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Temporal variations of rhizosphere and bulk soil chemistry in a Douglas fir stand

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Abstract

Rhizosphere soil can play a central role in the maintenance of the soil–plant system and influencing the biogeochemistry of forest ecosystems. However, rhizospheric studies *in situ* to understand the ecosystem functions are still lacking. Therefore, the objectives of the present study were to examine the differences in the chemical properties such as the pH, organic C, exchangeable base cations ($EBC = Mg^{2+} + Ca^{2+} + K^+$), exchangeable acidity and cation exchange capacity (CEC) of three soil fractions (Bulk, B; Rhizosphere, R and Rhizosphere Interface, RI) and the evolution of chemical properties of soil samples collected in March and June from a Douglas fir ecosystem located in the Beaujolais Mounts in France.

Most of the variables measured (organic matter, CEC and EBC) increased significantly in the same order ($B < R < RI$), indicating that the rhizosphere was a favorable interface for tree nutrition. These processes were more pronounced in June than in March, as the temperature and biological activities are normally higher in June than in March. The temporal variations of Al charge in R and B seem to depend on OH^- , organic complexation and H^+ production by roots and/or the organic matter degradation in the bulk soil. In the rhizosphere, the H^+ or OH^- production depends on the N cycle. The results of this study and the support of independent mineralogical study using the same soil fractions, and of other field studies on the same site have all pointed at the importance of rhizosphere as an excellent indicator for the understanding of the ecosystem dynamics in both short- and long-term.

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1. Introduction

The rhizosphere, defined as the volume of soil influenced by root activity, differs in many aspects from the bulk soil due to the root uptake (water and nutrients), the root exudates, the root respiration and the higher microbial and fungal activity. The evidence of these profound chemical changes that occur in the rhizosphere have been reviewed by several authors in recent years (e.g. Curl and Truelove, 1986; Darrah, 1993; Marschner, 1995). In this zone, the weathering rate of soil minerals can be increased due to root and microflora activity and that can be

manifested by, for example, pH decrease, higher organic acid production or differences in the oxydo-reduction potential (April and Keller, 1990; Hinsinger et al., 1992; Drever, 1994). These root effects on soils suggest to some investigators that soil can be considered, in part, as a product of plants and soil biota (Van Breemen, 1993).

In spite of the small volume that the rhizosphere occupies in the mineral soil, it plays a central role in the maintenance of the soil–plant system and influence the biogeochemistry of forest ecosystems (Gobran et al., 1998). However, *in situ* rhizospheric studies aimed at understanding ecosystem functions such as nutrition or aluminum toxicity are still lacking. This could be due to the complex nature of the ecosystem conditions where the dynamic nature of the ecosystem functions controlling the performance of plant, especially during the growing season, cannot be mimicked by experimental controlled conditions. Therefore, there is a strong need for more ecosystem studies

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geared to integrate mechanisms controlling the functional relationships between soil–plant–microorganisms. Apart of the field studies conducted and reviewed by Gobran et al. (1998, 2005) on coniferous forests growing on podzols to fully understand rhizosphere processes *in situ*, and Séguin et al. (2004) who studied extractable metal in the rhizosphere of forested soil, literature lacks greatly such studies under different climates and species. As rhizosphere is the soil that is influenced by the plant activities (above- and below-ground), it is hypothesized that rhizosphere must reflect the behavior of the plant during the active growing season. For example, biological activity in the rhizosphere including the dynamics of fine root growth (Ponti et al., 2004) and the vast dynamic of nutrient uptake by roots and their exudates during the growing season ought to be reflected by vast changes in the rhizosphere.

The objectives of this study were to 1) examine *in situ* in a forest site covered by a stand of 45-year-old Douglas fir the extent to which the biological activity can modify rhizosphere chemistry, and 2) relate the chemical changes in the three soil fractions (B, R and RI) in three different horizons to temporal effects occurring during March (M) and June (J), where biological activity changes drastically.

2. Materials and methods

2.1. Ecosystem description

A 45-year-old monospecific stand of Douglas fir (*Pseudotsuga menziesii* (Mirb) Franco) on the Beaujolais Mounts in France (46°30'N, 4°38'E) was chosen. This together with other that are covered by stands of 20 and 60 years old have been under intensive monitoring studies during 7 years (1993–1999). The chemical data obtained on the rhizosphere in this present study could be discussed in the light of the data obtained at the ecosystem scale. The chosen site is located at an altitude of 780 m on a gentle slope (<10°). Average annual air temperature is 7 °C and annual rainfall averages 1000 mm. The humus was a moder type and the soil was a typical Dystrachrepts (Soil Survey Staff, 1998) developed from a consolidated volcanic tuff dating from the upper visean (Ezzaïm et al., 1999a). The stocks and fluxes of elements in the vegetation and the soils were quantified in the chronosequence of three stands (Marques et al., 1996, 1997; Ranger and Turpault,

1999). The potential mineralizing and nitrifying capacity of the soil were also determined (Jussy et al., 2000). It is necessary to mention here that the mean annual flux of N–NO₃⁻ in the soil solution of the studied site represents 90% and 93% of total N at depths of 15 and 30 cm, respectively. The studies performed by Ezzaïm et al. (1999b) showed that weathering processes at this site have lead to a poor soil in nutrients from a relatively rich rock, to acidic and under saturated soils and to loamy soils (Table 1). Although chemical analysis of tree leaf does not show any nutrient deficiency, the nutrient budgets calculated for the whole stand was found negative for major cations like Ca, Mg and K (Ranger and Turpault, 1999). However, the deficit of K was less than those of Ca and Mg. Such deficits seem to decrease with the stand age, particularly K in stand of 60 years old (Ranger and Turpault, 1999). In addition, the chemistry of rhizosphere solutions sampled at three depths (0–20; 20–40 and 40–60 cm) from the same site in March 1999 was investigated and showed that the concentration of all elements increased in the rhizosphere solutions as compared to the bulk soil solutions, except for P (Turpault et al., 2005).

2.2. Soil sampling

A representative area of 42 × 30 m was selected and divided into small subsections of 6 × 6 m. At the intersections between the grid formed in this manner, a systematic soil sampling was performed, except in places where obstacles such as tree trunks and stumps were in the way. Thirty soil pits of 30 cm width × 70 cm length were dug in both the beginning of March and end of June 1998. All the pits were filled up again with the same soil sampled from each layer systematically under the humus layer from layer 1 (0–5 cm), layer 2 (5–15 cm) and layer 3 to limit soil perturbation. The pits sampled in June were dug at 50 cm and at the top of the slope of the old pits dug in March. At each sampling time, 30 mineral soil samples were taken (15–30 cm). At the site, roots <2 mm were carefully removed by hand and the adherent soil aggregates >1 cm on the root were discarded. The soil fraction that was free of roots was collected to give the bulk soil fraction (B). To limit the root–soil interactions after sampling, the roots with the adherent soil aggregates <1 cm were immediately dried in a steam-air dryer at a maximum temperature of 30 °C. The soil fraction that was detached from the roots after drying was collected to give the

Table 1
Description and selected properties of the soil (<2 mm) used in this study

Profile	Depth cm	pH H ₂ O	Cation exchange capacity cmol _c kg ⁻¹ dry soil	Exchangeable acidity	Organic C	Oxalate extractable			Clay	Silt	Sand
						Fe	Al	Si			
						g kg ⁻¹ dry soil					
A1	0–10	4.4	10.2	9.0	3.3	4.9	4.7	0.9	194	352	454
A1/Ap	10–20	4.5	6.1	5.5	2.8	4.3	4.5	0.7	222	380	399
Ap2	20–30	4.5	5.8	5.3	2.2	3.6	2.8	0.3	191	396	413
A/(B)	30–45	4.5	5	4.5	0.9	3.8	2.6	0.2	186	390	425
(B)1	45–65	4.7	4.7	4.3	0.4	2.7	2.1	0.2	181	374	446
(B)2	65–85	4.8	4.1	3.6	0.2				120	334	546
(B)/C	85–110	4.8	4.6	4.2	0.2	1	0.9	0.1	87	321	592
C	110–120	5.2	5.4	3.9	0.2	1.3	0.8	0.1	125	344	531

rhizosphere (R). The remaining dry root–soil fraction was gently shaken to separate some of the soil film covering the roots to give the rhizosphere interface (RI). The soil samples B were air-dried at about 25 °C. Due to insufficient samples of R and RI in layer 1, the two soil fractions were mixed to form a composite sample that was called hereinafter R.

The three soil fractions (B, R and RI) were sieved at 200 µm for the chemical analyses. The chosen size 200 µm should give a comparable particle size distribution in all soil fractions (Turpault et al., 2005).

2.3. Statistical analysis of rhizospheric and temporal effects

To assess the rhizospheric effect and the temporal variation of the mature trees *in situ*, it is necessary to consider the followings:

1. The collected soil samples were treated individually to give 30 replicates for each soil layer and sampling season,

2. The moisture content of the soil samples B collected during both sampling seasons (M and J) was not statistically different ($p < 0.05$; data not shown) Accordingly, we assumed that the moisture content of the soil samples R was not different in the 30 replicates, and

3. The weight of soil fraction R represented about 0.30, 0.18 and 0.05% of the total samples collected from layers 1, 2 and 3 respectively. These percentages were the same for all soil samples. This suggested that there was no sampling distortion during the sampling.

Student–Fischer test was used to establish significant differences at 5% level between each individual ($n=30$) for soil fractions (B, R and RI) and seasons (M and J). This test excluded the spatial field variability.

2.4. Chemical analyses

The soil samples from three layers and the three soil fractions (B, R and RI) for all 30 sampling points during the two seasons

Table 2
Mean chemical characteristics of 30 soils samples (B=bulk; R=rhizospheric; RI=rhizospheric interface) sampled in March and in June at three soil layers (1, 2 and 3)

	Layer	March			June		
		B	R	RI	B	R	RI
pH	1	3.93 (0.13) ^{ax}	3.94 (0.09) ^{ax}		3.90 (0.12) ^{Ax}	3.98 (0.16) ^{Bx}	
	2	4.30 (0.12) ^{ax}	4.39 (0.13) ^{bx}	4.39 (0.12) ^{bx}	4.31(0.12) ^{Ax}	4.43 (0.13) ^{Bx}	4.47 (0.14) ^{Cy}
	3	4.40 (0.06) ^{ax}	4.53 (0.09) ^{bx}		4.42 (0.05) ^{Ax}	4.55 (0.10) ^{Ax}	
C g kg ⁻¹	1	118 (25) ^{ax}	120 (24) ^{ax}		125 (19) ^{Ax}	122 (22) ^{Ax}	
	2	49 (8) ^{ax}	56 (7) ^{bx}	61 (9) ^{cx}	49 (6) ^{Ax}	55 (9) ^{Bx}	61 (11) ^{Cx}
	3	27 (6) ^{ax}	35 (6) ^{bx}	40 (8) ^{cx}	29 (7) ^{Ax}	35 (7) ^{Bx}	45 (13) ^{Cy}
CEC cmol _c kg ⁻¹	1	17.0 (2.1) ^{ax}	16.9 (2.2) ^{ax}		18.3 (2.2) ^{Ay}	18.8 (2.5) ^{Ay}	
	2	10.7 (1.6) ^{ax}	11.8 (1.4) ^{bx}	12.0 (1.4) ^{bx}	11.1 (1.3) ^{Ax}	12.1 (1.9) ^{Bx}	12.7 (1.6) ^{Cy}
	3	7.3 (1.0) ^{ax}	7.8 (1.0) ^{bx}	8.4 (1.2) ^{cx}	7.9 (1.3) ^{Ax}	8.4 (1.4) ^{By}	9.9 (1.7) ^{Cy}
BS %	1	24.0 (4.4) ^{ax}	24.1 (7.3) ^{ax}		22.5 (3.5) ^{Ax}	24.1 (6.6) ^{Ax}	
	2	11.1 (3.0) ^{ax}	12.2 (2.7) ^{ax}	17.1 (4.1) ^{bx}	12.0 (3.0) ^{Ax}	14.6 (4.9) ^{By}	22.5 (5.2) ^{Cy}
	3	10.1 (3.9) ^{ax}	13.2 (4.3) ^{bx}	18.7 (5.5) ^{cx}	11.0 (3.6) ^{Ax}	14.9 (5.0) ^{Bx}	24.4 (6.6) ^{Cy}
K/CEC%	1	3.0 (0.4) ^{ax}	5.6 (1.6) ^{bx}		3.7 (2.4) ^{Ax}	7.0 (3.0) ^{By}	
	2	2.6 (0.4) ^{ax}	5.6 (1.4) ^{bx}	8.7 (2.7) ^{cx}	3.1 (2.0) ^{Ax}	8.2 (3.8) ^{By}	13.3 (4.0) ^{Cy}
	3	2.9 (0.7) ^{ax}	7.4 (3.1) ^{bx}	10.5 (2.8) ^{cx}	2.6 (0.7) ^{Ax}	9.9 (3.8) ^{By}	16.0 (4.6) ^{Cy}
Mg/CEC%	1	4.5 (1.5) ^{ax}	3.6 (1.2) ^{bx}		4.1 (0.9) ^{Ax}	2.9 (1.0) ^{Bx}	
	2	2.9 (1.9) ^{ax}	1.9 (0.7) ^{bx}	2.7 (1.6) ^{ax}	3.0 (1.5) ^{Ax}	1.5 (1.5) ^{Bx}	2.8 (1.4) ^{Ax}
	3	3.2 (3.2) ^{ax}	1.8 (0.9) ^{bx}	2.9 (1.6) ^{ax}	3.0 (1.8) ^{Ax}	0.9 (1.5) ^{By}	1.9 (1.7) ^{ABy}
Ca/CEC%	1	16.5 (3.6) ^{ax}	15.0 (5.0) ^{bx}		14.6 (2.7) ^{Ay}	14.2 (3.8) ^{Bx}	
	2	5.6 (1.6) ^{ax}	4.7 (1.2) ^{bx}	5.7 (1.3) ^{ax}	5.9 (1.6) ^{Ax}	4.8 (1.6) ^{Bx}	6.4 (1.5) ^{Ax}
	3	4.1 (1.6) ^{ax}	4.0 (1.5) ^{ax}	5.3 (2.0) ^{bx}	5.5 (2.2) ^{By}	4.0 (1.7) ^{Ax}	6.5 (2.2) ^{Cy}
EA/CEC%	1	76 (4) ^{ax}	76 (7) ^{ax}		77 (3.5) ^{Ax}	76 (6.6) ^{Ax}	
	2	89 (3) ^{ax}	88 (3) ^{ax}	83 (4) ^{bx}	88 (3) ^{Ax}	85 (5) ^{By}	77 (5) ^{Cy}
	3	90 (4) ^{ax}	87 (4) ^{bx}	82 (5) ^{cx}	89 (4) ^{Ax}	85 (5) ^{Bx}	76 (7) ^{Cy}
Ht/CEC%	1	14.5 (2.3) ^{ax}	11.2 (1.6) ^{bx}		16.0 (1.8) ^{Ay}	15.6 (2.4) ^{Ay}	
	2	9.0 (1.1) ^{ax}	5.2 (3.6) ^{bx}	5.3 (3.0) ^{bx}	8.85 (1.2) ^{Ax}	8.8 (1.1) ^{Ay}	8.7 (1.5) ^{Ay}
	3	8.1 (2.5) ^{ax}	4.9 (3.8) ^{bx}	4.0 (3.9) ^{bx}	7.7 (2.3) ^{Ax}	7.9 (0.9) ^{Ay}	7.6 (2.6) ^{Ay}
Alt/CEC%	1	62 (4) ^{ax}	65 (8) ^{bx}		62 (4) ^{Ax}	60 (6) ^{Ay}	
	2	80 (3) ^{ax}	83 (4) ^{bx}	78 (5) ^{ax}	79 (3) ^{Ax}	77 (5) ^{By}	69 (5) ^{Cy}
	3	82 (4) ^{ax}	82 (6) ^{ax}	77 (6) ^{bx}	81 (4) ^{Ax}	77 (5) ^{By}	68 (6) ^{Cy}
Ald/CEC%	1	76 (8) ^{ax}	72 (10) ^{bx}		65 (7) ^{Ay}	72 (8) ^{Bx}	
	2	96 (6) ^{ax}	91 (13) ^{bx}	89 (12) ^{bx}	81 (5) ^{Ay}	93 (10) ^{Bx}	85 (12) ^{Ax}
	3	98 (9) ^{ax}	90 (12) ^{bx}	83 (11) ^{cx}	83 (7) ^{By}	90 (10) ^{Ax}	79 (9) ^{Cx}

CEC: cation exchange capacity; BS: Base saturation; EA: Exchangeable acidity; Alt: titrated aluminium; Ald: Aluminium determined by inductively coupled plasma emission spectrometry and affected of three charges (+); Mean followed by standard deviation in between parentheses. The letters a, b and c are used to compare B, R and RI soils sampled in March; A, B and C are used for B, R and RI soils sampled in June; x and y are used to temporal effect between March and June for each soil (B, R and RI). Different letters indicate that the differences are significant at 95%.

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(M and J) were chemically analyzed. Soil sample of 0.5 g was shaken overnight in 40 ml deionized water. The soil pH was measured in the soil suspension using a Mettler TS2DL25 pHmeter. Due to insufficient soil samples of R and RI, the pH was not determined in all samples. The total carbon of soil fractions was estimated using the TOC-5050 Shimadzu apparatus. In this type of soil where carbonates are absent, total carbon corresponds to the organic carbon. The exchangeable phase of the soil samples was extracted following the methods developed by Espiau and Peyronel (1976) and described in details by Turpault et al. (1996). Using a 1 M KCl soil extract, Al^{3+} (Ald), Mg^{2+} and Ca^{2+} were determined by inductively coupled plasma emission spectrometry (ICP; JYC 38 Plus). Potassium (K^+) was extracted by 1 M NH_4Cl and determined by the same ICP. The 1 M KCl soil extract also was titrated with the same automatic titrimeter (Mettler TS2DL25) to estimate exchangeable Ht (H^+) and Alt (Rouiller et al., 1980).

2.5. Calculations

Exchangeable acidity (EA) was calculated by taking the sum of Ht+Alt. Cation exchange capacity (CEC) was calculated by taking the sum of the salt extracted exchangeable base cation ($\text{EBC} = \text{Mg}^{2+} + \text{Ca}^{2+} + \text{K}^+$) plus EA. Base saturation (BS) = $100 \times \text{EBC} / \text{CEC}$ and ion saturation (%) = $100 \times (\text{ion}) / \text{CEC}$.

The mean charge of titratable Alt (McAl) was calculated by the equation used by Rouiller et al. (1980): $\text{McAl} = 3 \times (\text{Alt} / \text{Ald})$. Although this method is not free of criticism for several reasons, it provides a simple means for comparing soil samples under this study.

3. Results

The statistical analyses comparing the soil chemical properties in the three soil fractions (B, R and RI) collected in March (M) and in June (J) are presented in Table 2.

3.1. Rhizospheric effects

Generally, the analyzed elements show significant differences between rhizospheric and bulk soil, especially in layers 2 and 3. There was an increasing trend in pH, C, CEC and BS followed the order $\text{B} < \text{R} < \text{RI}$. It is also worth mentioning here that the increase in CEC in layers 2 and 3 was due generally to the increase of all the cations and principally K and Alt (data not shown).

Regarding the base cations (K, Ca and Mg), Table 2 shows that K saturation (K/CEC%) always increased significantly in the same order of $\text{B} < \text{R} < \text{RI}$. On the contrary, Ca saturation (Ca/CEC%) and Mg saturation (Mg/CEC%) decreased in R compared to B and increased again in RI. Accordingly, the accumulation gradient in BS ($\text{B} < \text{R} < \text{RI}$) was mainly due to the increased K/CEC%.

The acidity expressed as EA/CEC% decreased in the order of $\text{B} > \text{R} > \text{RI}$, especially in the layers 2 and 3. Notice also that the decrease in EA/CEC% was more in June than in March samples. This trend coincided with pH increases between 0.08

and 0.13 units when R is compared to B. Such decrease in the EA/CEC% seemed to depend mainly on Ht/CEC% in March and on Alt/CEC% in June. Apparently, the changes in Ht/CEC%, Alt/CEC%, and Ald/CEC% in the rhizosphere seemed to depend on the season.

3.2. Temporal effects

The temporal effects on soil samples were pronounced in the rhizosphere (R) and even more pronounced in the RI than on the B soil. For example, Table 2 indicates that the temporal changes from M to J had a positive effect on the CEC and Ht/CEC% while as the effect was negative on Ca/CEC% and Ald/CEC%. Note, that the CEC increased and in the same samples, but the increase was not significant. On the contrary, in the rhizosphere of all the soil layers, the increase in CEC, BS, K/CEC%, Ht/CEC% and the decrease of Alt/CEC% and EA/CEC% were generally observed between March and June. Despite all these changes observed in the rhizosphere, there was no significant change in either the pH or total C. The significant decrease of Mg/CEC% was only observed in layer 3 of rhizosphere between March and June.

4. Discussion

Table 2 generally shows that most of the measured soil variables were significantly different in the rhizosphere (R and RI) when compared to the bulk soils, especially in the layers 2 and 3. The temporal effects were especially manifested in the rhizosphere of layers 2 and 3 and particularly in the rhizosphere interface. These rhizospheric effects were more pronounced in June than in March.

4.1. Effects in layer 1

4.1.1. Organic matter

In forest soils, litterfall, throwfall, stemflow, organic matter decomposition, the resultant leaching of dissolved organic carbon and the rhizodeposition must have qualitative effects on soil fractions (Marques et al., 1996, 1997). We also understand that seasonal variations affecting the abiotic and biotic processes should create different impacts on the properties of soil fractions (Weaver and Forcella, 1979; Haines and Cleveland, 1981). For example, the decomposition of OM and the nitrification which are normally high during the growing season in this site (Jussy et al., 2000) lead to the production of high protons.

This first layer is rich in organic matter and contains high root density compared to the lower two layers. This could partially explain why carbon content in this layer (Table 2) did not change much either between bulk and rhizosphere soils or between M and J. Table 2 illustrates that the differences of most of the other measured variables between B, R and RI in this first layer had the same trend as in the other layers but with a much lower extent. This could be attributed to the effect of the high C content in this layer that masks the rhizospheric and seasonal effects.

Nevertheless, as mentioned above, the temporal effects in the bulk soil of this first layer were manifested by a significant increase of CEC and Ht/CEC% and a decrease of Ca/CEC%. These effects deviated from the general trend observed in the other two lower layers.

4.2. Effects in layers 2 and 3

4.2.1. Organic matter

As expected, OM increased in the order of B < R < RI during both seasons (M and J). However, the absence of seasonal effect on C content of soil fractions could be due to the same processes explained above for layer 1. Due to high rhizodeposition during summertime, we should expect higher accumulated C in the rhizosphere soils collected in June than in March. This was not the case as this mechanism could be offset by a significant higher mineralization of OM in R compared with B (Colin-Belgrand et al., 2003).

It also is interesting to mention here that the relationship between the increase in C and CEC in the rhizosphere soil compared with the bulk soil was not a straightforward relationship ($0.01 < R^2 < 0.3$), suggesting other factors to be considered such as pH, quality of OM, and Al complexation by the OM and clay minerals.

4.2.2. pH

There was a significant increase in pH in the R compared with B in both sampling times (M and J), but the difference between M and J was generally not significant. Although the changes in pH ranged between 0.08 and 0.13, many and considerable chemical reactions occurred in the soil that buffered the acid base conditions (Gobran and Bosatta, 1988). Five important factors affecting acid-base conditions in the rhizosphere can be discussed here: (1) the production of CO₂ from respiration, (2) the excretion of organic acids, (3) microbial production of acids following assimilation of released root carbon, (4) ion uptake, and (5) plant genotype. The dominant mechanism responsible for pH changes in the rhizosphere is the net release of H⁺, HCO₃⁻ or OH⁻ in response to the imbalance between cation and anion uptake by roots (Nye, 1986). For example, in soils where NO₃⁻ is the primary N form, the amounts of anions taken up by plants tend to exceed cations thus plants are required to release HCO₃⁻ or OH⁻ to maintain electrical neutrality across the soil–root interface. This causes an increase of the rhizosphere pH when compared to the bulk soil. This phenomenon is so well established that a method to manipulate rhizosphere pH has been elaborated by using different N sources (Riley and Barber, 1971; Sarkar et al., 1979).

A separate study evaluating ion uptake at the site used for this research was conducted by Marques (1996). The calculated uptake is the sum of ions immobilized in biomass, contained in litterfall and washed off by rain from plant tissues (Ranger and Turpault, 1999). The uptake data of this study was used to calculate the theoretical percentage of nitrate taken up by the trees as the uptake of cations must equal the uptake of anions on equivalent charge bases (mol_c ha⁻¹ y⁻¹). We could estimate the

form of N taken up using the following equation (organic N uptake was neglected):

$$x + a(\text{N-NO}_3^-) + b(\text{N-NH}_4^+) = 0 \quad (1)$$

$$\text{where } a + b = 1 \text{ and } x = \text{H}_2\text{PO}_4^- + \text{K}^+ + \text{Ca}^{2+} + \text{Mg}^{2+} + \text{SO}_4^{2-} \quad (2)$$

According to these Eqs. (1) and (2), we found that the uptake of NO₃⁻ was about 83% of the total N uptake (Fig. 1). These results could explain why the rhizosphere pH was higher than bulk pH. It is important to mention that the dominance of NO₃⁻ in our site has been commonly found in separate and independent studies. For example, the soil solution collected by lysimeters confirms constant high NO₃⁻ compared to NH₄⁺ concentrations (Marques et al., 1996). Also in incubation studies where a soil extraction using KCl was performed, the dominant form of N was always in NO₃⁻ (Jussy et al., 2000). In addition, the *in situ* incubation experiment on the site that was designed to estimate the leaching, production and uptake of N form during 3 years (Oct. 94 to Oct. 97) by Jussy et al. (2000) showed also that the N uptake was principally as nitrate. The N uptake was of about 93% in nitrate during the April–September period and of about 83% during October–March period. The data of 1997 was used in Fig. 1 to illustrate that the dominant form of N taken up was NO₃⁻ (>83%) during the soil sampling in June.

All these differences and the use of independent experiments confirm that the uptake of anions exceeds the one of cations during the growing season on our site under investigation. Under such conditions, plants are required to release OH⁻ to maintain electrical neutrality across the soil–root interface, the rhizosphere (Nye, 1986). This explains the significant increase in pH and decrease of EA/CEC% and Ht/CEC% in the R compared with B in June.

Fig. 1 also suggests that before and after the growing season where the uptake is low, the uptake of cations exceeds anions,

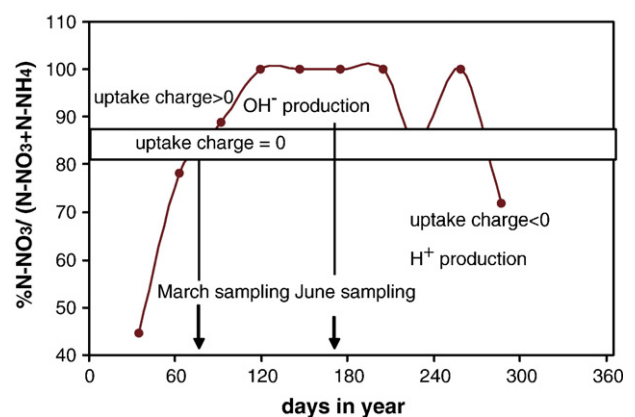


Fig. 1. Seasonal variation of nitrate percentage produced during the year 1997 (data from Jussy et al., 2000) compared to the calculated percentage of nitrate uptake as cations uptake must equal anions uptake.

resulting in a release of protons, which in turn could be consumed by the protonation of Al.

4.3. Temporal effects on acid-base and the changes of Al charge

The general view of the changes in McAl depicted in Fig. 2 shows that McAl varied in all the soil fractions (B, R and RI) depending on the growing season (M or J). From M to J, the increasing trend Ia in the bulk soil could be explained by the increased production of protons (Fig. 1, trend Ia) due to the increase in nitrification process (Jussy et al., 2000) and the increased production of dissolved organic carbon in soil solution (Marques et al., 1997). These two studies reported high mineralization of organic matter and high production of nitrates during springtime due to high soil temperature soil moisture content. As a small part of the produced nitrate is taken up by the trees which normally favor N-NH₄, nitrification process results in a positive proton budget in the top of this soil (Fig. 1, trend Ia). However, this reaction could be offset by the increased OM mineralization, hence increasing Al-OM complexation and a drop of Al charge. The produced protons could also be easily buffered by dissolution of soil minerals and by following buffering reaction:



The above buffering reaction could explain why the seasonal effect did not have any significant differences in the pH of B, where the influence of the roots and other biological reaction are small. It is worth mentioning that the increased charge of Al (Fig. 1, trend Ia) is also supported by an independent miner-

alogical study on the same soil samples (B, R and RI) (data not shown). The latter investigators found that Al in the interlayer of vermiculite was more extractable by Na-citrate in J compared to M in the bulk clay fraction. Moreover, in similar sites in France, hydroxyl-Al polymers have been shown a low fixation by the clay minerals in summer than in winter (Dambrine et al., 1989; Ranger et al., 1991), suggesting an increase in the charge of Al is to be expected (Fig. 1, trend Ia).

The increase in McAl between B and R soils sampling in March (Fig. 1, trend Ib) could be a result of the proton production from the active roots in autumn period. This rhizospheric effect was not seen in samples collected in June (Fig. 2, trend Db) nor during the growing season from M to J (Fig. 2, trend Da). Such a drop in McAl maybe attributed to the production of OH⁻ due to uptake process (Fig. 1) or organic acids production which increased Al-organic complexation and/or mineral weathering.

4.4. Nutrients

Table 2 shows that K saturation (K/CEC) increased significantly for all sample in the order of B<R<RI during both seasons, even to a higher degree in J than in M. This trend of rhizospheric accumulation is in a good agreement with the conceptual model developed by Gobran and Clegg (1996). Soil solution extracted by the centrifugation of the soil samples used in this study indicated that K concentration in R was always higher than in B (Turpault et al., 2005). Many studies supporting this observation in forest soils have been reported e.g. *in vitro* studies (Bakker et al., 1999; Bakker et al., 2004), and *in situ* studies (Clegg and Gobran, 1997; Wang and Zabowski, 1998; Dieffenbach and Matzner, 2000).

Furthermore, K budget has not been regarded as a growth limiting factor for our Douglas ecosystem (Ranger and Turpault, 1999). On the contrary, Ca and Mg budgets have been negative in such an ecosystem (Ranger and Turpault, 1999). Such shortage in Ca and Mg is reflected by the decrease in Ca saturation (Ca/CEC) and Mg saturation (Mg/CEC) in the R compared to B in the three soil layers (Table 2). It is also interesting to note that due to the increased uptake during J, the depletion of Mg seemed to be higher than Ca when B is compared with R. This observation suggests that the shortage in Mg may become more limiting in this site, especially during the growing season.

5. Conclusion

The differences in the chemical properties of soil fractions and how these variables were affected by the growing season of the Douglas fir ecosystem were statistically assessed. The results indicated that all the measured variables except EA/CEC%, Alt/CEC%, Ald/CEC% and Ht/CEC% increased significantly in the same order (B<R<RI). For example, the total C and CEC were always higher in the rhizosphere than in the bulk soil. Our results suggest that roots, associate microorganisms, and plant nutrient uptake have a regulating ability favoring their own system by establishing nutrient-rich conditions.

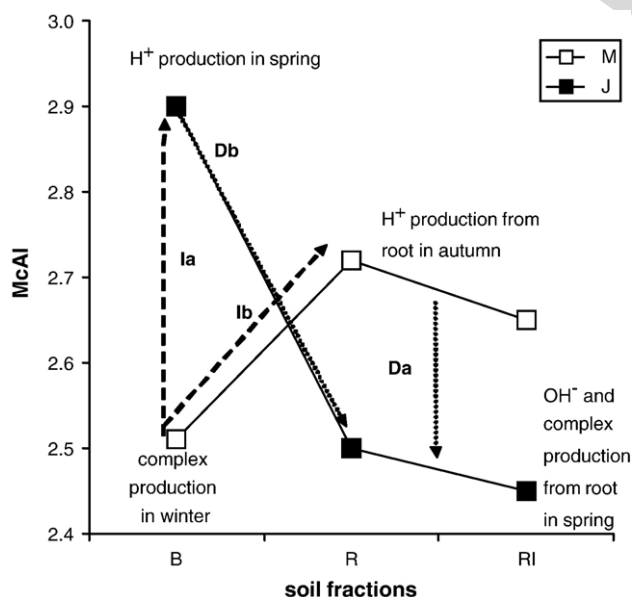


Fig. 2. Variation of mean charge of Al exchangeable (McAl) in the three fractions (B, R and RI) during March (M) and June (J) in layer 2. Ia and Ib correspond to McAl increase respectively between March and June in the bulk soil (B) and from the bulk soil (B) to rhizospheric soil (R) in March. Da and Db correspond to McAl decrease respectively between March and June in the rhizosphere and from bulk soil to rhizosphere in March.

We concluded that rhizosphere is indeed an excellent indicator to understand the dynamics of the ecosystem changes in both short- and mid-term. For example, the temporal effects due to soil nitrification and NO_3^- uptake during March and June were rapidly reflected by a pronounced change in the rhizosphere properties and not in the bulk, i.e. increased pH, complexation of Al. Furthermore, the changes in K, Ca and Mg in the rhizosphere and not in the bulk soil corresponded well with the whole ecosystem nutrient budget of these nutrients.

Our study suggests that rhizospheric processes deserve further attention for the study of ecosystem sustainability. Studying these processes *in situ* calls for a multidisciplinary approach and collaboration.

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