



Soil type determines the distribution of nutrient mobilizing bacterial communities in the rhizosphere of beech trees



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ABSTRACT

Rhizosphere represents a nutrient-rich environment and a hotspot of bacterial activities compared to the surrounding bulk soil. However, few studies have investigated how this rhizosphere effect depends on the soil conditions, and never for trees. Contrary to annual plants, trees need decades to grow and strongly depend on the access and recycling of soil nutrients and water. In this context, we aimed at understanding if contrasted soil types impact the taxonomy and functions of bacterial communities inhabiting beech rhizosphere. To test this hypothesis, we considered the natural toposequence of Montiers, which is characterized by a same land cover dominated by beech (*Fagus sylvatica*) trees of the same age, growing under the same climatic conditions and under the same forestry practices. We used a combination of *in vitro* bioassays and 16S rRNA gene sequences analyses on a collection of 370 bacterial strains generated from beech rhizosphere and surrounding bulk soil samples collected in the organo-mineral horizon along the toposequence. Our study highlighted an increasing beech rhizosphere effect from the nutrient-rich to nutrient-poor soils, with specific bacterial functions related to inorganic nutrient mobilization largely and exclusively enriched in the rhizosphere of the nutrient-poor soils. This functional selection in the rhizosphere came with an enrichment of bacterial strains assigned to the *Burkholderia* and *Collimonas* genus, which appeared to be the dominant and most effective mineral-weathering bacteria. Our data corroborate the hypothesis of a variable selection of specific rhizosphere bacterial communities by beech trees according to the soil conditions and the tree nutritional requirements.

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1. Introduction

Forests are often developed on nutrient-poor soils. The low nutrient availability occurring in these soils and the absence of fertilization make nutrient access and recycling key factors for forest ecosystem functioning and sustainability (Uroz et al., 2011a). However, depending on the soil conditions (i.e., soil type, pH, humidity), these nutrients are often present in insoluble forms such as in primary and secondary minerals or in organic matter, not directly bioavailable to plants and soil biota (Augusto et al., 2000). Moreover, the nutrients present in the soil solution have a high reactivity with soil constituents, on which they can adsorb and become less biologically available depending on the soil conditions. Such

reactivity is notably observed for phosphorus ions (Hinsinger, 2001). In basic conditions, phosphorus ions are known to form complexes with calcium ions or clay particles, while in acidic conditions they form complexes with aluminum or iron (Vance et al., 2003). Nutrient limitations can also come from forestry practices. Indeed, harvest intensification of trees leads to removal of nutrients accumulated by trees in their biomass during their lifetime, making them less available in soil. In this context, the mobilization of nutrients via biotic and abiotic geochemical processes such as organic matter degradation or mineral weathering is crucial to provide the nutritive elements required by trees for their growth.

To deal with these variable soil conditions, plants have developed several adaptive strategies (Chapin, 1980; Cooper, 1975). Indeed, plants are capable of perceiving environmental changes such as nutrient limitation, toxicity, acidity or water stress and of adjusting their physiology and functioning accordingly (Dakora and Phillips, 2002; De Feudis et al., 2016; Hofmann et al., 2016). Notably,

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nutrient limitation has been shown to modify photosynthesis rates and in certain case growth rates (Cooper, 1975; Jenny et al., 1969). In this sense, development of pygmy trees has been evidenced in response to the nutrient limitations occurring along the Mendocino chronosequence in north California (USA) (Jenny et al., 1969; Yu et al., 1999). Plants can also adjust their root architecture to the nutrient availability conditions by stimulating lateral root growth in nutrient limiting conditions to extend their supply area (Leuschner et al., 2006; López-Bucio et al., 2003; Marzec et al., 2013; Richter et al., 2013; Sun et al., 2014; Yuan and Chen, 2010). Besides these adaptations, plants can also modify the parameters of the soil close to their root system to fit with their nutritional needs. Indeed, it has been demonstrated that the root zone (i.e., rhizosphere) presents a nutrient enrichment compared to the surrounding bulk soil (Hartmann et al., 2008; Rovira, 1969; Turpault et al., 2005). This phenomenon, also termed rhizosphere effect, is due to the action of root exudates (i.e., organic acids, protons, phytosiderophores, carbohydrates, enzymes), which directly improve plant access to nutrients and indirectly through the stimulation of processes mediated by beneficial bacterial communities (Dakora and Phillips, 2002; Neumann and Römheld, 2002). Notably, plants have been shown to adjust the amount of root exudates according to the soil conditions (Neumann et al., 2014).

The selection and stimulation of specific bacterial communities in the plant root vicinity has now been evidenced in several field and microcosm based studies (Calvaruso et al., 2010; Dias et al., 2013; Frey-Klett et al., 2005; Haichar et al., 2008; Marschner et al., 2004; Uroz et al., 2007). It corresponds to a subset of the soil bacterial communities adapted to the physico-chemical conditions occurring in the root vicinity and for some of them capable of consuming the metabolites contained into the root exudates (Haichar et al., 2008; Lynch and Whipps, 1990; Sørensen et al., 1997). Initially demonstrated using culture-dependent approaches, it was confirmed in culture-independent studies using DNA Stable isotope probing technic, genetically modified organisms (GMO) or artificial root exudates (Dias et al., 2013; Haichar et al., 2008; Shi et al., 2011). Indeed, comparing a soil type planted or not in microcosm condition treated with $^{13}\text{CO}_2$, Haichar et al. (2008) highlighted a significant differentiation of the rhizosphere bacterial communities from those of the bulk soil. The same analysis also demonstrated that this selection was plant species dependent, suggesting that the composition of root exudates varied among species and selected different microbial communities. Notably, a single modification of the root exudates due to a gene mutation can drastically modify the structure of the rhizosphere bacterial communities as illustrated by Dias et al. (2013) considering potato cultivars altered or not in their starch content. The importance of the composition of the root exudates was confirmed by Shi et al. (2011). Using artificial root exudates varying in composition, these authors showed that organic acids had a stronger effect than carbohydrates on the richness and composition of the bacterial communities. Interestingly, several studies based on functional genes or functional screening of culturable bacteria revealed that these variations of structure and composition also corresponded to the enrichment of specific functions in the rhizosphere (Berg et al., 2006; Li et al., 2014a,b,c; Maougal et al., 2014; Mendes et al., 2014; Uroz et al., 2013, 2007). In this sense, several functions related to nutrient access such as phytate hydrolysis, mineral weathering or carbohydrate degradation were reported to be enriched in the rhizosphere compared to the surrounding bulk soil (Calvaruso et al., 2010; Collignon et al., 2011; Frey-Klett et al., 2005; Li et al., 2014a,b,c; Maougal et al., 2014; Mendes et al., 2014; Uroz et al., 2007). Enrichment of bacteria with antagonistic activity towards plant pathogens in the rhizosphere was also evidenced

(Berg et al., 2006). Altogether, these studies suggest that plants enrich specific taxa in their root vicinity, some of them being capable of improving plant nutrition and health.

Whether the rhizosphere effect was evidenced for several plants species and for different soil types, it was rarely tested jointly for a same plant species planted in different soil types (Berg and Smalla, 2009; Haichar et al., 2008; Marschner et al., 2004). To our knowledge, such questioning was mainly addressed in pot experiments or in geographically distant sites, but rarely under natural field conditions and under similar climatic conditions, and never for trees (Schreiter et al., 2014). However, it is now well established that soil parameters (i.e., pH, soil type, nutrient availability) strongly affect the structure, composition and function of soil bacterial communities (Fierer and Jackson, 2006; Fierer et al., 2012; Geisseler and Horwath, 2009; Griffiths et al., 2011; Jeanbille et al., 2016; Landesman et al., 2014; Lauber et al., 2009; Lepleux et al., 2013; Wang et al., 2005). In this context and particularly in the frame of agriculture and forestry practices, but also of climate changes that induce plant migration, it becomes essential to understand how plant species can adapt to different soil conditions. In this study, we aimed at determining how the soil parameters impact the structure and functional abilities of forest soil bacterial communities. To do this, we compared through a culture-dependent approach the bacterial communities from beech rhizosphere and from the surrounding bulk soil in the toposequence of Montiers. This long-term observatory (LTO) is characterized by a short-distance sequence of adjacent Cambisol soils with contrasted nutritive potentials ranging from Hyperdistic to Calcaric, developed under similar climatic conditions and dominated by beech trees (*Fagus sylvatica* L.) of the same age. Our hypothesis was that beech trees enriched specific taxa and functions in their rhizosphere according to the nutrient availability occurring in each soil type and depending on their nutritional needs. To address this hypothesis, a total of 370 bacterial strains were isolated from the beech rhizosphere and the surrounding bulk soil along the toposequence of Montiers. The functional abilities of each bacterial isolate to mobilize organic and inorganic nutrients were evaluated using *in vitro* bioassays and their metabolic potential was determined by the Biolog method. The bacterial isolates were also genotypically characterized by amplifying and sequencing a portion of their 16S rRNA gene sequence. The 16S rRNA gene sequences of the isolates were compared with the dataset of 16S rRNA sequences generated by pyrosequencing on the same soil samples.

2. Materials and methods

2.1. Site description

The LTO of Montiers (48.53N, 5.32E) is located in the Meuse department (in northeastern France) and is part of the SOERE F-ORE-T (Environmental research monitoring and experimentation systems) and French Infrastructure for Analysis and Experimentation on Ecosystems (AnaEE-France) networks. This experimental site is co-managed by the ANDRA, French national radioactive waste management agency; Permanent Environment Observatory (OPE) (ANDRA OPE) and the INRA (BEF Unit; <http://www.nancy.inra.fr/en/Outils-et-Ressources/montiers-ecosystem-research>). The LTO harbours a semi-continental climate (cold winters and hot summers), with average annual precipitation and temperature of 1100 mm and 12.6 °C, respectively. The LTO is characterized by a toposequence (SS2) (Jeanbille et al., 2016), covering a distance of ca. 1.5 km and composed of three adjacent soil types. Due to the size of the toposequence, each soil type is characterized by the same climatic conditions. The bedrock is made of two geological layers: a Jurassic calcareous (Tithonian) layer overlaid by detrital sediments

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