees. Tree age is an example of these internal factors: older trees spend more resources on maintenance than on tissue growth, allocating more resources into the production of fine absorbing roots and fewer into large structural roots (Pregitzer, 2002; West et al., 1999). However, (Zanetti et al., 2015) recently proved that root structure and growth are influenced more by soil and environmental factors than by genetic determinants. The availability of water and nutrients activates a series of genes/proteins at the root level, which inhibit or accentuate root growth (Gallais and Hirel, 2004; Giehl et al., 2014). For example, drought usually causes decreased root growth (Teskey and Hinckley, 1981).

The plant-soil interface commonly designated the rhizosphere, is the portion of soil under the influence of plant roots. These significantly modify water and nutrient availabilities, pH and microbial activity of the soil around them (Hinsinger et al., 2009) via rhizodeposition, i.e. the release of C by plant roots (Lynch and Whipps, 1990). Rhizodeposition strongly stimulates microbial activity in the vicinity of roots

DOI of original article: <http://dx.doi.org/10.1016/j.apsoil.2017.05.004>

<sup>☆</sup> This article is a reprint of a previously published article. For citation purposes, please use the original publication details; Applied Soil Ecology, 117–118, pp. 106–116.

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<https://doi.org/10.1016/j.apsoil.2018.03.014>

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Please cite this article as: Delaporte, A., Applied Soil Ecology (2017), <https://doi.org/10.1016/j.apsoil.2018.03.014>

(Lynch and Whipps, 1990) and is a major component of the C balance of trees: it is estimated that between 40% and 70% of the assimilated C is transferred to the rhizosphere (Grayston et al., 1997). Plant roots interact with a wide array of microorganisms, and partially control the processes of organic matter degradation/transformation and nutrient release (Taiz and Zeiger, 2013; Walker et al., 2003). Plants and microorganisms interact, exchanging molecule-signals which modify the behaviour and growth of the root system (Puga-Freitas and Blouin, 2015; Zhuang et al., 2013). However, soil microbial communities can also have negative effects on plant growth: either directly by acting as pathogens, or indirectly by competing with plants for nutrients (van der Heijden et al., 2008). Plants and rhizospheric micro-organisms interact tightly and depend highly on each other, so plants and soil can be considered as a continuum (Hogberg and Read, 2006).

The C balance of trees may be altered during decline (Anderegg et al., 2014; McDowell et al., 2008). More precisely, their photosynthetic C assimilation could be reduced (Anderegg et al., 2014) and/or C transport by phloem could be impaired (Sevanto et al., 2011). Girdling experiments have shown that interrupting C transport by phloem prevented rhizodeposition, and therefore limited the availability of resources to rhizospheric microorganisms (Hogberg et al., 2001). Moreover, when phloem transport is impaired by girdling, the stoichiometry of nutrients in the soil is altered: the inorganic N concentration increases (Hogberg et al., 2007; Weintraub et al., 2007), while organic C and N concentrations decrease (Dannenmann et al., 2009; Ekberg et al., 2007; Weintraub et al., 2007). Since rhizodeposition is a major source of labile C for soil microorganisms (Hogberg and Read, 2006), a reduction of the quantity and/or a modification of the quality of rhizodeposits may result in a decrease of total microbial biomass (Dannenmann et al., 2009; Hogberg and Hogberg, 2002), and of the diversity of the microbial community (Koranda et al., 2011; Schulze et al., 2005). Moreover, when rhizodeposition is altered by girdling, this can lead to decreased microbial activity in the soil (Hogberg and Read, 2006). The sensitivity of soil microbial communities to quantity and quality of C and N provided by tree roots is therefore highlighted by girdling experiments.

The C flux from tree roots to soil micro-organisms can also be altered by environmental factors. For example, (Ruehr et al., 2009) showed that C transfer from beech trees to soil micro-organisms was significantly delayed under drought conditions. Moreover, it has been hypothesized that during a drought, adult beech trees could decrease the activity of free-living soil microorganisms by reducing rhizodeposition (Dannenmann et al., 2009). This decreased microbial activity could in turn affect the nutritional status of the tree, either positively by shifting the competitive balance for N in favour of the tree rather than of soil microorganisms (Dannenmann et al., 2009), or negatively by decreasing the microbial mineralisation (Kreuzwieser and Gessler, 2010), resulting in altered nutrient contents in trees (Sardans et al., 2008a, 2008b).

It is therefore possible that such impairment of the transfer of C to the roots and soil might lead to changes in rhizosphere microbial community during drought-induced tree decline, consequently affecting the nutritional status of trees. However, the relationship between tree decline and C flux to roots and soil is still very poorly documented. A study of unexplained *Eucalyptus* decline showed that diminished tree crown health was associated with a modification of soil functional diversity, which could indicate an alteration of the chemical composition of rhizodeposits in declining trees (Cai et al., 2010).

Since rhizodeposition cannot be assessed directly, we relied on several proxies to estimate quantity and quality of rhizodeposits. Root soluble organic carbon (Marchand, 2003), rhizospheric soluble organic carbon (Haynes and Francis, 1993), and microbial biomass (Haynes and Francis, 1993) were used as proxies of the quantity of rhizodeposits. Bacterial abundance in the rhizospheric soil was used as a proxy for both quantity and quality of rhizodeposits, by discriminating between copiotroph and oligotroph bacteria (Dennis et al., 2010). The functional

diversity of soil bacteria was used as an indicator of the chemical diversity of rhizodeposits (Baudoin et al., 2002).

More than biological soil properties, physico-chemical properties and pedological characteristics of the soil could largely influence soil functioning. Indeed, soil properties are intimately linked with biotic processes through complex feedbacks controlling notably nutrient availability and *in fine* tree health. For example, in the Fontainebleau forest, a scheme of functioning of *Fagus sylvatica* soil-tree system under Luvisol and Podzsol was proposed by Ponge et al. (1999). Tree height could be explained with the help of the following three variables: litter quality, soil-dwelling earthworms and access to lime. These authors showed that the calcium cycle and in particular its availability at the soil surface, related to the presence of active anecic species of earthworms, was positively correlated to trees dimensions. Soil properties may also influence the microbial community. For example, soil pH can affect the contribution made by different functional groups and the total size of the microbial community (Anderson and Domsch, 1993; Wardle, 1992).

In this study, we wondered whether the decline of mature beech trees observed at the crown level could be related to changes in the belowground compartment, and so we investigated three aspects of the belowground soil-plant continuum: soil profiles, root-related features (rooting depth, root mass and root growth); and rhizodeposition-related features (quantity and quality of rhizodeposits). More precisely, we sought answers to the following questions:

- Is tree decline associated with changes in soil quality (horizons, main chemical characteristics)?
- Are root features (mass and growth) altered by the health status of trees?
- Is the quantity and/or quality of rhizodeposits associated with tree decline?

## 2. Material and methods

### 2.1. Site description and sampling design

The study was carried out in the Fontainebleau state forest, France (48°22'N, 02°36'E, mean elevation 120 m a.s.l.), during 2013. This forest extends over 17,000 ha, 60 km southeast of Paris. The climate is temperate, with a mean annual temperature of 10.6 °C and a mean annual cumulative precipitation of 749 mm, well distributed throughout the year (averages for the period 1960–2010). The study site is a mature, even-aged, monospecific beech (*Fagus sylvatica* L.) stand with a surface of 5 ha, where in 2011 the mean tree age was 95 years and the dominant height 27 m. It has shown signs of decline since the late 1990s. Trees were growing on a rather shallow soil (mean depth 0.6 m), with a C:N ratio of 18.7 and an extractable soil moisture of 101 mm.

From the dominant storey, five trees with altered crowns (“declining”) and five trees with intact crowns (“healthy”) were chosen for the present survey. These trees are distributed throughout the plot described above. Crown loss was evaluated using the DEPEFEU (DEPErissement des FEUillus) protocol (Nageleisen, 2010), which quantifies crown thinning on a scale from 0 (healthy tree) to 4 (dead tree). Selected healthy trees had large, dense crowns and abundant fine ramification (average DEPEFEU score: 0.9), while declining trees had reduced crown areas, very transparent crowns, only one or two main branches remaining and very limited fine ramification (average DEPEFEU score: 3.6). On average, declining trees had 70% less leaf area than healthy trees, as estimated with the DEPEFEU protocol. Mean diameters at breast height ( $45.9 \pm 5$  cm) and heights of the two groups ( $26.5 \pm 4$  m) were similar.

The soil profile at the foot of each tree was characterized. The pH of the soil solution was measured in the laboratory by mixing 5 g of air dried and sieved (< 2 mm) soil samples collected at depths of

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