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REGULAR ARTICLE

Temporal dynamics of exchangeable K, Ca and Mg in acidic bulk soil and rhizosphere under Norway spruce (*Picea abies* Karst.) and beech (*Fagus sylvatica* L.) stands

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Abstract
Aims The aim of this study was to assess the seasonal influence on the dynamics of exchangeable nutrients (K, Ca and Mg) in acidic and nutrient-poor forest soils, where nutrients can become limiting for tree growth.
Methods The amounts of exchangeable base cations (K^++Ca^{2+}+Mg^{2+}) were measured in soil samples collected in three soil compartments (Bulk, Outer Rhizosphere, and Inner Rhizosphere) and in 4 months (November, February, May and August) under two stands of 31-year-old Norway spruce and beech in an acidic temperate forest.
Results In all season, both rhizosphere compartments were enriched in exchangeable nutrients compared to bulk soil. This suggests that tree roots and root-associated microorganisms (bacteria and mycorrhizal fungi) increased nutrient availability through mineral weathering or mineralization processes, and thus could contribute to forest sustainability in nutrient-poor conditions. Interestingly, in contrast to beech, a drastic decrease of exchangeable base cations was observed in bulk soil of spruce between November and February (higher than 80% for K and Mg, and 100% for Ca). The relation between this decrease, Al solubility, and nitrate concentration are evoked in the discussion.
Conclusion This study reveals that processes resulting from interactions between trees, microorganisms and soil influence not only the seasonal dynamics of nutrients in the root vicinity but also the bulk soil function.

Keywords Soil nutrients · Temporal variations · Rhizosphere · Bulk soil · Exchangeable base cations · Norway spruce · Beech · Sustainable forest ecosystem

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Introduction

With the actual development of bio-energy from wood, the intensification of forestry managements may affect nutrient dynamics and availability in soils (Belleau et al. 2006; Keller et al. 2006), particularly in nutrient-poor ecosystems such as acidic soils. In view of a sustainable forest management, it is important to characterize the dynamics of major nutrients, such as Ca, Mg and K, in these forest soils. The fraction of those cations occupying the cation exchange capacity (CEC) is a measurement of their relative storage in soil and thus of their potential availability for tree nutrition. In acidic soils, the exchange reactions (adsorption/desorption reactions) between the soil solution and the exchange site are mainly dominated by element concentration in solution, inputs of acidity, speciation of Al and ionic strength of the soil solution (Ross et al. 2008). Although the chemistry of soil solutions reacts rapidly with the seasonal changes (Ranger et al. 2001; Vestin et al. 2008), it is generally admitted that the quantity of exchangeable cations is relatively stable or evolves very slowly in the time (over a 10 year period), due to soil acidification process (Johnson et al. 1990; Gbondo-Tugbawa and Driscoll 2003; Courchesne et al. 2005). However, previous studies have reported a weak decline (less than 50%) in the exchangeable nutrients (Ca, Mg and K) between late winter and summer in bulk soil of forest ecosystems (Haines and Cleveland 1981; Peterson and Rolfe 1982; Kelly and Mays 1999). These observations suggest thus that the stock of exchangeable nutrients can be influenced by the seasonal variations, particularly during the growing season when the nutrient uptake by vegetation is important.

The rhizosphere, defined as the volume of soil surrounding the roots (Darrah 1993), is the zone where water and nutrient uptake by tree takes place. The chemical characteristics of the rhizosphere can be very different from those of bulk soil due to root nutrient uptake but also to root exudation and microbial activities (Marschner 1995). The nutrient availability in the rhizosphere depends on the difference between element output fluxes, principally by plant uptake, and element input fluxes, principally by mass flow, mineral weathering and organic matter mineralization (Hinsinger et al. 2009). It is also known that the release of organic substances from roots is a key process influencing nutrient availability in the rhizosphere (Grayston et al. 1997; Lambers et al. 2009). Firstly, the release of organic acids, protons and enzymes influence directly the mobilization of essential nutrients through processes such as organic matter mineralization (Clegg and Gobran 1997; Wang and Zabowski 1998) and mineral weathering (April and Keller 1990; Courchesne and Gobran 1997; Bakker et al. 2004; Calvaruso et al. 2006). Secondly, root exudates enhance nutrient availability indirectly through their use as carbon substrates, by increasing microbial growth and activities in the rhizosphere. Indeed, rhizospheric microorganisms (mycorrhizal fungi and free bacteria and fungi) contribute to tree nutrition by releasing nutrients from soil minerals (Uroz et al. 2009; Courty et al. 2010) or organic matter (Phillips and Fahey 2008). Interestingly, the accumulation of exchangeable nutrients is generally observed in the tree rhizosphere compared to bulk soil (Clegg and Gobran 1997; Wang et al. 2001; Séguin et al. 2005; Turpault et al. 2005). However, little is known about the impact of seasons on the availability of exchangeable nutrients in the tree rhizosphere (Turpault et al. 2007).

In the nutrient-poor and acidic soil of the Breuil-Chenue experimental forest site, a recent study (Calvaruso et al. 2011) showed that the rhizosphere of different tree species (such as Norway spruce and beech) was enriched in exchangeable cations (such as K, Mg and Ca) during the summer. However, this observation raises a question: does the accumulation of exchangeable nutrients in the rhizosphere occur in all the seasons? The objective of this study was thus to examine, in the Breuil-Chenue experimental forest site, (i) the impact of seasonal variations on the availability of exchangeable nutrients (such as Mg, K and Ca) between the rhizosphere and the bulk soil and (ii) the seasonal evolution of the concentration of those exchangeable cations in three soil compartments (Bulk soil, Outer Rhizosphere and Inner Rhizosphere). The nutrient concentration has been analysed under two contrasted tree species, Norway spruce (*Picea abies* Karst.) and beech (*Fagus sylvatica* L.), at three different depths and for four seasons (autumn: November, winter: February, spring: May and summer: August).

Materials and methods

Study site and soil properties

This study was conducted in the Breuil-Chenue experimental forest site located in the Morvan (47°18′N, 4°5′E, France). The forest is situated on a plateau at an altitude of 638 m. The native forest was partially clear-cut and replaced in 1976 by monospecific plantations distributed in plots of 0.1 ha of different species such as beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* Karst.). The soil derives from 'Pierre qui Vire' granite (Seddoh 1973) and is acidic, well-drained, and classified as a Typic Dystrochrept (USDA 1999) with depths ranging from 120 to 140 cm. The granite composition is quartz: 34%, albite: 31.1%, K-feldspar: 24.2%, muscovite: 1.2%, and chlorite: 0.5%. The bulk soil has a sandy-loam texture (55% sand and less than 20% clay) and is acidic (pH_{KCl} 3.1–4.3). In the native forest, the cation exchange capacity (CEC) is small (ranged from 9.2 to 2.7 $cmol_c\ kg^{-1}$) and mainly occupied by aluminium with a base saturation (BS) lower to 10% (Mareschal et al. 2010). Humus is present as moder (Zeller et al. 2007) in the native forest and carbon (C) concentration is 7.3% in the A1 horizon.

Soil sampling

Soil samples were collected under beech and Norway spruce stand in November 2007 (autumn), February 2008 (winter), May 2008 (spring) and August 2008 (summer). For each season and both stands, soil samplings were carried out in four replicates. Each stand was separated into four areas and pits (120× 80 cm) randomly distributed and dug in each area. After removing the forest floor, soil sampling was carried out systematically at three depths (layer 1: 0–3 cm, layer 2: 3–10 cm and layer 3: 10–23 cm). 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 both Norway spruce and beech stands (Calvaruso et al. 2011). For each pit, soil material was cut and extracted from the profile by layer (0–3, 3–10, and 10–23 cm). At the site, roots with diameters <2 mm were carefully removed by hand from each soil layer. The soil without roots was collected to give the bulk soil compartment (B). The roots with adherent soil aggregates <1 cm were collected to separate rhizospheric soils from two hand-shaking operations according to Turpault et al. (2005). The first one was done in the field. The soil falling from freshly roots was collected to give the rhizosphere outer (Ro). The second hand-shaking operation was performed in the laboratory from roots dried in a steam-air dryer at 30°C. The roots were then shaken even more gently to collect soil particles covering the roots and to give the rhizosphere inner (Ri).The three soil compartments (B, Ro and Ri) were dried and sieved at 200 μm for the chemical analyses, to eliminate the roots and to obtain a comparable particle size distribution in three soil compartments, following the method described by Turpault et al. (2005).

Solid soil phase chemical analysis

Four replicates of soil samples from three layers (0–3, 3–10 and 10–23 cm) and three soil compartments (B, Ro and Ri) for the 4 months were chemically analysed. Exchangeable cations in soil samples were extracted in either 1 M KCl for Mg^{2+}, Ca^{2+} Mn^{2+} and Fe^{3+}or 1 M NH_4Cl for K^+, according to Espiau and Peyronel (1976), and determined by 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 titrated (Rouiller et al. 1980). Cation exchange capacity (CEC) was calculated as the sum of extracted exchangeable cations ($Mg^{2+} + Ca^{2+} + K^+ + Mn^{2+} + Fe^{3+} + H^+ +$ Al titrated) and expressed to $cmol_c\ kg^{-1}$ soil. The results concerning Mn, Fe, H and Al are not presented in this study. 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 (<1% of the CEC; Calvaruso et al. 2011). Base saturation (BS) was calculated as the sum of $Mg^{2+} + Ca^{2+} + K^+$. The good linear relation observed by Calvaruso et al. (2011) between the CEC values extracted by cobaltihexamin and by the method described by Espiau and Peyronel (1976) suggests that our extraction procedure (e.g., 1 M KCl and 1 M NH_4Cl) is adapted to exchangeable cation measurements in forest soils.

The limit of detection was lower than 0.04 mg L^{-1} for K, than 0.02 mg L^{-1} for Ca and than 0.02 mg L^{-1} for Mg. The measurement uncertainty of analysis was lower than 12.5% for K (0.05 to 3 mg L^{-1} range), than 8.7% for Ca (0.04 to 4 mg L^{-1} range) and than 5.2% for Mg (0.02 to 4 mg L^{-1} range).

The amount of carbon (C%) in soil fractions was estimating using a CHN analyser (ThermoQuest NCS 2500).

Solution extraction and analysis

The soil solutions of B and Ro soils have been extracted for the 3 months (November, February and May, only), the three layers and the two tree species. The soil samples used for soil solution extractions were placed in air-tight bags and stored at 4°C while awaiting centrifugation, which was carried out within 72 h. Both bulk soil and rhizosphere outer were sieved (2 mm mesh) and homogenized. The soil solutions from these two soil fractions were then extracted by centrifugation (15°C, 20 min, 3,000 rpm; JOUAN KR422) and filtered at 0.45 µm. In August, the volume of solutions extracted from several soils was insufficient to conduct chemical analysis. The nitrate concentrations in the solutions were determined by ion chromatography using a Dionex DX 300 model.

Statistical analyses

The mean values (CEC, BS/CEC, K/CEC, Ca/CEC and Mg/CEC) were calculated from four replicates ($n=4$) and are given with standard errors. For each tree species, each depth and each soil compartment, a one-factor variance analysis (ANOVA) was used to assess significant differences between the different seasons, at the threshold of $p<0.05$. The normality of distribution and the homoscedasticity of variances were tested. Average comparisons were made using the Student-Newman-Keuls test. Before analysis, all percentages were arcsine transformed. The paired t-Student test was performed to establish significant differences for CEC and BS between the three soil compartments (not independent samples) for each tree species, each depth and each season at the threshold level of $p<0.05$. Relationships between soil characteristics were analysed using simple correlation and regression. Statistical analyses were completed with the UNISTAT software (Unistat version 5.0, 2002, England).

Results

Climatic conditions

The climatic conditions (air temperature and rainfall) measured during the period of the study in the region of Breuil-Chenue site are presented in Fig. 1. Minimum and maximum temperatures were recorded in December 2007 (−3.2°C) and June 2008 (23.6°C), respectively. The annual precipitations were from 1,300 mm. The lowest soil moisture was measured in the samples collected in August (data not shown).

Cation Exchange Capacity (CEC) and carbon concentration (C)

In both beech and Norway spruce stands, CEC was low (7.5 to 23.3 $\mathrm{cmol_c\ kg^{-1}}$ of soil) and decreased with depth (Table 1). The CEC varied little during the year and was higher in rhizospheric soils (Ro and Ri) than in bulk soils (B). The statistical analyses showed that the differences between the three soil compartments (Ro-B; Ri-B and Ri-Ro) were higher under Norway spruce stand than under beech stand. In addition, this soil compartment effect was more pronounced in February compared to the other months for both tree species.

Base saturation (BS = $Ca^{2+} + K^{+} + Mg^{2+}$)

Figure 2 represents the evolution of BS and each exchangeable cation (Ca, K and Mg) expressed as a percentage of CEC occupied. Generally, BS/CEC, K/CEC, Ca/CEC and Mg/CEC decreased with depth and their concentration increased in the same order: B<Ro<Ri. Independently from the season and from the depth, BS/CEC was significantly higher in Ri soils than in B soils (Table 2).

The BS/CEC values of Ri soils presented the same evolution in both stands. In layer 1, BS/CEC showed the lowest values in August. As regards to the Norway spruce, the BS/CEC decrease observed between February and August was principally due to a decrease of both exchangeable K ($p=0.0582$) and exchangeable Mg ($p=0.0585$). In contrast, under beech stand, the BS/CEC decrease resulted from a decrease of Ca ($p=0.0529$) and K ($p=0.0015$). In

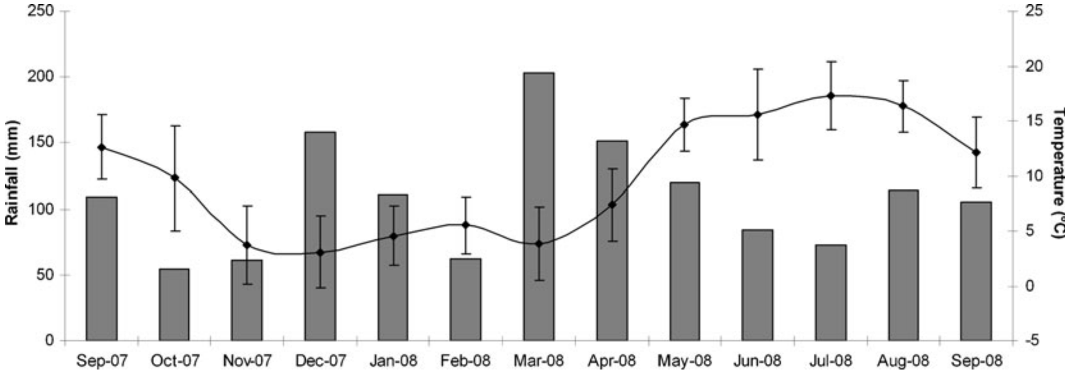


Fig. 1 Rainfall and air temperature during the whole study (METEO FRANCE). The values of rainfall and air temperature correspond to monthly total precipitation and monthly mean temperature, respectively (adapted from Collignon et al. 2011)

layers 2 and 3 of both stands, BS/CEC of Ri soils was higher in May compared to those of the other months, principally due to high levels in exchangeable K during this period. A strong variability of BS/CEC values was observed in Ri soils of Norway spruce in May.

The temporal evolution of BS/CEC in B soils was significantly different between the Norway spruce and beech. Under the Norway spruce stand, BS/CEC was significantly lower in February compared to that of November in layer 2 and compared to those of the three other months in layer 3. Accordingly, the lowest values of BS measured in February resulted from an absence of exchangeable Ca as well as a decrease of K and Mg. It is also necessary to note that the absence of Ca was observed in Ro soils of layer 3, whereas the Ri soils was always rich in exchangeable Ca. In contrast, under beech stand, BS/CEC was significantly higher in February than in the other months in layer 3 due to an increase of exchangeable K (0.0225).

The carbon concentration was significantly higher in both soils around roots (Ro and Ri) than in bulk soil and it was significantly correlated with BS under Norway spruce stand (BS=0.2773%C - 1.2846, R^2= 0.63; $p<0.0001$) and under beech stand (BS= 0.2605%C - 0.5717, R^2=0.75; $p<0.0001$) (Fig. 3).

Complementary analyses revealed a significant increase of both exchangeable aluminium and nitrate concentration in soil solution between November and February in the bulk soil of Norway spruce in layer 3 (data not shown). In addition, Fig. 4 showed that the BS concentration was significantly negatively correlated with Al/CEC (R2=0.63, $p<0.0001$) and nitrate concentration (R2=0.44, $p<0.0186$) in B soil of Norway spruce stand. In contrast, the analysis did not show correlations between BS evolution and both Al/CEC and quantity of nitrate in B soil of beech in the layer 3.

Discussion

Rhizosphere effect on nutrient availability

Active plant roots have been recognized to influence the biogeochemical parameters of soil in their vicinity (Hinsinger et al. 2006), i.e. the rhizosphere that differs in many aspect from the bulk soil. In accordance with previous studies (Dieffenbach and Matzner 2000; Braun et al. 2001; Wang et al. 2001), our work confirmed the presence of nutrient concentration gradients between the root surface of trees and the bulk soil. These gradients can result from gradients of mass flow and exudation of protons, release of organic acids or enzymes by roots and associated microorganisms (Hinsinger et al. 2009). In the present study the CEC and BS were higher in the beech and spruce rhizospheres than those in the bulk soils in November, February, May and August (with B< Ro<Ri). These results thus suggest for the first time that the soil around tree roots is enriched in nutrients compared to the bulk soil for all season.

The relationship between the BS and the carbon quantity suggests that the increase of BS in the rhizosphere can be partially linked to an increase in organic carbon. This result confirms the observations

Table 1 Average values of CEC expressed in cmolc kg^{-1} of soil for the three compartments (Bulk soil [B], Outer Rhizosphere [Ro] and Inner Rhizosphere [Ri]) and the season sampling (November, February, May and August) under Norway spruce and beech stands

Tree species	Layer	CEC cmolc.kg-1																							
		November						February						May						August					
		B	Ro	Ri	Ro-B	Ri-B	Ri-Ro	B	Ro	Ri	Ro-B	Ri-B	Ri-Ro	B	Ro	Ri	Ro-B	Ri-B	Ri-Ro	B	Ro	Ri	Ro-B	Ri-B	Ri-Ro
Norway spruce	1	16.7 (±1.1)	21.7 (±2.4)	23.3 (±3.8)	*	*		15.1 (±0.6)	18.2 (±0.7)	24.4 (±1.4)	*	***	**	17.2 (±2.1)	16.8 (±2.9)	21.6 (±1.9)				14.3 (±0.7)	15.8 (±0.7)	20.2 (±1.0)		**	*
	2	14.3 (±2.2)	16.0 (±2.2)	16.0 (±1.5)				13.1 (±0.8)	15.0 (±1.1)	16.8 (±0.8)	*	**		12.6 (±0.9)	14.5 (±1.2)	14.8 (±3.2)	*	*		13.0 (±0.3)	13.8 (±0.6)	17.5 (±1.4)		**	**
	3	8.6 (±1.5)	10.5 (±1.5)	12.1 (±1.7)		*		7.9 (±0.2)	10.1 (±0.5)	13.3 (±0.9)	**	**	*	8.6 (±0.4)	11.3 (±1.0)	12.0 (±0.8)	**	***		8.1 (±0.7)	11.4 (±0.7)	14.8 (±2.8)	**	**	
Beech	1	16.1 (±2.5)	19.2 (±3.3)	21.3 (±3.3)				16.1 (±1.0)	16.4 (±1.0)	19.3 (±0.5)		**	**	17.0 (±1.2)	16.1 (±0.5)	18.8 (±2.0)				15.5 (±1.1)	16.4 (±2.0)	19.2 (±3.3)			
	2	13.3 (±2.1)	14.5 (±2.6)	15.9 (±2.8)				13.7 (±1.0)	14.8 (±1.4)	16.0 (±1.9)				12.7 (±1.3)	14.3 (±1.4)	14.4 (±1.2)				14.7 (±2.2)	15.1 (±2.1)	16.3 (±3.3)			
	3	9.5 (±1.9)	10.7 (±1.4)	11.7 (±2.0)				8.7 (±1.4)	10.3 (±0.9)	12.0 (±1.0)		*	*	7.5 (±0.8)	9.5 (±0.9)	10.6 (±0.2)	*	***		10.4 (±1.8)	11.6 (±2.4)	13.0 (±2.5)			

CEC cation exchange capacity

Layer 1 : 0 to 3 cm, Layer 2 : 3 to 10 cm and Layer 3 : 10 to 23 cm

Mean followed by standard error in between parentheses

The presence of asterisks in the columns Ro-B, Ri-B and Ri-Ro indicates significant differences between Ro and B soils, between Ri and B soils and between Ri and Ro soils respectively, according to a paired t-Student analysis at the threshold of $p=0.05$ (*), $p=0.01$ (**) and $p=0.001$ (***)

of Clegg and Gobran (1997) under Norway spruce stand. The release of carbon from roots into the surrounding soil, called rhizodeposition (Jones et al. 2004; Jones et al. 2009), includes the carbon derived from photosynthates that are produced during the growing period and the fine-root decomposition that can even occur in winter (Meinen et al. 2009). The large quantities of organic matter in the rhizosphere could enhance the nutrient availability through an increase of CEC (increase of exchange sites) and a stimulation of microbial growth and activities which favours organic matter mineralization and mineral weathering (Lambers et al. 2009).

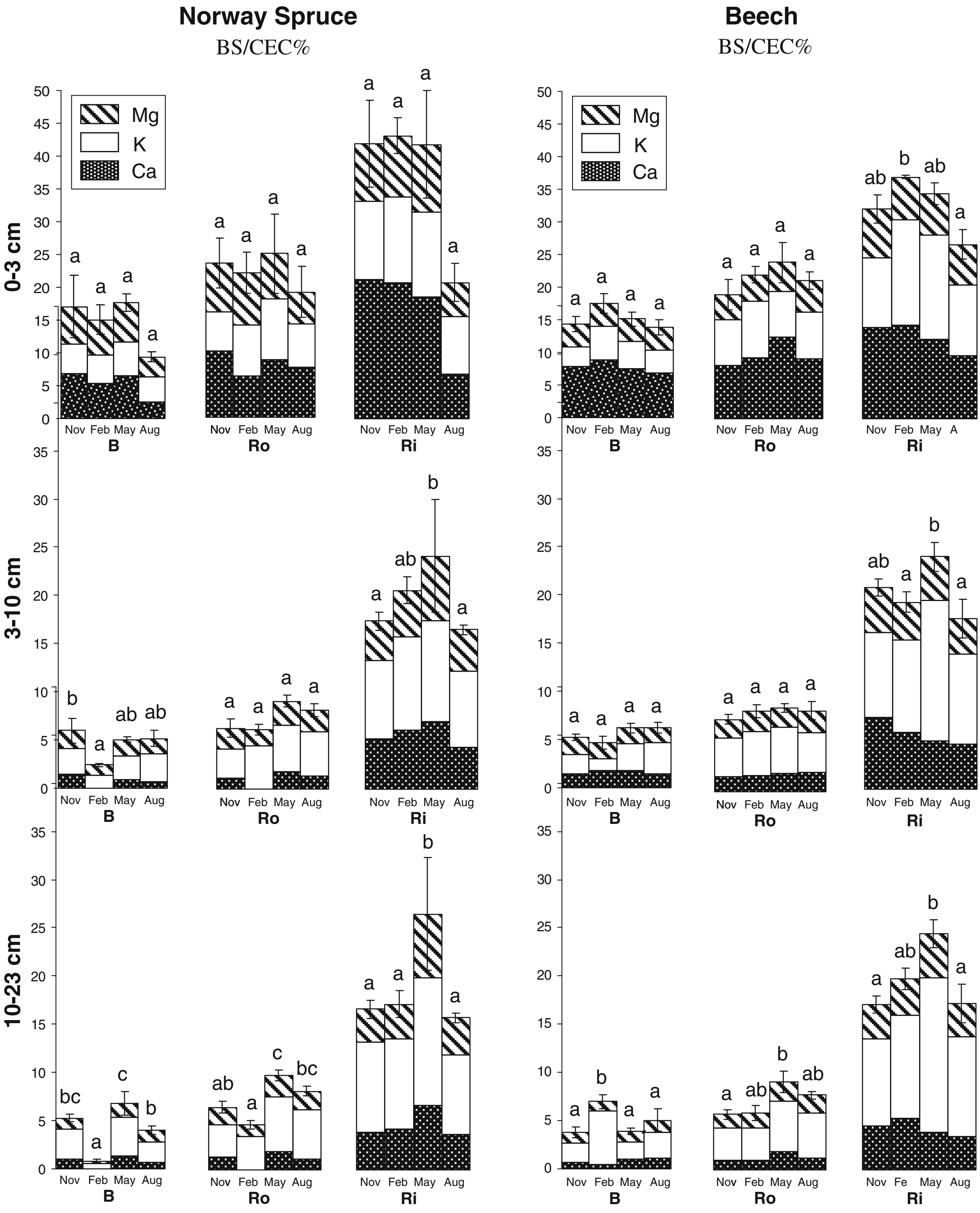
Furthermore, our results highlighted that the content of K, Ca and Mg in the rhizosphere was higher than in the bulk soil for the four seasons and both tree species. The accumulation of exchangeable cations in the tree rhizosphere has already been observed by other authors in rhizotron experiments (Bakker et al. 1999b; Wang et al. 2001) and in soil samples collected in situ during the winter (Turpault et al. 2005), the spring (Calvaruso et al. 2011) and the summer (Gobran and Clegg 1996; Séguin et al. 2005). Our study confirmed independently from the season the conceptual model proposed by Gobran and Clegg (1996) and Gobran et al. (1998), thus supporting the hypothesis that interactions between soil, microorganisms and roots create a mutually supportive system that can raise nutrient availability in the rhizosphere compared to the bulk soil.

Previous studies led in the Breuil-Chenue site during spring showed an accumulation of exchangeable nutrients in Norway spruce and beech rhizosphere (Calvaruso et al. 2011), and an increase of the rates of organic matter decomposition (Colin-Belgrand et al. 2003) and mineral weathering (Calvaruso et al. 2009) in the rhizosphere compared to bulk soil for hardwoods and coniferous. Furthermore, Uroz et al. (2007) and Calvaruso et al. (2010) have reported that bacterial strains with a high mineral weathering efficiency were enriched in the ectomycorrhizosphere of beech and oak compared to bulk soil in the autumn period. Similarly, we showed that the rhizosphere was enriched in high mineral weathering potential bacteria compared to bulk soil for the four seasons under beech and in autumn and summer under Norway spruce (Collignon et al. 2011). All these observations suggest that in a nutrient-poor ecosystem such as the Breuil-Chenue forest, tree roots and root-associated microorganisms could contribute to the increase of nutrients in the rhizosphere, thus creating a favourable environment for tree nutrition.

Temporal evolution of exchangeable nutrients in the rhizosphere

The nutrient uptake by plants can lead to a decrease of nutrients in the rhizosphere (Marschner 1995). For example, the depletion of cations (such as K, Mg and Ca) was already observed in the rhizospheric solutions during tree growth (Dieffenbach et al. 1997; Bakker et al. 1999a; Dieffenbach and Matzner 2000). In the present study, BS/CEC in the Ri soils decreased between February and August in Norway spruce and beech stands, suggesting that this decrease could result from nutrient uptake by trees at the end of the vegetation period. These results are in accordance with Turpault et al. (2007) who have observed a decrease in stocks of exchangeable Ca and Mg in the rhizosphere of Douglas fir between March and June.

Additionally, the BS/CEC in the Ri soil values showed a strong variability in May under Norway spruce stand, suggesting that the rhizosphere is a dynamic environment characterized by temporal and spatial heterogeneities related to variations of nutrient inputs (mass flow, mineral weathering and organic matter mineralization) and outputs (principally tree uptake). Furthermore, the BS/CEC values of Ri soils were highest in May compared to the other sampling periods, due principally to an increase of exchangeable K. This observation is in accordance with the work of Calvaruso et al. (2009), who showed, in the same forest site, that the illite-like minerals (stemming from the K fixation in 2:1 interlayer phyllosilicates) were enriched in the tree rhizosphere compared to the bulk soil. Accumulation of easily available K in the rhizosphere, as observed in situ for Douglas-fir (Turpault et al. 2005) and Norway spruce (Clegg and Gobran 1997), can result from the weathering of K-bearing phyllosilicates such as mica (Hinsinger et al. 2006). Indeed, in the same experimental site, Mareschal et al. (2010) showed that K represented around 62% of the total reserve in bases of soil, suggesting that the soil minerals constitute an important reservoir of K in the Breuil-Chenue site.


Norway Spruce
BS/CEC%
Beech
BS/CEC%
Mg
K
Ca
0-3 cm
3-10 cm
10-23 cm
0
5
10
15
20
25
30
35
40
45
50
Nov Feb May Aug
B
Ro
Ri
Nov Feb May A
Nov Fe May Aug
a
ab
b
bc
c

◀ **Fig. 2** Temporal variations of mean base saturation (BS = Mg2+ + Ca2+ + K+) expressed as a percentage of CEC occupied (BS/CEC%) in Norway spruce and beech stands, for the three compartments (Bulk soil [B], Outer Rhizosphere [Ro] and Inner Rhizosphere [Ri]) and the sampling season (November-07 [Nov], February-08 [Feb], May-08 [May] and August-08 [Aug]) and in the three soil layers (Layer 1 [0–3 cm], Layer 2 [3–10 cm] and Layer 3 [10–23 cm]). Error bars indicate standard deviations (n=4). For each depth and each soil compartment, bars with the same letter (**a**, **b**, **c**) are not significantly different according to a one-factor (season) ANOVA and the Student-Newman-Keuls test (p<0.05)

Consequently, the increase of the exchangeable K could be due to a high mineral weathering in May linked to production of weathering agents (such as protons, organic acids and complexing organic acids) by roots and microorganisms. Hence, these results suggest that the recycling of nutrients is effective in the vicinity of roots and that tree needs could be assured in spring by mineral weathering in the rhizosphere. This hypothesis is in agreement with Turpault et al. (2008), who observed an increase of mineral weathering in the rhizosphere of Douglas-fir between March and June.

Temporal evolution of exchangeable nutrients in the bulk soil

Contrary to previous studies (Haines and Cleveland 1981; Peterson and Rolfe 1982; Kelly and Mays 1999), our results did not show a decrease of exchangeable cations (Ca, Mg and K) between late winter and summer in bulk soil. In bulk soil of beech, the exchangeable K showed the highest values in February, whereas under Norway spruce stand, the concentration of exchangeable cations exhibited a drastic decline ranging from 80 to 100% between November and February in the layers 2 (3–10 cm) and 3 (10–23 cm). In addition, this decrease of base saturation observed in February under Norway spruce stand was accompanied by a significant increase of exchangeable aluminium (data not shown). Furthermore, our analysis revealed a negative correlation between the evolution of the base saturation and of the exchangeable Al under spruce and not under beech in the layer 3. Thus, these results suggest that a competition between aluminium and base cations for cation-exchange sites could induce a decrease of nutrients on CEC in winter. This hypothesis is

Table 2 Average values of BS (BS = $Mg^{2+} + Ca^{2+} + K^{+}$) expressed as a percentage of CEC occupied (BS/CEC%) for the three compartments (Bulk soil [B], Outer Rhizosphere [Ro] and Inner Rhizosphere [Ri]) and the sampling season (November, February, May and August) under Norway spruce and beech stands

Tree species	Layer	BS/CEC%																							
		November						February						May						August					
		B	Ro	Ri	Ro-B	Ri-B	Ri-Ro	B	Ro	Ri	Ro-B	Ri-B	Ri-Ro	B	Ro	Ri	Ro-B	Ri-B	Ri-Ro	B	Ro	Ri	Ro-B	Ri-B	Ri-Ro
Norway spruce	1	17	24	41		*		15	22	43		***	***	18	25	41		*		9	19	20	*	**	
	2	6	6	17		**	***	2	6	21	***	***	**	5	9	24	**	***	***	5	8	16	*	***	***
	3	5	6	17		***	***	1	5	17	***	***	***	7	10	26		**	*	4	8	16	**	***	***
Beech	1	14	19	32		***	*	18	22	36		***	***	15	24	34		***	*	14	21	26	**	**	
	2	5	7	21	**	***	***	5	8	19	**	***	***	6	9	24	**	***	***	6	8	18		***	***
	3	4	6	17		***	***	7	6	20		***	***	4	9	24	**	***	***	5	8	17		**	**

BS Base saturation; *CEC* cation exchange capacity

Layer 1 : 0 to 3 cm, Layer 2 : 3 to 10 cm and Layer 3 : 10 to 23 cm

The presence of asterisks in the columns Ro-B, Ri-B and Ri-Ro indicates significant differences between Ro and B soils, between Ri and B soils and between Ri and Ro soils respectively, according to a paired t-Student analysis at the threshold of p=0.05 (*), p=0.01 (**) and p=0.001 (***)

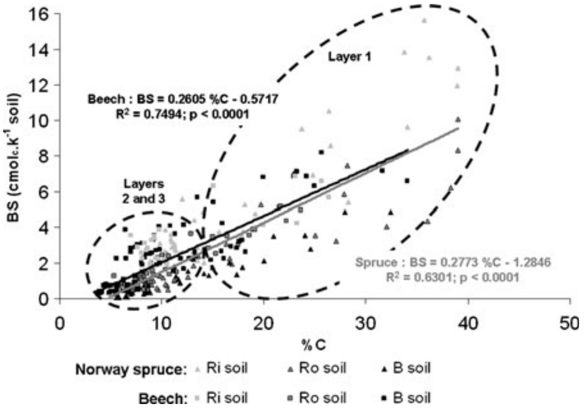


Fig. 3 Relationship between base saturation (BS) and carbon concentration under Norway spruce (*triangle*) and beech (*square*) stands. The three compartments are presented by different colors: Bulk soil [B] (*black*), Outer Rhizosphere [Ro] (*dark gray*) and Inner Rhizosphere [Ri] (*light gray*)

supported by Ranger and Nys (1994), who showed under Norway spruce stand that aluminium fixed on the resins (cationic and chelating) was higher in winter than in summer, suggesting that aluminium could take up a large proportion of the exchange site in winter. In addition, the evolution of the base saturation was negatively correlated with nitrate contained in soil solutions of Norway spruce. It is also known that the increase of nitrate with soil depth is often followed by an increase in dissolved aluminium in forest soils (Nielsen et al. 1999; Maitat et al. 2000).

Conclusion

In the present study, the availability of exchangeable cation (K, Mg and Ca) differed between the soil around tree roots and the bulk soil. Except a decrease of exchangeable nutrients during the vegetation period that could result from tree uptake; the rhizosphere was enriched in exchangeable nutrients compared to the bulk soil for all season. These results thus suggest that high biological activities (organic matter mineralization and mineral weathering by tree roots and rhizospheric microorganisms) favour an efficient recycling of nutrients in the vicinity of roots and thus contribute to ecosystem sustainability. In addition, our results demonstrated that the temporal dynamics of exchangeable cations in the bulk soil was significantly different between beech and Norway spruce. Indeed, in contrast to beech, a strong decrease of exchangeable nutrients has been observed in February under Norway spruce stand which could result from an increase of Al solubility. Examination of both mineralogical and Al form changes should permit a better understanding of the mechanisms involved in the seasonal evolution of nutrient cations in soils. Further studies at long-term are also required to reach clearer conclusions and generalizations. The results of this study showed that seasonal variations of biological and physicochemical processes within soils must be taken into account to evaluate precisely the temporal evolution of

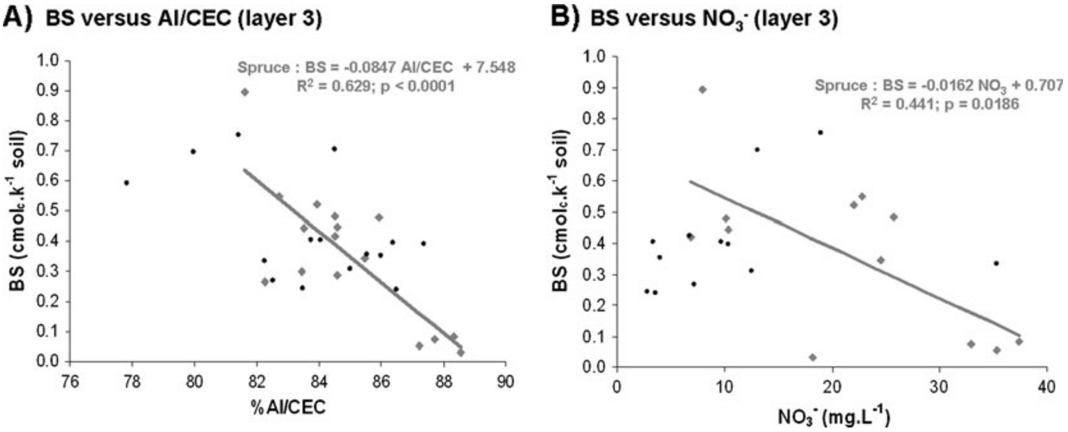


Fig. 4 Relationships between the base saturation and (**a**) the exchangeable Al (expressed as a percentage of CEC) and (**b**) the nitrate concentration (mg.L^{-1}) in soil solutions extracted by centrifugation in the bulk soil sampled in November-07, February-08 and May-08 under Norway spruce (*gray triangle*) and beech (*black square*) stands in the soil layers 3 (10–23 cm)

nutrients at medium- and long-term and to conclude on the influence of tree species on nutrient dynamics in soils.

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