REGULAR ARTICLE

Impact of common European tree species and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) on the physicochemical properties of the rhizosphere

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Abstract Trees play a crucial role in nutrient cycling and ecosystem fertility, notably through rhizosphere processes. The aim of this study was to compare soil physicochemical properties between bulk soil and rhizosphere of several tree species, and to compare rhizosphere properties between fertilized and non-fertilized conditions. The soil sampling was performed in Breuil-Chenue forest (North-East of France) in seven stands: native forest (old beech (*Fagus sylvatica* L.) and oak (*Quercus sessiliflora* Smith) coppice with standards; CwS), beech, oak (*Quercus petraea* [Matt.] Liebl.), Douglas-fir and fertilised Douglas-fir, Norway spruce (*Picea abies* Karst.) and fertilised Norway spruce. Systematic soil sampling was performed at 0–3, 3–10, and 10–23 cm in 20 calibrated pits. The rhizosphere of the different species was generally enriched in C, N, Ca, Mg, and K. Interestingly, the same positive effect was observed in the fertilised plots. The rhizosphere effect varied between tree species for C, "base" cations, pH_{water} and cation exchange capacity. This study reveals that interactions between roots, microorganisms and soil can enrich the pool of nutrients in the rhizosphere compared to bulk soil whatever the soil fertility conditions, and that the magnitude of the rhizosphere effect depends on tree species.

Keywords Fertilisation · Forest ecosystem · Rhizosphere · Soil physicochemical properties · Tree species

Introduction

Changes in tree species in a temperate forest ecosystem, generally a nutrient-poor ecosystem (Fisher and Binkley 2000), can lead to soil acidification and nutrient impoverishment through effects on nutrient uptake and storage, interception rates of atmospheric pollutants, production of acidic organic matter, as well as mineralization, nitrification, and weathering rates (Binkley 1995; Binkley and Giardina 1998). Plant species effects can thus be as or more important than abiotic factors, such as climate, in controlling nutrient cycling and ecosystem fertility (Hobbie 1992; Augusto et al. 2002; Binkley and Menyailo 2004; Mareschal et al. 2010).

The rhizosphere, defined as the volume of soil surrounding the roots which is affected by it (Darrah 1993), constitutes the interface between the soil solid phase, soil solution, and root system, and is the zone where major processes take place. Because of its specific function and its ecological importance (Hinsinger et al. 2009), the study of the rhizosphere is necessary to assess biogeochemical cycles and

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dynamics of forest ecosystems (Gobran et al. 1998; Turpault et al. 2009). The biological and physico-chemical characteristics of the rhizosphere may be drastically different from those of the bulk soil mainly due to root and microbial activities (for a review, see Hinsinger et al. 2005). Notably, it has been demonstrated that roots and root-associated micro-organisms such as bacteria and ectomycorrhizal fungi produce a great variety of acid compounds, i.e. protons, organic acids, and complexing organic acids (Jones 1998; Kelly et al. 1998; Welch et al. 1999; Liermann et al. 2000; Landeweert et al. 2001; Jones et al. 2009) which are important factors controlling mineral weathering and nutrient availability (Drever and Stillings 1997; Lambers et al. 2009) particularly in low-nutrient environments such as forest ecosystems (Marschner 1995; Grayston et al. 1996; Dakora and Phillips 2002). The rhizosphere is thus a highly dynamic environment characterized by spatial and temporal heterogeneities (Hinsinger et al. 2005). The magnitude of the rhizosphere effect depends not only on the edaphic and climatic factors but also on the activities of root and root-associated microorganisms which appear to be related to tree species and soil fertility conditions. For example, Philips and Fahey (2006) demonstrated that tree roots stimulated nutrient availability in the rhizosphere in the upper soil horizon (0–4 cm), and observed distinctive rhizosphere effect between arbuscular mycorrhizal and ectomycorrhizal tree species for the C, N and P cycling. Calvaruso et al. (2009) also showed that the clay-sized fraction weathering in the upper horizon of a forest soil (0–3 cm) was three to five times higher in the rhizosphere of Norway spruce related to that of the oak. In addition, Philips and Fahey (2007, 2008) observed that fertilization of a forest soil reduced fine root biomass, microbial biomass and activity, and that the magnitude of such effects was generally greater in the rhizosphere than in the bulk soil. This observation suggests that soil fertility may mediate the intensity of rhizosphere processes.

New researches are, however, needed to quantify the influence of different tree species on nutrient availability through rhizosphere processes, and for various soil fertility conditions. The main objectives of the present study were thus i) the comparison of soil physicochemical properties (e.g., pH_{water}, base saturation, cation exchange capacity, exchangeable acidity, carbon, nitrogen) between bulk soil and rhizosphere of several common European tree species such as beech, oak and Norway spruce as well as Douglas-fir, and (ii) the comparison of rhizosphere properties between fertilized and non-fertilized conditions, for the coniferous. We hypothesized that (i) tree species improve nutrient availability in the rhizosphere, (ii) the magnitude of rhizosphere effects differs between native forest, hardwoods and coniferous, and (iii) fertilisation influences rhizosphere properties. To our knowledge, this study is the first to quantify rhizosphere effects on soil physicochemical properties for various soil fertility levels and under several different tree species, all growing under field conditions in a common soil.

Materials and methods

Study site

The soil samples were collected at the Breuil-Chenue experimental forest site located in the Morvan (47°18′ N, 4°5′ E, France) which was set up in 1976 specifically to compare biogeochemical cycles between tree species. The forest is situated on a plateau at an altitude of 638 m, on a slight, northwest facing slope. Mean annual air temperature is 9°C and the annual precipitation averages 1280 mm yr^{-1}. The native forest was a 150 year-old Coppice with standards (CwS) stand dominated by beech (*Fagus sylvatica* L.) and oak (*Quercus sessiliflora* Smith). This initial forest was partially clear-felled and replaced in 1976 by monospecific plantations distributed in plots of 0.1 ha of different species. The stands studied in this study were the reference CwS, beech, oak (*Quercus petraea* (Matt.) Liebl.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and Norway spruce (*Picea abies* Karst.). The fertilisation was applied only on Douglas-fir and Norway spruce plots in two steps: in Spring 1979, basal application on each tree (0.25 m^2: 36 g of P_2O_5, 15 g of K_2O, and 3.4 g of nitrogen as ammonitrate) and in Spring 1983 on the whole plot (35×35 m, 160 kg.ha^{-1} (4 g for 0.25 m^2) of P_2O_5 and 1120 kg.ha^{-1} (28 g for 0.25 m^2) of CaO). The parent material is the "Pierre qui Vire" granite (Seddoh 1973). According to Dejou (1966), Bonneau et al. (1977), and Mareschal (2008), this granite is homogeneous in term of texture (big-size

grain granite) and composition in the CwS, beech, oak, Douglas-fir, and Norway spruce stands. Its composition is quartz: 34%, albite: 31.1%, K-feldspath: 24.2%, muscovite: 1.2%, and chlorite: 0.5%. The soil deriving from this granite is acidic, well drained, and is classified as a Typic Dystrochrept (USDA 1999). The bulk soil has a sandy-loam texture (55% sand and less than 20% clay) and was acidic (pH_{KCl} 3.1–4.3). The cation exchange capacity (CEC) was low and mainly occupied by aluminium (Al) (Mareschal et al. 2010). Base saturation (BS) was less than 10%. The humus form is a moder (Zeller et al. 2007) in the native forest, and carbon (C) concentrations were 7.3±0.8% in the A1 horizon.

Sampling and sample preparation

The sampling of soil materials was performed in June 2000 in seven stands: native forest (CwS), beech, oak, Douglas-fir and fertilised Douglas-fir, Norway spruce and fertilised Norway spruce. After removing the forest floor, systematic soil sampling was performed at three depths (layer I: 0–3 cm, layer II: 3–10 cm, and layer III: 10–23 cm) in 18 to 20 calibrated pits each with a dimension of 80 by 35 cm (0.28 m^2; metal border limiting the sampling zone), distributed throughout each plantation plot. The volumes of soil collected in the 0 to 3, 3 to 10, and 10 to 23 cm horizons of each pit were thus 8.4, 19.6, and 36.4 dm^3, respectively. The choice of 0–3, 3–10, and 10–23 cm was motivated by the fact that these depths correspond approximately to the limits of three distinct and homogeneous soil horizons (from organo-mineral to mineral soil horizons) in the different plots (Mareschal 2008).

The separation of soil samples into bulk and rhizosphere fractions was conducted in the field. For each pit, soil material was cut and extracted from the profile by layer (0–3, 3–10, and 10–23 cm). Living roots with diameters <2 mm were then carefully removed by hand from each soil sample. Root-free soil fraction was collected and immediately air-dried in a steam-air dryer at 30°C to give the bulk soil sample (B). Roots with adhering soil aggregates <1 cm in diameter were immediately air-dried in a steam-air dryer at 30°C. The soil fraction that spontaneously came off from the roots after drying was collected as the rhizosphere sample (R). To discard root debris present in soil samples and to compare samples of same particle size, bulk soil and rhizosphere were sieved at 200 μm. In total, 798 soil samples were collected. For each layer, the whole collected roots <2 mm in diameter were washed, air-dried in a steam-air dryer at 65°C and weighed. The fine root density corresponds to the dry root biomass divided by the volume of soil collected. It is important to note that the fine root density in the soil was underestimated because part of the fine roots was lost during sieving.

Soil analysis

The pH of soil samples was measured in distilled water with a soil to solution gravimetric ratio of 1:5 (pHmeter Mettler DL21).

Exchangeable cations in soil samples were extracted using either 1 M KCl for Mg^{2+}, Ca^{2+}, Na^+, Fe^{2+}, Mn^{2+} assay or 1 M NH_4Cl for K^+ assay, according to the method described by Espiau and Peyronel (1976), and then determined by inductively coupled plasma atomic emission spectrometry (ICP–AES; JY180 ULTRACE). The 1 M KCl soil extract was also titrated on an automatic titrimeter (Mettler DL70ES) to assess exchangeable H^+ and Al_t (Rouiller et al. 1980). Exchangeable acidity (EA) was calculated by taking the sum of H^+ and Al_t. The CEC was calculated from the sum of extracted exchangeable "base" cations (Mg^{2+}, Ca^{2+}, K^+), Fe^{2+}, Mn^{2+}, and EA (H^+, Al_t). The Na^+ measurements were not considered in the CEC calculation because of pollution of some samples in this element during analyses. However, the Na^+ concentrations were very low in these soils (<0.05 $cmol_c.kg^{-1}$ of soil, <1% of the CEC; Mareschal 2008). An independent measure of the CEC with cobaltihexamin [$Co(NH_3)6Cl_3$ 0,05 N] was also realized on the mean samples of each stand for each layer by dosage by colorimetry at 472 nm (Beckman DU 70) (1 g of soil for 10 ml of reactive; Orsini and Rémy 1976; Ciesielski and Sterckeman 1997). The results showed a good linear relation ($y=0.97x$ and $r^2=0.95$; data not shown) between the two methods indicating that our extraction procedure (e.g., 1 M KCl and 1 M NH_4Cl) is adapted to exchangeable cation measurements and CEC calculation in forest soils. Base saturation (BS) is the percentage of exchangeable "base" cations in the CEC: $BS=100 \times (Mg^{2+} + Ca^{2+} + K^+)/CEC$.

Using a 1 M KCl soil extract, Al^{3+} (Al_d) was determined by ICP–AES (JY180 ULTRACE). The mean charge of Al (McAl) was calculated by the equation used by Rouiller et al. (1980): McAl=3 x (Al_t/Al_d).

The total amount of C and N in soil fractions was estimated using a CHN analyzer (ThermoQuest NCS 2500).

For each soil variable, rhizosphere effects were calculated in the 0–23 cm horizon as the percentage difference between paired rhizosphere and bulk soil samples. A positive rhizosphere effect indicates a greater flux in the rhizosphere, while a negative rhizosphere effect indicates a greater flux in the bulk soil.

Statistical analyses

The descriptive statistical approach (mean, standard deviation, variation coefficient…) as well as the variance analysis (ANOVA) were carried out using the UNISTAT software. The normality of distribution and homoscedasticity of variances were checked. The Bonferroni-Dunn test was performed to test fine root density by layer under the different tree species at the threshold level of a P value of 0.05. The Bonferroni-Dunn test was also performed to establish significant differences between tree species regarding the rhizosphere effect in the 0–23 cm layer for the different soil physicochemical properties at the threshold level of a P value of 0.05. The paired t-Student test was performed to establish significant differences between bulk soil and rhizosphere (not independent samples) by layer under the different tree species for the different soil physicochemical properties at the threshold level of a P value of 0.05. The Student-Newman-Keuls test was performed to establish significant differences between treatments (fertilisation or not) by layer for the different physicochemical properties of the rhizosphere and bulk soil at the threshold level of a P value of 0.05.

Results

Fine root density and rhizosphere

In the surface layer (0 to 3 cm), the fine root (<2 mm) density in the soil was significantly higher under

Norway spruce compared to that of the other species (Table 1). Contrary to Norway spruce of which the great majority of roots were located in the 0–3 cm layer (about 10 g of fine roots by dm^3 of soil in the upper layer and <1 g of fine roots by dm^3 of soil in the deeper layer), the amount of roots produced by Douglas-fir was relatively stable with depth and remained high in the 10–23 cm layer (about 2.5 g of fine roots by dm^3 of soil in the upper layer and >1.5 g of fine roots by dm^3 of soil in the deeper layer) (Table 1). Interestingly, the fine root density in the fertilised plots was lower than that of the non-fertilised ones for Douglas-fir and Norway spruce (Table 1).

The rhizosphere collected represented a mass of about 1.2% of the global soil and ranged from about 0.1% to 5% (data not shown). Whatever the tree species, the treatment (fertilisation or not), and the layer, the amount of rhizosphere collected was significantly related to the fine root density in the soil (Fig. 1; r^2=0.58 and P=0.0132).

Rhizosphere effect on soil properties in non-fertilised plots

Regardless of tree species and layer, the C, N, CEC, BS, K/CEC, Mg/CEC, Ca/CEC, Fe/CEC and to a lesser extent Mn/CEC values were generally higher in the rhizosphere compared to those of the bulk soil (Table 2). In contrast, the EA/CEC and Al_t/CEC values were lower in the rhizosphere compared to those of the bulk soil (Table 2).

The percentage of enrichment of the rhizosphere in C was higher in the native forest (CwS) compared to that of beech, but did not differ between the different species planted in 1974 (Fig. 2). The percentage of enrichment of the rhizosphere in exchangeable "base" cations (Ca^{2+} + K^+ + Mg^{2+}) was higher in the Douglas-fir stand compared to that of CwS and beech stands (Fig. 2). The positive rhizosphere effect for the CEC was higher in the Norway spruce stand compared to the other stands (Fig. 2). As regards to the pH_{water}, no difference between bulk soil and rhizosphere was observed for CwS, beech, oak, and Douglas-fir (Table 2 and Fig. 2). In contrast, a significant decrease of the pH_{water} (increase of H^+) was measured in the rhizosphere under Norway spruce for all layers (Table 2 and Fig. 2). Finally, the McAl values were lower or equivalent in the

Table 1 Fine root density (in g.dm^{-3} of soil) collected in the three soil layers (0–3, 3–10 and 10–23 cm) for the different tree species (native forest (CwS), beech, oak, Douglas-fir, and Norway spruce) at the experimental site of Breuil-Chenue (France). Each value is the mean value of 18 to 20 replicates ± standard deviation. For each variable, values followed by the same letter are not significantly different according to a one-factor (tree species) ANOVA ($P=0.05$), and the Bonferroni-Dunn test

Layer	Tree species						
	CwS	Beech	Douglas	Spruce	Oak	Fertilised Douglas	Fertilised spruce
I	3.2±1.5 ab	3.8±2.5 b	2.4±1.0 ab	9.8±4.3 d	2.4±1.5 ab	1.3±1.0 a	6.4±2.8 c
II	1.7±1.4 bc	2.6±1.0 c	2.2±0.7 bc	1.7±1.0 bc	0.6±0.2 a	1.6±1.2 bc	1.2±0.5 bc
III	1.1±0.3 ab	1.0±0.5 ab	1.5±0.7 b	1.0±0.7 ab	0.4±0.1 a	0.9±0.4 ab	0.7±0.5 ab

rhizosphere compared to those of the bulk soil for all species except for CwS (Table 2).

Fertilisation effect on rhizosphere and bulk soil properties

As observed in the non-fertilised plots, the C, N, CEC, BS, K/CEC, Mg/CEC, Ca/CEC, Fe/CEC and Mn/CEC values were generally higher in the Douglas-fir and Norway spruce rhizosphere of the fertilised plots compared to those of the bulk soil (Table 2).

In Douglas-fir stands, the CEC, and K, Mg, and Mn saturations of the rhizosphere and bulk soil did not differ between the non-fertilised and fertilised plots (Table 2). The BS, pH$_{water}$, and Ca saturation were higher in the rhizosphere and bulk soil of the

fertilised Douglas-fir stand compared to those of the non-fertilised ones (Table 2). In contrast, EA/CEC and Al$_t$/CEC ratio were lower in the rhizosphere and bulk soil of the fertilised Douglas-fir stand compared to those of the non-fertilised ones (Table 2).

In Norway spruce stands, the CEC, pH$_{water}$, BS, EA/CEC, and Mg saturation of the rhizosphere and bulk soil did not differ between the non-fertilised and fertilised plots (Table 2). In contrast, total C and N concentrations, and Fe saturation were generally higher in the rhizosphere and bulk soil of the fertilised plot compared to those of the non-fertilised ones (Table 2).

Discussion

According to Binkley (1995), the main parameters allowing the comparison of soils are: soil and parent material homogeneity, proximity of the different stands, identical microclimate (e.g., temperature, moisture, rainfall), exposition, and slope. The experimental site of Breuil-Chenue (France) used in our study meets the above criteria because the different plots are juxtaposed and soils (e.g., pH$_{water}$, exchangeable cations, CEC, particle size distribution…) and parent material (e.g., composition and texture) are homogeneous (Bonneau et al. 1977).

In our study, Norway spruce produced an important root system in the upper soil layer which decreased drastically with depth whereas the observed fine root density under Douglas-fir remained constant and relatively high in the soil profile. Interestingly, the fine root density was lower when the stands were fertilised. This can be due to the fact that in conditions of high nutrient bioavailability, trees considerably diminish the allocation of carbon to the roots because
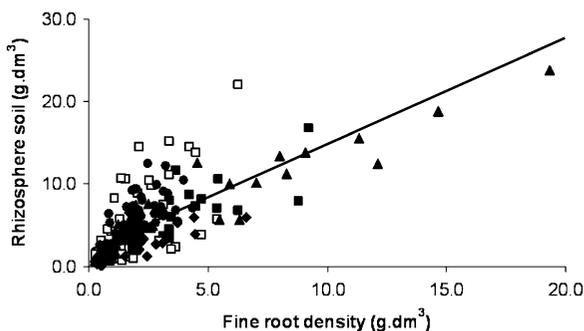
Fig. 1 Relationship between the fine root density (in g.dm^{-3} of soil) and the amount of rhizosphere (in g.dm^{-3} of soil) for the different tree species for the three soil layers (0–3, 3–10 and 10–23 cm) at the experimental site of Breuil-Chenue (France). The clear square, the dark square, the dark rhomb, the dark circle, and the dark triangle represent the native forest (CwS), beech, oak, Douglas-fir, and Norway spruce, respectively. The equation and the coefficient of determination of the linear regression are $y=0.44x + 0.23$ and $r^2=0.58$

Table 2 Physicochemical properties of rhizosphere (R) and bulk soil (B) of the different tree species (native forest (CwS), beech, oak, Douglas-fir, Norway spruce) for the three soil layers (I: 0–3 cm, II: 3–10 cm, and III: 10–23 cm) and the two treatments (fertilised or not) at the experimental site of Breuil-Chenue (France). Each value is the mean value of 18 to 20 replicates. The columns R-B and Rf-Bf presents the results of statistical analyses for each tree species and each layer regarding the "rhizosphere effect" on soil physicochemical properties in the non-fertilised and in the fertilised stands, respectively. For each variable, the presence of an asterisk indicates significant differences between bulk soil and rhizosphere according to a paired t-Student analysis at the threshold of $P=0.05$. The columns R-Rf and B-Bf presents the results of statistical analyses for Douglas-fir and Norway spruce and for each layer regarding the "fertilisation effect" on physicochemical properties of rhizosphere and bulk soil, respectively. For each variable, the presence of an asterisk indicates significant differences between rhizosphere or bulk soil of the non-fertilised and fertilised plots according to a Student-Newman-Keuls analysis at the threshold of $P=0.05$. f Fertilised, CEC Cation exchange capacity, EA Exchangeable acidity, Al_t Titrated Al, BS Base saturation, $McAl$ Mean charge Al, nd Not determined

	Layer	CwS			Beech			Oak			Douglas-fir								Norway spruce							
Tree species		R	B	R-B	R	B	R-B	R	B	R-B	R	B	R-B	Rf	Bf	Rf-Bf	R-Rf	B-Bf	R	B	R-B	Rf	Bf	Rf-Bf	R-Rf	B-Bf
N_t (g.kg^{-1})	I	20,6	15,4	*	7,9	6,0	*	nd	nd		nd	nd		6,8	6,6	*			nd	nd		10,7	7,8	*		*
	II	6,9	4,7	*	5,5	4,5	*	5,0	4,0	*	5,4	4,9	*	5,7	4,7	*	*	*	4,9	4,1	*	5,7	4,9	*	*	*
	III	3,6	2,9	*	3,6	2,9	*	3,2	2,4	*	3,7	2,7	*	4,0	2,7	*	*	*	3,3	2,5	*	4,0	3,1	*	*	*
C_t (g.kg^{-1})	I	351	260	*	128	100	*	nd	nd		nd	nd		120	117	*			nd	nd		196	145,9	*		*
	II	122	85	*	90	74	*	84	68	*	92	79	*	98	83	*	*	*	87	72	*	103	84,7	*	*	*
	III	65	51	*	62	49	*	58	44	*	63	46	*	70	47	*	*	*	61	44	*	70	52,3	*	*	*
pH$_{water}$	I	3,8	3,8	*	4,2	4,2	*	4,0	4,1	*	4,0	3,9	*	4,5	4,5	*	*		3,8	4,0	*	3,8	3,9			
	II	3,9	4,0	*	4,5	4,5	*	4,4	4,3	*	4,1	4,0	*	4,4	4,4	*	*		4,1	4,3	*	4,0	4,1			
	III	4,6	4,5	*	4,7	4,7	*	4,7	4,7	*	4,5	4,4	*	4,4	4,6	*	*		4,5	4,7	*	4,4	4,5			
CEC (cmol$_c$.kg^{-1})	I	23,6	19,3	*	15,1	14,2	*	16,6	13,9	*	19,3	17,3	*	17,7	17,9	*			19,4	15,0	*	20,4	17,2	*		
	II	17,1	15,0	*	12,3	11,4	*	14,5	12,9	*	15,2	13,7	*	14,4	13,6	*	*		14,9	12,6	*	15,6	13,8	*		
	III	10,9	9,4	*	8,6	7,5	*	10,2	8,6	*	11,1	8,8	*	10,4	8,3	*	*		10,4	7,6	*	11,1	8,7	*		
EA/CEC	I	53,4	65,5	*	72,7	80,2	*	69,2	80,9	*	54,4	64,7	*	39,3	34,7	*		*	65,8	77,9	*	57,8	69,2	*		*
	II	79,9	85,8	*	84,3	89,4	*	80,9	89,8	*	82,0	89,3	*	63,2	70,0	*	*	*	86,1	91,0	*	80,8	86,9	*	*	
	III	85,6	87,4	*	85,5	91,7	*	83,4	90,3	*	83,0	92,4	*	80,1	88,0	*	*	*	85,3	93,4	*	87,9	92,4	*		
Al$_t$/CEC	I	22,2	35,0	*	60,6	67,4	*	53,2	69,8	*	38,9	51,4	*	32,5	29,4	*		*	47,4	63,5	*	38,9	52,4	*		*
	II	62,8	74,3	*	77,3	83,0	*	74,7	86,1	*	72,7	80,1	*	56,9	64,0	*	*		80,2	86,3	*	70,4	78,1	*	*	
	III	81,6	84,8	*	82,0	89,3	*	81,0	88,1	*	79,8	89,3	*	76,9	86,2	*	*		81,8	91,3	*	84,6	90,0	*		
BS (%)	I	39,2	26,1	*	18,5	12,5	*	24,2	14,6	*	37,2	28,4	*	54,2	58,6	*		*	26,1	16,2	*	34,6	23,6	*		*
	II	11,4	6,9	*	11,3	7,0	*	15,5	8,1	*	13,5	8,1	*	32,1	26,0	*	*	*	9,1	6,1	*	13,4	8,1	*	*	
	III	10,5	4,9	*	11,6	5,9	*	14,6	8,3	*	14,5	4,9	*	17,0	9,4	*	*	*	11,2	5,2	*	9,4	5,5	*		
K/CEC	I	12,5	6,0	*	6,7	3,8	*	11,9	6,3	*	7,9	5,7	*	6,2	3,9	*			7,3	5,0	*	6,2	3,9	*		*
	II	6,3	2,9	*	6,5	3,2	*	10,7	4,8	*	7,0	2,9	*	6,2	2,8	*	*		4,5	3,3	*	3,6	2,5	*	*	
	III	6,7	2,2	*	7,1	3,2	*	10,6	5,5	*	9,7	2,0	*	8,3	2,4	*	*		6,4	3,8	*	4,0	1,9	*	*	*

Mg/CEC	I	11,9	8,3	3,4	2,5	4,6	3,2	7,2	6,3	5,7	5,5	5,9	3,7	5,3	3,0
	II	3,3	2,2	2,3	1,8	2,8	2,0	3,3	2,4	4,0	3,1	2,7	1,7	4,4	1,8
	III	2,4	1,6	2,2	1,4	2,3	1,9	1,9		3,1	1,7	2,8	1,1	2,2	1,4
Ca/CEC	I	14,8	11,8	8,4	6,2	7,6	5,1	22,1	16,5	42,3	49,1	12,9	7,5	23,1	10,7
	II	1,9	1,8	2,4	2,0	2,0	1,3	3,2	2,8	21,9	20,1	1,8	1,1	5,4	1,4
	III	1,4	1,2	2,2	1,3	1,7	0,9	1,8	1,1	5,7	5,4	2,0	0,3	3,3	1,2
Fe/CEC	I	4,4	6,0	5,7	4,1	3,6	1,9	3,6	2,7	2,2	1,7	5,2	3,5	6,2	6,1
	II	8,1	6,7	3,1	2,0	2,4	1,3	3,7	1,5	3,3	2,4	3,9	2,1	5,3	4,6
	III	2,5	6,5	0,9	0,5	0,7	0,6	1,1	1,5	1,4	1,1	2,0	0,3	1,6	1,2
Mn/CEC	I	3,0	2,4	3,1	3,2	3,0	2,5	4,8	4,2	4,3	5,0	3,0	2,3	1,4	1,1
	II	0,6	0,6	1,4	1,7	1,1	0,9	0,9	1,1	1,5	1,6	0,8	0,9	0,5	0,4
	III	1,4	1,2	2,0	1,9	1,3	0,8	1,4	1,2	2,5	1,5	1,6	1,2	1,0	0,8
McAl	I	2,7	2,3	2,7	2,9	2,7	3,0	2,5	3,0	2,6	2,8	2,6	2,8	2,6	2,6
	II	2,8	2,6	2,9	3,0	2,9	3,0	2,8	2,7	2,7	2,7	2,8	2,9	2,8	2,8
	III	3,0	3,0	3,0	3,0	3,0	3,0	3,0	2,7	3,0	2,9	2,8	2,9	3,0	3,0

of easy access to nutrients (Schmidt and Linke 2007). Indeed, root development is remarkably sensitive to the variations of mineral nutrient supplying and distribution in soils (Hodge 2004; Hodge et al. 2009). Also, numerous studies demonstrated the ability of roots to modify the morphology and the architecture of root system in response to nutrient localization and availability (Robinson 1994; Schöttelndreier and Falkengren-Grerup 1999; Forde and Lorenzo 2001). As observed by Philips and Fahey (2008), the percentage of collected rhizosphere is positively related to the amount of roots produced by the different species. In our study, the rhizosphere represented in average 1.2% of the total soil. This value is in agreement with that obtained by Gobran and Clegg (1996) in a Norway spruce stand where the rhizosphere represented 1 to 2% of the total soil.

Significant differences appeared between bulk soil and rhizosphere. Whatever the tree species and layer, N, C, BS, and Ca, Mg, K, Fe, Mn saturations generally increased in the rhizosphere compared to the bulk soil. These results confirm those obtained by Clegg et al. (1997), Wang and Zabowski (1998), Turpault et al. (2005) in forest sites despite of the low availability of cations in the soils. Also, Gobran and Clegg (1996) observed in a Swedish forest that the CEC and BS were higher at the soil-root interface and the rhizosphere of Norway spruce compared to the bulk soil. They attributed this to the accumulation of organic matter in the rhizosphere (for example, 23% of organic matter in the rhizosphere vs. 10% in the bulk soil of the E horizon). In addition, numerous studies demonstrated the capacity of roots and soil microorganisms to mobilize elements such as K, Mg, Ca… through the weathering of mineral phases (for reviews, see Barker et al. 1997; Berner et al. 2005; Gadd, 2007; Uroz et al. 2009). Finally, the uptake of water by plant generates a rapid transport of solution containing elements from the bulk soil to the vicinity of the roots by mass flow (Turpault et al. 2007). These soluble elements (from mineral weathering and mass flow) can thus be fixed on the organic matter and on the mineral surfaces thus enriching the rhizosphere. Glowa et al. (2004) even demonstrated in coniferous forests that properties of rhizosphere are strongly influenced by the presence of ectomycor- rhizae. These authors observed that total C and N, CEC as well as exchangeable K^+, and Na^+ were significantly higher in soils influenced by ectomycor-
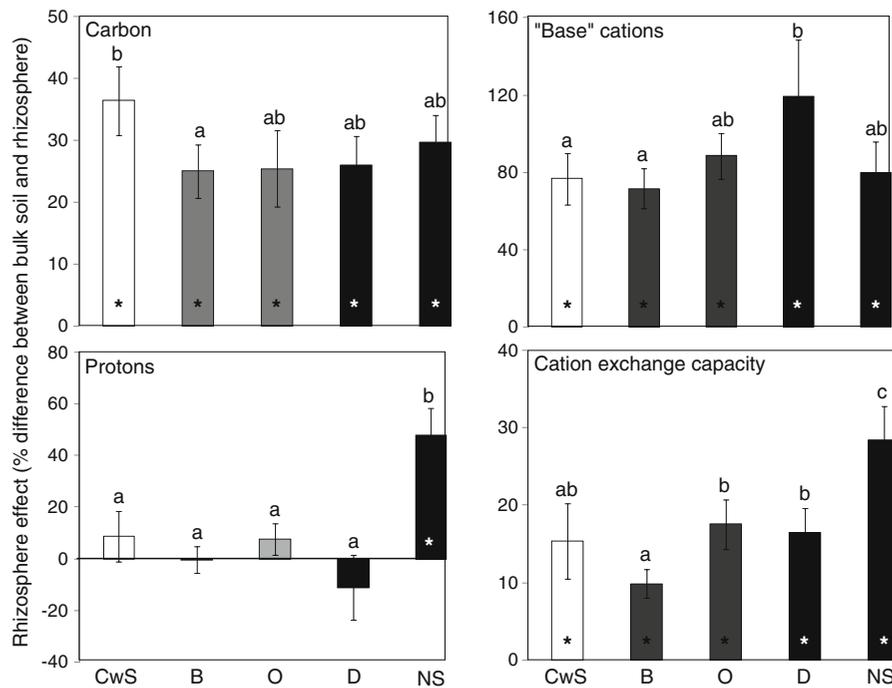
Fig. 2 Rhizosphere effect (% difference between bulk soil and rhizosphere) for the different species in the 0–23 cm layer at the experimental site of Breuil-Chenue (France), for carbon, "base" cations, cation exchange capacity, and protons. A positive rhizosphere effect indicates a greater flux in the rhizosphere, while a negative rhizosphere effect indicates a greater flux in the bulk soil. Histograms represent the mean value of 54 to 60 replicates. Bars represent standard deviations. Values with an asterisk are significantly different from 0 according to a Student-Fischer analysis at the threshold of $P=0.05$. Values with the same letter are not significantly different according to a one-factor (tree species) ANOVA ($P=0.05$) and the Bonferroni-Dunn test. *White*: native forest (old beech and oak coppice with standards: CwS); *grey*: hardwoods (beech: B, oak: O); *black*: coniferous (Douglas-fir: D, Norway spruce: NS)

rhizal fungi. Interactions between roots, microorganisms and soil can thus create a mutually supportive system that can raise nutrient availability by enriching the pool of cations in the rhizosphere compared to the bulk soil. Interestingly, similar to the non-fertilised stands, the rhizosphere of the fertilised Douglas-fir and fertilised Norway spruce stands were generally enriched in N, C, Ca, K, and Mg suggesting that the enrichment of the rhizosphere in nutrients would not be dependent on the level of nutrient availability in the ecosystem.

We also showed that EA/CEC, Al_t/CEC and McAl generally decrease in the rhizosphere. The decrease in Al charge in the rhizosphere mainly results from the exudation of complexing agents by roots and root-associated microorganisms (Curl and Truelove 1986; Marschner et al. 1986; Gobran and Clegg 1996). Organic acids produced by roots and soil microorganisms (e.g., oxalic, citric, lactic, malic acids) act through their hydroxyl and carboxyl groups ("ligand-

promoted mechanism") and through their protons ("proton-promoted mechanism") (Berthelin 1983; Welch and Ullman 1996; Bennett et al. 2001) and can increase the mineral dissolution more than the simple action of protons. These organic acids form soluble complexes with Al (Al-OH) or Fe (Fe-OH) which increase the dissolution of Al-Fe bearing minerals by directly attacking mineral surface and/or by complexing Al and Fe in solution which generates disequilibrium between the solid phase and the soil solution (Drever and Vance 1994; Berner and Cochran 1998; Jones 1998). Due to their richness in carboxyl, phenol and hydroxyl groups, humic substances can also induce a decrease in Al charge in the rhizosphere by binding Al, notably in the upper soil horizon. According to Dessureault-Rompré et al. (2008), this process is, however, secondary in the rhizosphere in comparison to that originating in organic acids. In a previous study on the experimental site of Breuil-Chenue, Calvaruso et al. (2009) already

demonstrated that the clay-sized fraction collected in the rhizosphere of Norway spruce and oak was impoverished in Al and Fe compared to the bulk soil. These authors even observed the formation of mica-like minerals in the rhizosphere of Norway spruce and oak which they explained by a two-step mechanism when the initial mineral was hydroxy-interlayered vermiculite (HIV). First, the acid and complexing compounds produced in the rhizosphere release the interlayer Al of the HIV and generate vermiculite which is characterized by an expandable interlayer space. Second, the K enters the interlayer space, collapsing the structure to form a mineral with a mica-like spacing.

Our study also revealed differences between tree species regarding the magnitude of rhizosphere effects: CwS vs. beech for C, Douglas-fir vs. CwS and beech for "base" cations, and Norway spruce vs. other species for pH_{water} and CEC. Firstly, we observed that the rhizosphere of the native forest (CwS; 90% of beech) was more enriched in C than that of the beech. This effect could result from differences in root exudates' composition (qualitatively and quantitatively), linked (i) to plant species and age (mature forest of about 150 years for CwS vs. 24 years for the beech; Smith 1976; Bertin et al. 2003) and (ii) to the microbial communities associated to the roots (Rambelli 1973; Laheurte et al. 1990; Leyval and Berthelin 1993). Besides, through 454 pyrosequencing analysis, Buée et al. (2009) observed an extraordinary high diversity and heterogeneity of the fungal communities inhabiting the soil under the different tree species of the Breuil-Chenue forest. Secondly, we observed a higher enrichment of the rhizosphere in "base" cations in Douglas-fir stand compared to the other species. The accumulation of elements in the rhizosphere results from positive differences between element input fluxes, principally by mass flow, mineral weathering, and organic matter mineralization, and element output fluxes, principally by plant uptake in the rhizosphere. In consequence, the higher enrichment of the rhizosphere in "base" cations in Douglas-fir stand corresponds to higher input fluxes and/or lower output fluxes. Complementary studies regarding soil mineralogy and soil solutions are, however, needed to determine which process(es) prevails. Finally, we observed that only Norway spruce roots significantly acidified the rhizosphere. This acidification results from the production

by roots and root-associated microorganisms of a great variety of acid compounds such as protons, organic acids, and complexing organic acids (Leyval and Berthelin 1991; Hoffland 1992; Drever 1994; Jones and Darrah 1994; Kelly et al. 1998; Welch et al. 1999; Liermann et al. 2000; Landeweert et al. 2001). According to Calvaruso et al. (2009), this decrease of pH in the rhizosphere could be due to a massive production of protons by Norway spruce roots to compensate for the predominant uptake of N under NH_4^+ form in the Breuil forest. This acidification of the rhizosphere in the Norway spruce stands could also reveal differences in the activities among the microbial communities colonizing the Norway spruce roots and those colonizing the other species. For example, Glowa et al. (2004) demonstrated in a spruce forest, that the colonization of roots by certain species of ectomycorrhizal fungi can significantly decrease the pH of the rhizosphere. As observed by Calvaruso et al. (2009), the exudation of large amount of protons by Norway spruce roots and root-associated microorganisms generated an important loss of interlayer Al in the rhizosphere (clay-sized fraction), three times higher than that measured for the oak. This mechanism could thus explain the higher CEC increase in the rhizosphere of Norway spruce related to the other species. Indeed, the removal of interlayer Al in clay particles releases blocking positions and contributes to an increase in the CEC of the soil (Townsend and Reed 1971; De Kimpe and Laverdiere 1980).

The supply of Ca is still observable 17 years after site fertilisation in the fertilised plot of the Douglas-fir stand: about 40% of the CEC of the rhizosphere and 50% of the CEC of the bulk soil is occupied by Ca in the upper layer of the fertilised Douglas-fir plot vs. about 20% and 10% in the Norway spruce. Several mechanisms control Ca availability in soils. Some of these mechanisms are closely linked to tree growth while others are more related to abiotic factors (climate, soil parent material, relief), while often there is an interaction of both biotic and abiotic factors. As abiotic factors are almost identical in the Douglas-fir and Norway spruce plots used in our study, the differences in soil Ca availability were likely to result from tree growth. The accumulation of Ca in the rhizosphere and bulk soils of the fertilised Douglas-fir plot could thus be due to a faster growth of Douglas-fir than Norway spruce. Besides, in a recent study conducted on the Breuil-Chenue experimental site,

Sicard et al. (2006) demonstrated that Douglas-fir was more productive than Norway spruce: +28% for total tree biomass, +50% for ligneous biomass, and +53% for stem wood. The accumulation of Ca in the upper layer could thus result from the better potential of this species to take up and store Ca in its biomass (thus limiting drainage losses) and then to restitute it to the soil by way of litterfall. In addition, Douglas-fir is a species with slow litter decomposition rates thus building up thicker forest floors (Klopatek 2009), it may have higher amounts of Ca immobilized in the forest floor. Finally, as described previously, Douglas-fir has high fine root density in the deeper layer and thus may be able to pump Ca from deeper soil layers to the soil surface where the Ca eventually will return as leaf litter or with throughfall/stemflow (Johnson et al. 1985; Dijkstra and Smits 2002).

Conclusion

Our study demonstrates that common European tree species and Douglas-fir significantly impact the physicochemical properties of the rhizosphere. Whatever the tree species (beech, oak, Douglas-fir, Norway spruce) and the layer (0–3, 3–10, and 10–23 cm), the rhizosphere is generally enriched in C, N, Ca, Mg, and K revealing that interactions between roots, microorganisms and soil can enrich the pool of nutrients in the rhizosphere compared to the bulk soil. Interestingly, the same positive rhizosphere effect was observed in the fertilised plots for the coniferous suggesting that soil fertilization does not influence rhizosphere properties. Our study also revealed differences of magnitude of the rhizosphere effect between tree species for several soil properties (pH_{water}, C, "base" cations, CEC). Finally, Douglas-fir maintains the Ca-fertilization effect 17 years after site treatment which is not the case for Norway spruce. This difference could result from the fast growth of Douglas-fir which thus pumps and stores more Ca in its biomass than Norway spruce and then restitutes it to the soil by way of litterfall. In these temperate forest ecosystems, further researches are, however, required to assess (i) the temporal heterogeneity of the rhizosphere effect resulting from seasonal variations of rhizosphere processes as well as (ii) the spatial heterogeneity of the rhizosphere effect, notably resulting from the variations in the activities of fungi and bacteria colonizing the root system.

References

Augusto L, Ranger J, Binkley D et al (2002) Impact of several common tree species of European temperate forests on soil fertility. Ann For Sci 58:47–58

Barker WW, Welch SA, Banfield JF (1997) Biogeochemical weathering of silicate minerals. In: Banfield JF, Nealson KH (eds) Geomicrobiology: interactions between microbes and minerals. Miner Soc Am, Washington, DC, pp 391–428

Bennett PC, Rogers JR, Choi WJ et al (2001) Silicates, silicate weathering, and microbial ecology. Geomicrobiol J 18:3–19

Berner RA, Cochran MF (1998) Plant-induced weathering of Hawaiian basalts. J Sediment Res, Sect A Sediment Pet Proc 68:723–726

Berner EK, Berner RA, Moulton KL (2005) Plants and mineral weathering: present and past. In: Drever JI (ed) Surface and ground water, weathering and soils. Treatise on geochemistry series. Elsevier, Amsterdam, pp 169–188

Berthelin J (1983) Microbial weathering processes. In: Krumbein WE (ed) Microbial geochemistry. Blackwell Scientific Publications, Oxford, pp 223–262

Bertin C, Yang X, Weston L (2003) The role of root exudates and allelochemicals in the rhizosphere. Plant Soil 256:67–83

Binkley D (1995) The influence of tree species on forest soils: Process and Patterns. In: Mead DJ, Cornforth IS (eds) Proceeding of the trees and soil workshop. Agronomy Society of New Zealand Special Publication, Lincoln University, Canterbury, pp 1–33

Binkley D, Giardina C (1998) Why do tree affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89–106

Binkley D, Menyailo O (2004) Gaining insights on the effects of tree species on soils. In: Binkley D, Menyailo O (eds) Proceedings of the NATO advanced research workshop on trees and soil interactions, implications to global climate change. Springer, Dordrecht, pp 1–17

Bonneau M, Lacaze JF, Lelong F et al (1977) Modification de la fertilité des sols sous boisements artificiel des résineux purs. (Internal document-INRA)

Buée M, Reich M, Murat C et al (2009) 454 Pyrosequencing analyses of forest soils reveal an unexpectedly high fungal diversity. New Phytol 184:449–456

Calvaruso C, Mareschal L, Turpault MP (2009) Rapid clay weathering in the Rhizosphere of Norway Spruce and oak in an acid forest ecosystem. Soil Sci Soc Am J 73:331–338

Ciesielski H, Sterckeman T (1997) A comparison between three methods for the determination of cation exchange capacity and exchangeable cations in soils. Agronomie 17:9–15

Clegg S, Gobran GR, Guan X (1997) Rhizosphere chemistry in an ammonium sulfate and water manipulated Norway spruce [Picea abies (L.) Karst.] forest. Can J Soil Sci 77:515–523

Curl EA, Truelove B (1986) The rhizosphere. Springer, Berlin

Dakora DF, Phillips DA (2002) Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 245:35–47

Darrah PR (1993) The rhizosphere and plant nutrition: a quantitative approach. Plant Soil 155(156):1–20

Dejou J (1966) Le massif granitique à 2 micas de la Pierre qui Vire (Yonne et Nièvre). Etude pétrographique de ses différents faciès. Ann Agron 17:99–141

De Kimpe CR, Laverdiere MR (1980) Amorphous material and aluminum interlayers in Quebec spodosols. Soil Sci Soc Am J 44:639–642

Dessureault-Rompré J, Nowack B, Schulin R, Tercier-Waeber M-L, Luster J (2008) Metal solubility and speciation in the rhizosphere of Lupinus albus cluster roots. Environ Sci Technol 42:7146–7151

Dijkstra FA, Smits MM (2002) Tree species effects on calcium cycling: the role of calcium uptake in deep soils. Ecosystems 5:385–398

Drever JI (1994) The effect of land plants on weathering rates of silicate minerals. Geochim Cosmochim Acta 58:2325–2332

Drever JI, Vance GF (1994) Role of soil organic acids in mineral weathering. In: Pittman ED, Lewan MD (eds) Role of soil organic acids in geological processes. Springer, New York, pp 138–161

Drever JI, Stillings LL (1997) The role of organic acids in mineral weathering. Colloid Surf A-Physicochem Eng Asp 120:167–181

Espiau P, Peyronel A (1976) L'acidité d'échange dans les sols. Méthode de détermination de l'aluminium échangeable et des protons échangeables. Bull AFES 3:161–175

Fisher RF, Binkley D (2000) Ecology and management of forest soils. Wiley, New York

Forde B, Lorenzo H (2001) The nutritional control of root development. Plant Soil 232:51–68

Gadd GM (2007) Geomycology: biogeochemical transformation of rocks, minerals, metals and radionuclides by fungi, bioweathering and bioremediation. Mycol Res 111:3–49

Glowa KR, Arocena JM, Massicotte HB (2004) Properties of soils influenced by ectomycorrhizal fungi in hybrid spruce [Picea glauca×engelmannii (Moench.) Voss]. Can. J. Soil Sci 84:91–102

Gobran GR, Clegg S (1996) A conceptual model for nutrient availability in the mineral soil-root system. Can J Soil Sci 76:125–131

Gobran GR, Clegg S, Courchesnes F (1998) Rhizospheric processes influencing the biogeochemistry of forest ecosystems. Biogeochemistry 42:107–120

Grayston SJ, Vaughan D, Jones D (1996) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Appl Soil Ecol 5:29–56

Hinsinger P, Gobran GR, Gregory PJ et al (2005) Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. New Phytol 68:293–303

Hinsinger P, Bengough AG, Vetterlein D et al (2009) Rhizosphere: biophysics, biogeochemistry and ecological relevance. Plant Soil 321:117–152

Hobbie S (1992) Effects of plant species on nutrient Cycling. Tree 7:336–339

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol 162:9–24

Hodge A, Berta G, Doussan C et al (2009) Plant root growth, architecture and function. Plant Soil 321:153–187

Hoffland E (1992) Quantitative evaluation of the role of organic acid exudation in the mobilization of rock phosphate by rape. Plant Soil 140:279–289

Johnson DW, Richter DD, Lovett GM et al (1985) The effects of atmospheric deposition on potassium, calcium, and magnesium cycling in two deciduous forests. Can J Soil For Res 15:773–782

Jones DL (1998) Organic acids in the rhizosphere—a critical review. Plant Soil 205:25–44

Jones DL, Darrah PR (1994) Role of root derived organic-acids in the mobilization of nutrients from the rhizosphere. Plant Soil 166:247–257

Jones DL, Nguyen C, Finlay DR (2009) Carbon flow in the rhizosphere: carbon trading at the soil-root interface. Plant Soil 321:5–33

Kelly E, Chadwick OA, Hilinski TE (1998) The effect of plants on mineral weathering. Biogeochemistry 42:21–53

Klopatek JM (2009) Litter decomposition contrasts in second- and old-growth Douglas-fir forests of the Pacific Northwest, USA. Plant Ecol 196:123–133

Laheurte F, Leyval C, Berthelin J (1990) Root exudates of maize, pine and beech seedlings influenced by mycorrhizal and bacterial inoculation. Symbiosis 9:111–116

Lambers H, Mougel C, Jaillard B et al (2009) Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. Plant Soil 231:83–115

Landeweert R, Hoffland E, Finlay RD et al (2001) Linking plants to rock: ectomycorrhizal fungi mobilize nutrients from minerals. Trends Ecol Evol 16:248–253

Leyval C, Berthelin J (1991) Weathering of a mica by roots and rhizospheric micro-organisms of pine. Soil Sci Soc Am J 55:1009–1016

Leyval C, Berthelin J (1993) Rhizodeposition and net release of soluble organic compounds by pine and beech seedlings inoculated by rhizobacteria and ectomycorrhizal fungi. Biol Fertil Soils 15:259–267

Liermann LJ, Kalinowski BE, Brantley SL et al (2000) Role of bacterial siderophores in dissolution of hornblende. Geochim Cosmochim Acta 64:587–602

Mareschal L (2008) Effet des substitutions d'essences forestières sur l'évolution des sols et de leur minéralogie: bilan après 28 ans dans le site expérimental de Breuil (Morvan). PhD thesis. University of Nancy

Mareschal L, Bonnaud P, Turpault MP et al (2010) Impact of common European tree species on the chemical and physicochemical properties of fine earth: an unusual pattern. Eur J Soil Sci 61:14–23

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic, London

Marschner H, Romheld V, Kissel M (1986) Different strategies in higher plants in immobilisation and uptake of iron. J Plant Nutr 9:695–713

Orsini L, Rémy JC (1976) Utilisation du chlorure de colbalti-hexammine pour la détermination simultanée de la capacité d'échange et des bases échangeables des sols. Science du Sol 4:269–275

Philips RP, Fahey TJ (2006) Tree species and mycorrhizal associations influence the magnitude of rhizosphere effects. Ecology 87:1302–1313

Philips RP, Fahey TJ (2007) Fertilization effects on fineroot biomass, rhizosphere microbes and respiratory fluxes in hardwood forest soils. New Phytol 176:655–664

Philips RP, Fahey TJ (2008) The influence of soil fertility on rhizosphere effects in Northern hardwood forest soils. Soil Sci Soc Am J 72:45–53

Rambelli A (1973) The rhizosphere of mycorrhizae. In: Marks GC, Kozlowski TT (eds) Ectomycorrhizae: their ecology and physiology. Academic, New York, pp 299–343

Robinson D (1994) The responses of plants to non-uniform supplies of nutrients. New phytol 127:635–674

Rouiller J, Guillet B, Bruckert S (1980) Cations acides échangeables et acidités de surface. Approche analytique et incidence pédogénétique Bull AFES 2:161–175

Schmidt W, Linke B (2007) Nutrients as regulators of root morphology and architecture. In: Pinton R, Varanini Z, Nannipieri P (eds) The rhizosphere: biochemistry and organic substances at the soil plant interface, 2nd edn. Marcel Dekker Inc, New York, pp 135–150

Schöttelndreier M, Falkengren-Grerup U (1999) Plant induced alteration in the rhizosphere and the utilisation of soil heterogeneity. Plant Soil 209:297–309

Seddoh FK (1973) Altération des roches cristallines en Morvan (granites, granophyres, rhyolites). Etude Minéralogique, géochimique et micromorphologique. Doctoral dissertation, Université de Dijon, France

Sicard C, Saint-André L, Gelhaye D et al (2006) Effect of initial fertilisation on biomass and nutrient content of Norway spruce and Douglas-fir plantations at the same site. Tree 20:229–246

Smith WH (1976) Character and significance of forest tree root exudates. Ecology 57:324–331

Townsend FC, Reed LW (1971) Effects of amorphous constituents on some mineralogical and chemical properties of a panamanian latosol. Clays Clay Miner 19:303–310

Turpault MP, Uterano C, Boudot JP et al (2005) Influence of mature Douglas-fir roots on the solid soil phase of the rhizosphere and its solution chemistry. Plant Soil 275:327–336

Turpault MP, Gobran GR, Bonnaud P (2007) Temporal variations of rhizosphere and bulk soil chemistry in a Douglas fir stand. Geoderma 137:490–496

Turpault MP, Nys C, Calvaruso C (2009) Rhizosphere impact on the dissolution of test-minerals in a forest ecosystem. Geoderma 153:147–154

Uroz S, Calvaruso C, Turpault MP et al (2009) Mineral weathering by bacteria: ecology, actors and mechanisms. Trends Microbiol 17:378–387

USDA (1999) Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys, 2nd edn. Agriculture Handbook Number 436. U.S. Gov Print Office, Washington, DC

Wang X, Zabowski D (1998) Nutrient composition of Douglas-fir rhizosphere and bulk solutions. Plant Soil 200:13–20

Welch SA, Ullman WJ (1996) Feldspar dissolution in acidic and organic solutions: compositional and pH dependence of dissolution rate. Geochim cosmochim Acta 60:2939–2948

Welch SA, Barker WW, Banfield JF (1999) Microbial extra-cellular polysaccharides and plagioclase dissolution. Geochim Cosmochim Acta 63:1405–1419

Zeller B, Recous S, Kunze M et al (2007) Influence of tree species on gross and net N transformation in forest soils. Ann For Sci 64:151–158