Do deep tree roots provide nutrients to the tropical rainforest?

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Abstract. The contribution of deep tree roots to the nutrition of a tropical rainforest were studied along an edaphic transect in French Guyana. Soil types were mapped in relation to the texture of the upper horizons and the depth of occurrence of the loamy saprolite. The position of mature individuals of four common species, differing by they rooting depth, was identified and tree leaves were analysed for major nutrients and strontium (Sr) isotopic ratios. On average, the range of leaf isotopic ratio ($^{87}Sr/^{86}Sr$ = 0.714–0.716) was narrow compared to that of bulk soils ($^{87}Sr/^{86}Sr$ = 0.72–0.77). Steep gradients of increasing $^{87}Sr/^{86}Sr$ in roots with soil depth were found in all investigated profiles, which indicated that the flux of Sr deposited in rain and leached from the litter layer was tightly retained in the upper soil layers. Over the whole of the site, as well as within each soil unit, tree $^{87}Sr/^{86}Sr$ ratios were very similar whatever the species, and close to litter and near-surface roots $^{87}Sr/^{86}Sr$ ratios, suggesting no or very little Sr contribution from deep tree roots. Variations of Ca and Sr concentrations in leaves were strongly correlated but not with leaf $^{87}Sr/^{86}Sr$ ratios. These results support the theory that Sr and Ca uptake and cycling are mostly superficial in tropical rainforests.

Introduction

In forested ecosystems, plant available base cations in soils originate from two primary sources: atmospheric deposition and soil mineral weathering. These nutrients are essential for the vegetation, and play a major role in neutralising soil acidity and maintaining biological activity. The sustainability of forest ecosystem fertility depends on these primary fluxes, as well as on the efficiency of nutrient uptake and cycling within the ecosystem. Under wet tropical climate, mature soils developed from crystalline rocks are strongly weathered and extremely impoverished in alkaline and alkaline earth cations. Based on a comprehensive study of nutrient fluxes in the soil of a pristine forest of the Amazon, Jordan (1982) suggested that forest nutrients were mostly derived from the atmosphere. Lesack and Melack (1996) in a Central Amazon catchment showed that nutrient inputs from rain were fairly low but larger than nutrient outputs in streamwater, which indicate a very low rate of

soil mineral weathering at the catchment scale, and a strong retention of leached ions by tree roots. Tropical trees display a large variety of rooting patterns. Although fine roots always densely prospect the litter layer, many species have tap-roots down to several meters depth. In a literature study of maximum rooting depth in major biomes, Canadell et al. (1996) indicated a maximum rooting depth for tropical evergreen forests of 8 m ± 0.5 on average. A very significant contribution of deep tree roots to water uptake during the dry season has been demonstrated. Guehl (1984), in French Guyana rainforest and Nepstad et al. (1994), in a dryer area of Southern Amazon, showed large decreases in the water content of deep soil horizons (down to 1.6 m and 8 m depth, respectively) during the dry season. However, the contribution of deep tree roots to mineral uptake remains mostly unknown. In a comprehensive study of tree $\delta^{15}N$ in French Guyana, Roggy et al. (1999) suggested that low $\delta^{15}N$ values in deeply rooted non N-fixing tree species could be related to preferential uptake of ^{15}N-depleted NO_3 in deep mineral horizons. Besides, mycorrhizal fungi associated with roots were observed in deep mineral horizons (Ferry et al. 2000). Relations between soil factors, plant rooting patterns and symbioses and nutritional requirements may to a certain extent determine the distribution of plant species in the rainforest (Austin et al. 1972; Sabatier et al. 1997; Clark et al. 1999).

Tracers, and especially isotopic tracers, are welcome when the contribution of different sources to tree supply is to be established. Under favourable conditions, the $^{87}Sr/^{86}Sr$ ratios of the Strontium (Sr) deposited from the atmosphere and released by weathering differ. The $^{87}Sr/^{86}Sr$ ratio of atmospheric deposition is mostly influenced by the oceanic $^{87}Sr/^{86}Sr$ ratio and varies in the range 0.709–0.716 (Wickman 1996; Négrel and Lachassagne 2000). The $^{87}Sr/^{86}Sr$ ratio of rocks varies according to their age and their original Rb and Sr content (Faure 1986). Because the ionic radius of Sr is close to that of Ca, Sr is substituted to Ca in most Ca-bearing minerals. Besides Rb is substituted to K in most K-bearing minerals and the radioactive decay of ^{87}Rb produces ^{87}Sr (half-life 4.88 10^{10} years). Hence, in a given rock, the $^{87}Sr/^{86}Sr$ isotopic ratio of K-bearing minerals, with high Rb/Sr ratio, is higher than that of Ca-bearing minerals. The difference between isotopic signature of rain and weathering has been used to quantify the relative contribution of these two sources to Sr and base cation fluxes in ecosystems (Graustein and Armstrong 1983; Graustein 1989; Miller et al. 1993; Åberg 1995; Bailey et al. 1996; Capo et al. 1998). The main difficulty is identifying the weathering end-member because it depends on soil mineral composition which may vary considerably both laterally and vertically (Bailey et al. 1996). Moreover, the Sr isotopic composition of the bulk soil may be not related to that of the weathering solution, because the mineral that release Sr may be a minor fraction of Sr bearing minerals (Bain and Bacon 1994). The vertical variation of soil isotopic composition may be used to estimate the weathering end-member (Bailey et al. 1996; Bullen et al. 1997). However this assumes that the process, which has led to the vertical differentiation of the soil profile, is still active and that the soil profile is developed from an homogeneous parent material, which is often not the case. Leaching of soil materials with diluted mineral (Miller et al. 1993) or organic acids (Wickman and Jacks 1991, 1992) has

been used to estimate a weathering signature, although this method may yield variable results in soils poor in weatherable minerals (Probst et al. 2000; Taylor et al. 2000).

Because rain Sr is deposited on the soil surface, whereas soil weathering releases Sr from mineral horizons, the Sr isotopic ratio may form a depth gradient. The relation between the tree and soil bioavailable Sr isotopic ratios may then be used to measure the mean depth and sources of Sr uptake (Wickman and Jacks 1993; Dambrine et al. 1997). Sr is not essential to the plant, but the chemical structures of Ca and Sr are very close (Faure 1986) and their variation in waters and plant organs are correlated. However, a preferential uptake and translocation of Ca over Sr by some plants has been shown (Elias et al. 1982; Poszwa 2000). In spite of these different dynamics, this method has been successively used to quantify Ca sources in forests (Jacks et al. 1989; Miller et al. 1993; Bailey et al. 1996)

The aim of the following work was to study the contribution of deep tree roots to the base cation nutrition of a tropical rainforest in French Guyana. The study was designed to compare four common forest species with different rooting architectures, along an edaphic transect from sandy to loamy soils, typical to very large areas in French Guyana and the Amazon. Our hypothesis were that (1) deeply rooted tree species could act as a nutrient pump, recycling leached ions and returning nutrients through litterfall to the whole plant community, (2) the mean depth of nutrient uptake was influenced by soil texture and hydrologic regime and tree size. Because tropical soils are generally deeply leached, large $^{87}Sr/^{86}Sr$ isotopic changes of bioavailable Sr in relation to soil depth were expected in the study area. The nutrient content and Sr isotopic signature of tree leaves and soils were measured in order to compare the mean depth of root uptake of the different tree species and its relation to rooting patterns, tree nutrition, and soil physical and chemical properties.

Material and method

Site

The study site (5°20' N, 52°10' W) is located on the Northern edge of the Amazon forest, 30 km inland from the Atlantic coast of French Guyana, 30 km west from Kourou, near Petit Saut dam (Bonal et al. 2000; Ferry et al. 2000). The climate is of the humid tropical type with an average annual precipitation of 3000 mm, but with large interannual variations (1.5 to 4 m). Average monthly temperature is 26 °C all year round. The yearly average potential evapotranspiration is 1500 mm (Roche 1982). The dry season lasts on average about 2 months, with large interannual variations: the average monthly precipitation is close to or below 50 mm during September and October.

The landform is tabular and the elevation is low (<100 m a.s.l.). The geological substrate is schist and pegmatite from the Armina sedimentary succession of the

paleo-proterozoic (2.5–1.9 GA, Gruau et al. (1985)). It is deeply weathered. The loamy saprolite is covered by a sandy-clayey to sandy material, several meters thick, initially referred to as the "Série détritique de base" by geologists, who considered it as a sedimentary deposit from the Pliocene (Boye 1963), whereas Veillon (1990) showed on the northern plateaux of French Guyana, that this material may well result from an in situ pedological differentiation. This material always has a good macroporosity, either due to a microaggregate structure of the sandy-clay fine earth or to the sandy texture, which provide a free vertical drainage. In contrast, the loamy saprolite below the detritic cover has a massive structure, low macroporosity and permeability (Grimaldi and Boulet 1989) and generates a water table and lateral drainage during the rain season (Guehl 1984). The site is about 3 ha large and covers the upper part and the slope of a small hill (25 m height). Two main soil units were characterised in relation to their texture and position in the landscape (Ferry et al. 2000). The Thick Detritic Material soil unit (TDM) on the plateau was characterised by a thick (1–4 meters) sandy to sandy clay loam material. On the hillslope, the sandy material was eroded. The Saprolite Near the Surface (SNS) soil unit was characterised by the occurrence of a loamy saprolite in the first meter of the profile. TDM and SNS soil units have been described many times in French Guyana as DVD (deep vertical drainage) and SLD (superficial lateral drainage) in relation to their hydrological behaviour (see for instance Sabatier et al. (1997)). Subdivisions of these units in relation to the texture of the detritic material and the depth of occurrence of the loamy saprolite were mapped, except for soils near the stream, which were not characterised.

Most SNS soils contained in the top 40 cm a large amount of ferruginised quartz remains, several cm in diameter. Saprolite colour varied between red, yellow, light grey and white. We were not able to represent the extension of these different types of saprolites, but they occurred in distinct areas. White and grey saprolite (2.5 Y 8/3; N 8 /; N 7 /) occurred below thick detritic horizons, below thin detritic layers with hydromorphic conditions and below thin detritic horizons on the Eastern slope of the catchment. The red and reddish yellow saprolite (2.5 YR 4/8; 2.5 YR 5/8; 5 YR 5/8; 5 YR 6/8) occurred at shallower depth, only on the Southern-west and gentler slope. The different colours of the saprolites are related to either differences in the parent rock composition, or to the progressive transformation of the red saprolite into the white saprolite by weathering of muscovite into kaolinite and loss of Fe (Grimaldi et al. 1994; Grimaldi and Pédro 1996).

Species selection

A tropical rainforest covers the site. It was opened in some places in 1979 for selective timber exploitation, but the area where our study was carried out was mainly undisturbed. Three species were chosen for their very different rooting systems, described at the study site (Bonal et al. 2000; Ferry et al. 2000). *Eperua falcata* Aublet is a very common species of the forest reaching the top of the canopy. It is a legume, which is known to occur preferentially on poor soils, either very sandy, or with dense deep horizons and hydromorphic characteristics in surface horizons

(Barthès 1991; Bariteau 1992). In Surinam, it is common on the white sand covers (Schultz 1960). Its root system is characterised both by deep taproots and by an extensive network of horizontal near-surface roots exploring the litter. Tap roots down to 3.5 and 2 metres were found in the TDM and SNS soils respectively (Ferry et al. 2000). *Dicorynia guianensis* Amsh. is also a common legume reaching the top of the canopy, much in demand for its wood. This species is not strongly linked to specific soil types but is less abundant on badly drained depressions, close to the streams. Its root system is less hierarchical and more sensitive to obstacles; it has no deep taproots and horizontal near-surface roots in the litter are much less abundant than for *Eperua* (Grandval 1993). The deepest roots were found at 1.6 and 1 meter depth in TDM and SNS soils respectively. *Astrocaryum sciophilum* (Miq.) is a small size palm tree of the understorey. Large palms form a 3–5 meter wide funnel, which collect leaf litter falling from neighbouring trees. This species is densely rooted in the litter heap (about 50 cm height on average) resulting from the accumulation of litterfall at the foot of the stem. It was hypothesised that these palm trees would mostly take up nutrients from the decomposing litter. A legume which wood is much appreciated, *Vouacapoua americana* Aublet, was also studied, although it was represented only by a few trees on the site. This species occurs on well-drained soils and is almost absent on badly drained depressions (Collinet 1997) but no information was available concerning its root system.

All mature individuals of *Dicorynia guianensis* (Dg), *Eperua falcata* (Ef) and *Vouacapoua americana* (Va), with a diameter exceeding 20 cm, were located and their diameter was registered. From this set, we selected areas where trees of the different species with approximately similar diameters were grouped. *Astrocaryum sciophilum* (As) individuals growing closest to these areas were then located and added to the selection. The succession of soil horizons was described in 35 drill holes located below the selected trees. Upper crown leaves of 20 *Dicorynia*, 22 *Eperua* and 4 *Vouacapoua* were collected by shooting with a gun. Each sample per tree was composed of three twigs sharing several leaves. Pieces of palm were taken with a machete from 11 selected *Astrocaryum* individuals. *Dicorynia*, *Eperua* and *Vouacapoua* leaves were oven dried at 65 °C, then finely ground. 0.5 g of each sample was digested in 10 ml of high purity HNO_3 (Merk suprapur, 65%), in a digestion bloc system (Tecator 40 1016). *Astrocaryum* leaves were previously dry scrubbed from epiphytic organisms with a hard brush. Newly formed leaves, recognisable in the field by their smaller size and their lighter colour, or after analysis by their high P content and low C/N ratio, were not used.

Soil and root sampling and analysis

Four soil pits were opened: on the plateau (TDM soil unit), a deep sandy soil (profile 1) and a deep sandy clay soil (profile 2); on the hillslope (SNS soil unit), a sandy loam covering a red loamy saprolite (profile 3) and a loamy sand covering a white loamy saprolite (profile 4). Soils were sampled per horizon, sieved in the field and roots less than 2 mm in diameter (without other distinction) were separated. Roots within the decomposing litter were not separately collected. Leaf litter was

collected from the soil surface within a ten-meter-diameter circular area around each pit.

Soil density, texture, pH, C, N, cation exchange capacity and total nutrient contents were determined by conventional methods. Soil exchangeable base cations from the 4 profiles were extracted by shaking twice, during 1 hour, 10 g of soil in 50 ml of high purity NH_4Cl 1 molar. Aliquots of the fine earth of the major horizons were ground to uniform fine consistency in an agate mortar. 100 mg were digested overnight with 1 ml of HNO_3 (purified by double distillation) and 1 ml of high purity HF. After evaporation, total digestion of the bulk soil was obtained by adding a few drops of $HClO_4$ and H_2O_2, to remove Ca fluorides and organic mater residues. The fine roots from the 4 profiles were cleaned from soil particles in ultrapure water, using a paintbrush. Samples were dried at 65 °C in an oven, finely ground, then digested following the procedure used for leaves digestion.

Leaf, root and soil nutrient concentrations and isotopic measurements

Calcium, Sr, Mg, P and K in leaves, in roots and in soil NH_4Cl extracts were analysed by ICP AES (Jobin Yvon 38+). The total element contents of soils were measured by ICP-MS. For isotopic measurements, aliquots of samples containing about 500 ng of Sr were evaporated, treated with high purity $HNO_3 + H_2O_2$ in order to remove organic matter remains, then evaporated to dryness in Teflon beakers. Samples were dissolved with 2 molar HCl and passed through quartz glass ion exchange columns containing 8 ml of a Temex 50WX8, 200–400 mesh resin. Sr was collected after elution by HCl 2N and 4N and evaporation to dryness. Sr in chemical blanks was lower than 2 ng. The $^{87}Sr/^{86}Sr$ isotopic ratio of samples was measured by mass spectrometry (Finnigan Mat MS 261). NBS 987 standard was used to control and standardise the measurements. Measurement accuracy was always below $2\ 10^{-5}$.

Statistics

Species or site effects on concentrations or isotopic signatures in tree leaves on the whole site were tested using the Bonferroni t-test and analysis of variance. Significance of statistics ($p < 0.05$) was noted in the text. Grouping trees pairwise (according to closeness of location and soil characteristics) reduced the influence of edaphic variability when comparing the effect of species on isotopic signature. Results were then compared statistically using a paired t-test.

Results

Soil physical characteristics

TDM soil unit of the plateau: In profile 1 (P 1 on Figure 1), the proportion of sand (mainly coarse) increased from 70% above 0.6 m depth to more than 90% pure quartz sand below 1 m depth. In profile 2 (P 2 on Figure 1), the sand proportion was about 65%, with less than 10 % silt down to 1.7 m, and increased up to 90% between 2 and 3 m depth. The loamy saprolite appeared below 3.5 m. In profile 2, soil fine earth density increased from 1 to 1.4 g cm^{-3} down to 0.6 m depth, and decreased further down to 1.2 on average.

SNS soil unit of the hillslopes: In profile 3 (P 3 on Figure 1), the proportion of silt increased from 15% in upper layers to 50 – 65% below the depth of 0.8 m. Conversely, the proportions of coarse sand and clay decreased from about 25% close to the surface to less than 10 % at 1.75 m. In profile 4 (P 4 on Figure 1), the sand proportion was about 75% down to the depth of 0.55 m, with less than 10% silt. The silt proportion increased sharply (50%) in the weathered saprolite. In profile 3, soil density increased from 1.2 to 1.6 g cm^{-3} in the saprolite and remained stable further down.

Soil chemical characteristics

The exchange capacity was low and decreased rapidly with increasing depth according to the organic matter content (Ferry et al. 2000). Base saturation was low and the soil exchange complex was mainly occupied by exchangeable Al (Table 1). Exchangeable Ca and Sr concentrations in upper horizons (Figure 2) were higher in SNS soils on the hillslope than in TDM soils on the plateau. Below 30 cm depth, exchangeable Ca and Sr concentrations were very low, but generally higher in the weathered saprolite. Total Ca content in the fine earth was extremely low (< 80 μg kg^{-1}) and decreased in each profile according to soil depth (Table 1). Total Ca concentrations were higher in soils on the plateau (especially in the upper horizons) than on the hillslopes. Total Sr contents were similar in soils on the plateau and on the hillslopes and slightly increased in each profile according to depth (Table 1). The Sr/Ca molar ratio on the soil exchange complex (Figure 3a) decreased regularly down to 50 cm in the 4 profiles from 10^{-2} to 4 10^{-3}. Deeper, the Sr/Ca ratio stayed almost constant except in profile 1 where very low Ca and Sr concentrations gave irregular values of Sr/Ca. Bulk soil Sr/Ca ratio was much higher (between 0.1 and 1), in relation to very low total Ca contents. Total K concentrations (Table 1) were quite constant according to depth in the profile 2 on the plateau, while total K strongly increased in the weathered saprolite (profile 3) in relation to the muscovite content. The total iron content of the white saprolite (12 g kg^{-1}) was much lower than in the red saprolite (44 g kg^{-1}).
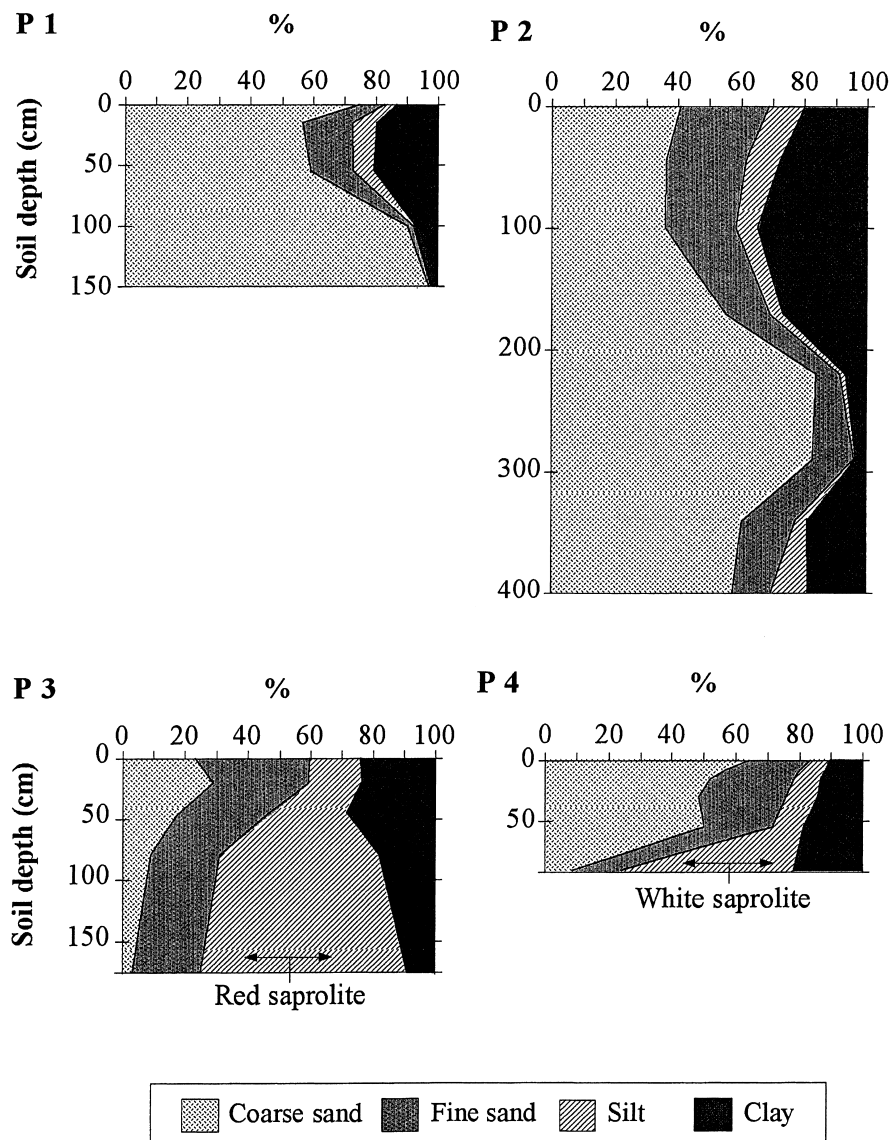
Figure 1. Particle-size distribution in fine earth (< 2 mm) in relation to depth, in profiles 1 (P1), 2 (P2), 3 (P3) and 4 (P4).

Leaf litter and root concentrations

Calcium (10 mg g^{-1}) and Sr (131.4 μg g^{-1}) concentrations in leaf litter from the area around profiles 2 and 3 were higher than from the 2 other profiles (Ca: 5 mg g^{-1} and Sr: 65.7 μg g^{-1}). Ca and Sr concentrations in near-surface roots were higher in profiles 3 and 4 on the hillslopes (data not shown). Fine root concentra-

Table 1. pH, C, N, total element contents and exchangeable element concentrations in profile 2 (P2), 3 (P3) and 4 (P4).

Depth (cm)	pH water	Total (g kg^{-1})							Exchangeable (* mmol(+) kg^{-1},$^{**}\mu$mol(+)kg^{-1})			
		C	N	Ca	Sr	K	Rb	Fe	Ca*	Sr**	K*	Al*
Profile 2, on the plateau (TDM soil unit)												
10–20	5	24.74	1.55	0.074	0.020	0.83	0.003	15.78	0.190	1.071	0.404	22.6
70–100	5.4	4.47	0.39	0.021	0.030	0.97	0.004	26.58	0.028	0.124	0.072	4.5
135–170	5.4	2.40	0.18	0.023	0.031	0.55	0.003	26.40	0.024	0.119	0.044	1.7
Profile 3, on the Southern-west slope (SNS soil unit)												
10–20	4.9	21.64	1.44	0.036	0.023	3.40	0.008	28.32	0.321	1.904	0.589	16.3
55–95	5.3	1.89	0.19	0.019	0.031	8.19	0.015	45.30	0.057	0.198	0.056	5.2
130–180	5.3	0.86	0.14	0.016	0.036	16.52	0.021	43.82	0.142	0.573	0.091	6.8
Profile 4, on the Eastern slope (SNS soil unit)												
10–20	4.5	14.20	0.99	0.016	0.006	nd	0.003	7.80	0.234	1.244	0.406	nd
70–110	4.9	nd	nd	0.034	0.029	nd	0.023	12.31	0.118	0.148	0.071	nd

tions decreased rapidly with increasing depth, with slightly higher Ca concentrations in roots from profile 3 (as for exchangeable Ca).

Leaf litter Sr/Ca ratio (around 6 10^{-3}) was lower than the Sr/Ca of near-surface fine roots. Roots Sr/Ca ranged from 7 to 15 10^{-3} between 0 and 50 cm, and increased in the weathered saprolite (Figure 3b).

Leaf concentrations

Over the whole of the site, Ca and Sr concentrations were strongly correlated in leaves of *Eperua*, *Dicorynia* and *Vouacapoua* (Figure 4) but not in *Astrocaryum* palms. On TDM soils, there was no significant difference in Ca and Sr concentrations in leaves between *Eperua* and *Dicorynia*, while concentrations in *Vouacapoua* leaves were lower. On SNS soils, leaf Ca and Sr concentrations in *Dicorynia* were significantly lower than in *Eperua* ($p < 0.005$), and higher than in *Astrocaryum* ($p < 0.02$) and *Vouacapoua*. The Sr/Ca molar ratio was higher ($p < 0.002$) in *Dicorynia* leaves (7.4 10^{-3}) than in *Eperua* leaves (6.2 10^{-3}) and in *Astrocaryum* leaves (5 10^{-3}). Calcium and Sr content in *Eperua* and *Dicorynia* leaves were higher in SNS soils as compared to TDM soils, but the site effect was much more significant for *Eperua* ($p < 0.03$).

Magnesium concentrations in *Eperua* and *Astrocaryum* leaves were significantly higher than in *Dicorynia* and *Vouacapoua* ($p < 0.006$), whatever the site (data not shown). There was no significant difference in leaf K concentrations according to species or site, excepted in *Astrocaryum* which concentrations were higher on SNS soils than on TDM soils ($p < 0.04$). There was no significant difference in leaf P concentrations according to species or site, excepted in *Astrocaryum* which concentrations were lower on TDM soils compared to the other species ($p < 0.002$).
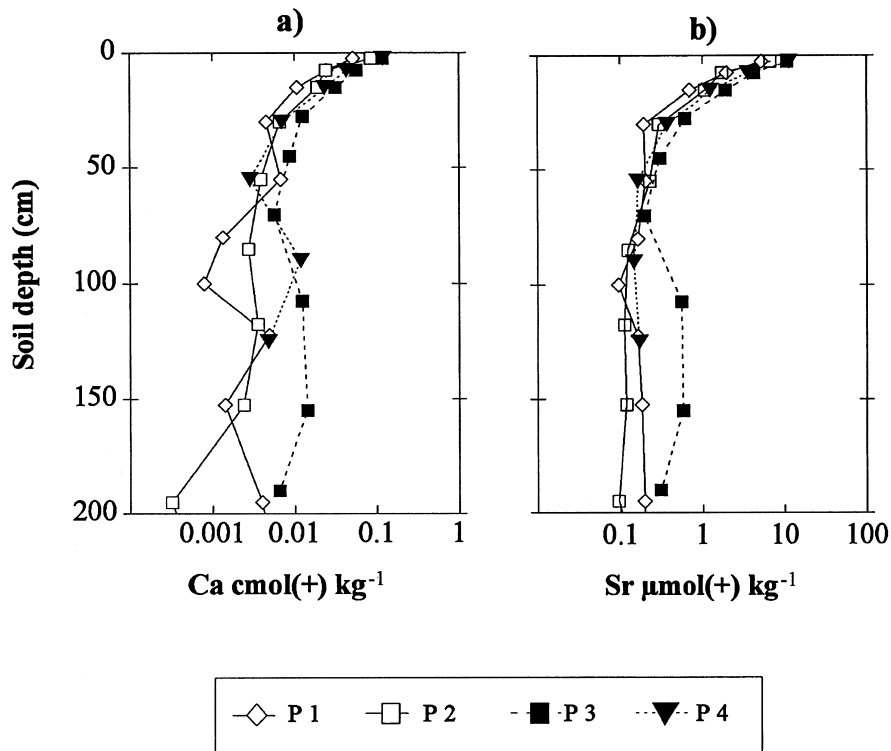
Figure 2. a) Soil exchangeable Ca concentration, and b) soil exchangeable Sr concentration, in relation to depth, in 4 soil profiles (P1, P2, P3, and P4).

$^{87}Sr/^{86}Sr$ isotopic ratio variations in soils, roots and leaves

The $^{87}Sr/^{86}Sr$ isotopic ratio of Sr in bulk TDM soils on the plateau (profile 2) was stable and close to 0.72 from surface to depth (Figure 5). The isotopic signature of bulk soils on the hillslope was close to 0.73 in the upper horizons, 0.76 in the red saprolite of profile 3 and 0.77 in the white saprolite of profile 4. In comparison, the $^{87}Sr/^{86}Sr$ isotopic ratio of exchangeable Sr in the upper mineral layer (0–5 cm) varied within a narrow range, between 0.7141–0.7150 in TDM soils and 0.7156–0.7164 in SNS soils. Fine root Sr isotopic ratio was equal to soil exchangeable Sr in the layer 0–5 cm (except in profile 1) and slightly but consistently higher (+0.0004) in the 5–10 cm layer (Figure 6).

In the 4 studied soils, the $^{87}Sr/^{86}Sr$ ratio of leaf litter was systematically 0.0002 to 0.0003 units lower than in root of the 0–5 cm layer (Figure 7). Root $^{87}Sr/^{86}Sr$ isotopic ratio increased in relation to soil depth but gradients were more accused in SNS soils, especially in profile 4 (Figure 7). In profile 1, roots $^{87}Sr/^{86}Sr$ ratio increased continuously from 0.7145 to 0.7160 from the soil surface to the depth of 30 cm, and stabilised deeper. In profile 2, roots $^{87}Sr/^{86}Sr$ ratio increased from 0.715 to 0.718 between 0 and 150 cm. In profile 3, roots $^{87}Sr/^{86}Sr$ ratio increased from
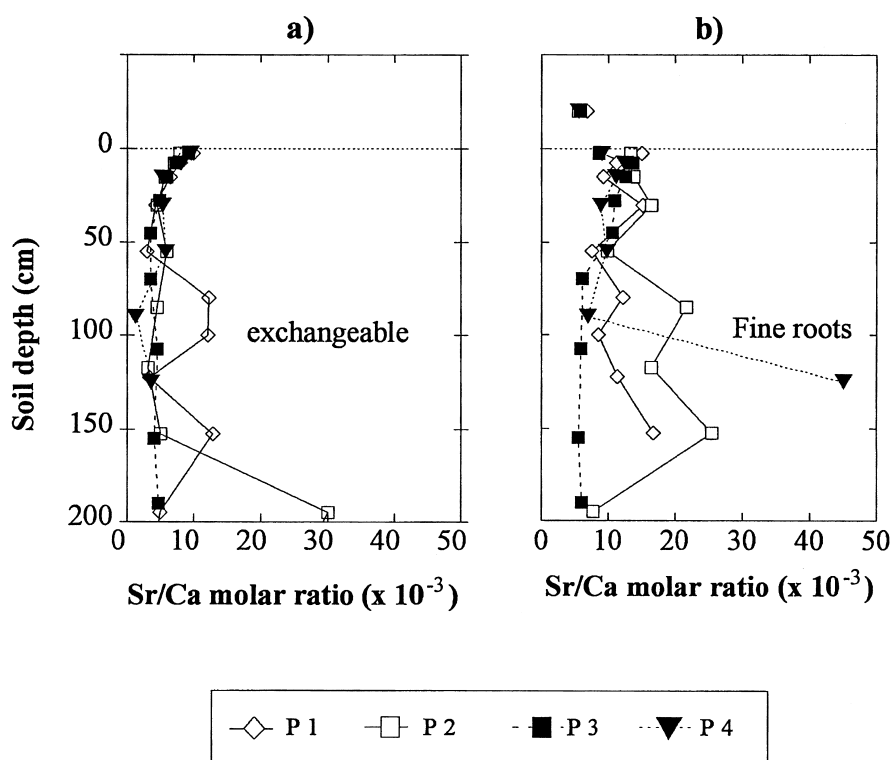
Figure 3. a) Soil exchangeable Sr/Ca molar ratio, and b) Sr/Ca molar ratio in litter and root, in relation to depth, in 4 profiles (P1, P2, P3, P4).

0.7155 to 0.7196 down to 70 cm depth and decreased deeper. In the profile 4, roots $^{87}Sr/^{86}Sr$ ratio increased slightly down to 20 cm depth and abruptly deeper in the weathered white saprolite.

At each site, the leaf $^{87}Sr/^{86}Sr$ isotopic ratio of the trees below which the pits were dug, as well as neighbouring trees, was always lower or close to the $^{87}Sr/^{86}Sr$ isotopic signature of fine roots in the upper 5 cm soil layer, with only one exception: one *Eperua* individual, near the profile 4, which signature (0.719), corresponded to the isotopic ratio of fine roots at a mean depth of about 40 cm.

Spatial relation between soil types, leaf isotopic ratio and leaf mineral content

Three distinct areas with increasing leaf $^{87}Sr/^{86}Sr$ ratio could be identified and related to soil units (Figure 8). The lowest isotopic ratios (mean = 0.7145, standard deviation: sd = 4 10^{-4}) were measured in leaves of trees growing on TDM soils (with a saprolite depth > 2m), on the plateau (area I). Slightly but significantly
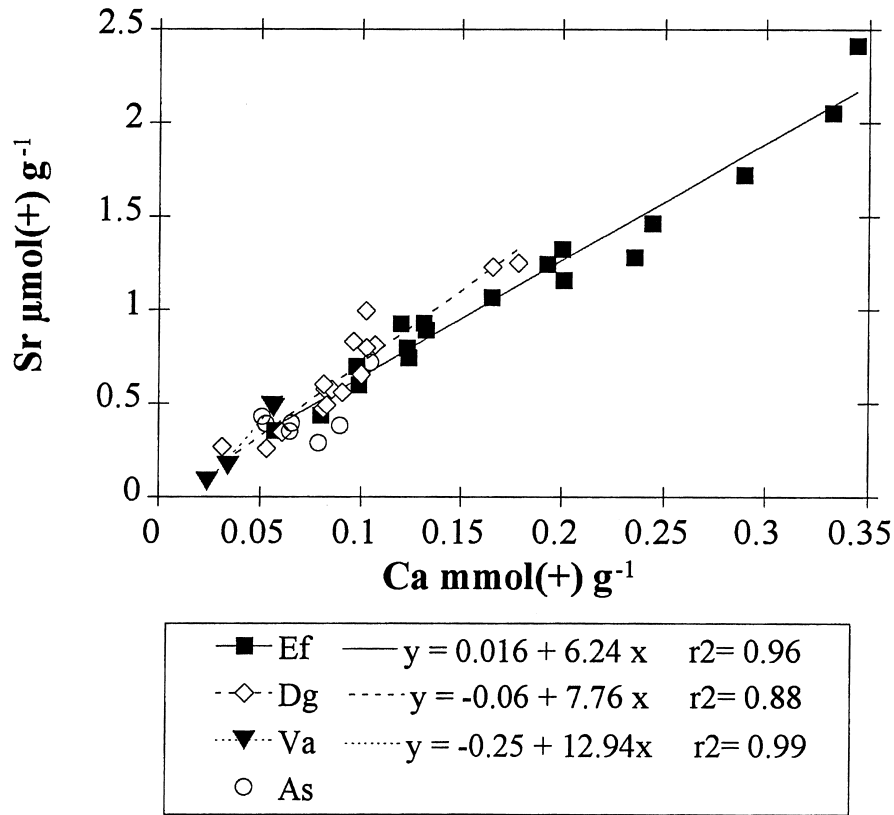
Figure 4. Correlation between leaf Ca and Sr concentrations in *Eperua falcata* (Ef), *Dicorynia guianensis* (Dg), *Vouacapoua americana* (Va) and *Astrocaryum sciophilum* (As).

higher $^{87}Sr/^{86}Sr$ values (mean = 0.7151, sd = 4 10^{-4}) were measured in leaves of trees growing on SNS soils, with or without hydromorphy, on the Southwest slope (area II). Much higher $^{87}Sr/^{86}Sr$ ratios (mean = 0.7165, sd = 10 10^{-4}) were observed in leaves of trees located on the Southeast slope (area III), on SNS soils with a white saprolite, or close to the stream, or on sandy clay soils 1–2 meter thick, over a white saprolite.

Considering the closest trees to each litter sampling areas, the comparison of leaf $^{87}Sr/^{86}Sr$ ratios (Figure 7) showed on average the following order *Astrocaryum < Eperua* = litter = *Vouacapoua < Dicorynia*. Nevertheless, these interspecific variations of leaf $^{87}Sr/^{86}Sr$ isotopic ratio were low (< 5 10^{-4}) compared to the edaphic variations between the different areas (6–20 10^{-4}). In order to assess statistically some interspecific differences, trees were grouped according to their geographic and edaphic proximity in 12 couples *Eperua – Dicorynia*, 7 couples *Dicorynia – Astrocaryum* and 8 couples *Eperua – Astrocaryum*. For all *Eperua – Dicorynia* couples except one, leaf $^{87}Sr/^{86}Sr$ ratio was higher in *Dicorynia* than in
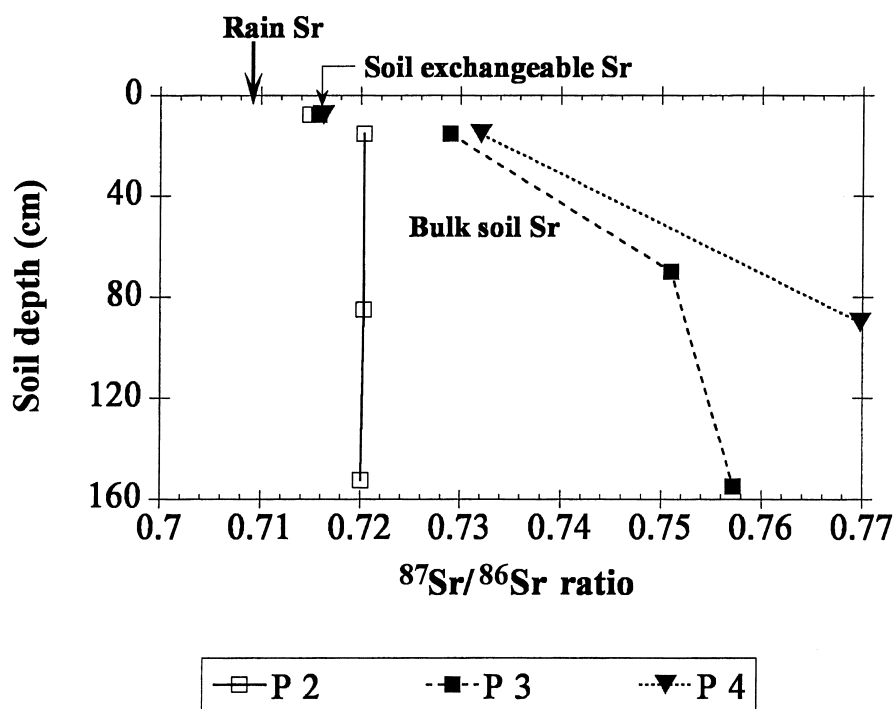
Figure 5. $^{87}Sr/^{86}Sr$ isotopic ratio of bulk soils of the plateau (profile 2: P2) and the hillslopes (profiles 3: P3 and 4: P4) and of soil exchangeable Sr at 5–10 cm depth.

Eperua (p = 0.015). *Astrocaryum* palm isotopic ratio was lower than *Dicorynia* leaf (p= 0.02) and *Eperua* leaf (p = 0.016).

Over the whole of the site, tree DBH varied between 20 and 70 cm, and was especially variable for *Eperua* growing on SNS soils. No relation was found between tree diameter and leaf $^{87}Sr/^{86}Sr$ ratio. A weak relation between Sr concentration and $^{87}Sr/^{86}Sr$ isotopic ratio was observed in leaves of *Eperua located* on the Southeast hillslope (area III) but very large variations in Sr concentration were measured in leaves of *Eperua* on the Southwest slope (area II) without any variation of isotopic ratio (Figure 9).

Discussion

Isotopic ratios of Sr sources

The oceanic $^{87}Sr/^{86}Sr$ ratio is 0.709. The $^{87}Sr/^{86}Sr$ ratio of major rains in the wet season was not measured, but should be close to this value because most rains come from the East, and the site is less than 30 km from the ocean. On the other hand, Négrel and Lachassagne (2000) measured higher values (on average 0.7118) in
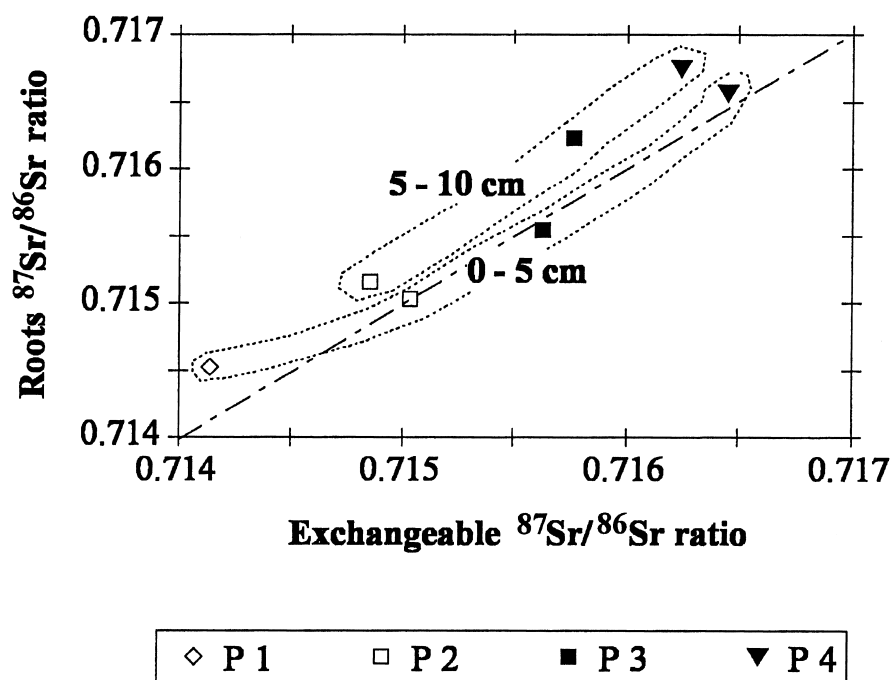
Figure 6. Comparison between isotopic ratio of root Sr and exchangeable Sr at two soil depth (0–5 and 5–10 cm), in 4 profiles (P1, P2, P3, P4).

rains of continental origin collected during the dry season along the Maroni river, 200–300 km inland. Given the small contribution of rains from the dry period in the total rain amount, and the proximity of the study site to the sea, the average volume weighted isotopic ratio of atmospheric deposition should be close to 0.710.

The mineralogical and Sr isotopic composition of primary schist in this area is unknown (Gruau et al. 1985). It is weathered into a red saprolite, composed mainly of muscovite and iron, which Sr isotopic ratio is close to 0.76. This transformation may be ascribed to preferential weathering of the most weatherable minerals such as feldspar. Transformation of the red or yellow muscovite-dominated saprolite into a white kaolinite-dominated saprolite, releases mainly K and Fe, but also Ca, as demonstrated by Grimaldi et al. (1994) in French Guyana, and certainly Sr (Table 1). The higher $^{87}Sr/^{86}Sr$ ratio in the white saprolite (profile 4) compared to the red saprolite (profile 3) suggests a preferential weathering of minerals with lower isotopic ratio than the bulk soil during this mineral transformation. However, the influence of spatial variations of the parent material composition cannot be ruled out from the data in hand. On the plateau, the stability of the Sr isotopic ratio in profile 2, in spite of large variations of clay and Sr contents, suggests that the isotopic ratio of the detritic cover is controlled by one mineral. On the hillslope, the decrease of the Sr isotopic ratio from the saprolites to the sandy upper layers may be ascribed to the progressive dissolution of muscovite, and to the conservation of
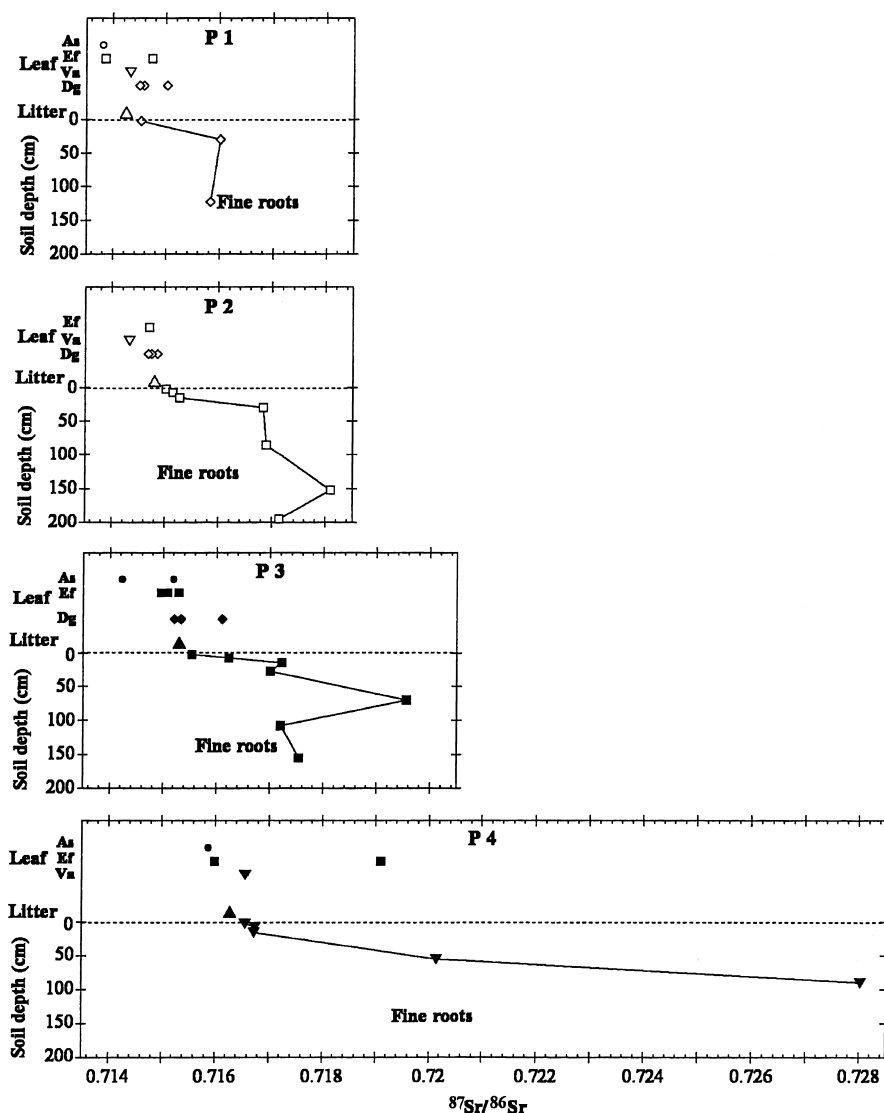
Figure 7. ^{87}Sr/^{86}Sr ratio in leaves of *Eperua falcata* (Ef), *Dicorynia guianensis* (Dg), *Vouacapoua americana* (Va) and *Astrocaryum sciophilum* (As), surrounding 4 soil profiles (P1, P2, P3, P4) and variation of root ^{87}Sr/^{86}Sr isotopic ratio with soil depth. Symbols as in Figure 4

Ca-bearing accessory minerals or the integration of atmospheric Sr into secondary minerals (Chadwick et al. 1999). It results also from the mixture in various proportions of materials from the saprolite and the detritic cover.

Root ^{87}Sr/^{86}Sr ratio is the closest indication of plant available Sr isotopic ratio in the root environment, as shown by the comparison between root Sr and exchangeable Sr isotopic ratio presented here (Figure 6), as well as at other sites
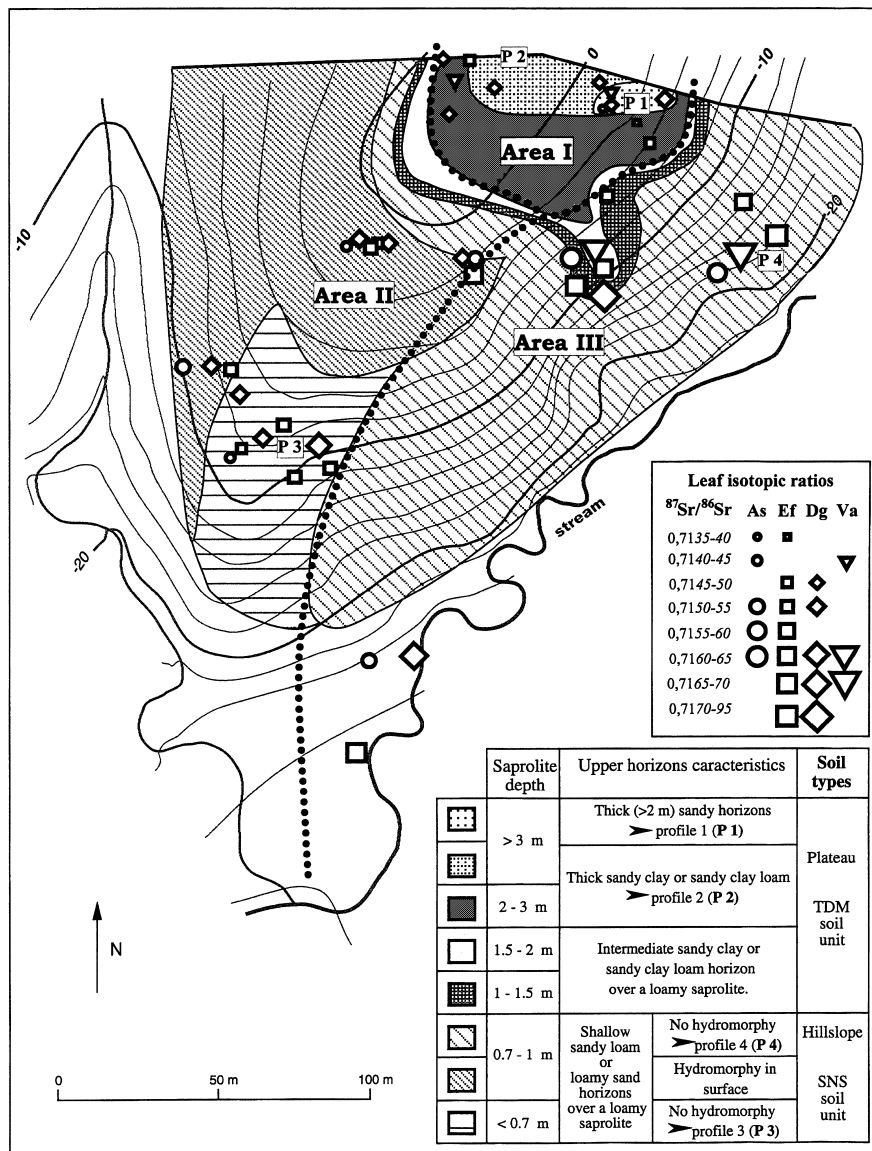
Leaf isotopic ratios

$^{87}Sr/^{86}Sr$	As	Ef	Dg	Va
0,7135-40	●	■		
0,7140-45	○			▽
0,7145-50		□	◇	
0,7150-55	○	□	◇	
0,7155-60	○	□		
0,7160-65	○	□	◇	▽
0,7165-70		□	◇	▽
0,7170-95		□	◇	

	Saprolite depth	Upper horizons caracteristics		Soil types
▨	> 3 m	Thick (>2 m) sandy horizons ➤ profile 1 (P 1)		
▨		Thick sandy clay or sandy clay loam ➤ profile 2 (P 2)		Plateau
▨	2 - 3 m			TDM soil unit
□	1.5 - 2 m	Intermediate sandy clay or sandy clay loam horizon over a loamy saprolite.		
▦	1 - 1.5 m			
▨	0.7 - 1 m	Shallow sandy loam or loamy sand horizons over a loamy saprolite	No hydromorphy ➤ profile 4 (P 4)	Hillslope
▨			Hydromorphy in surface	SNS soil unit
□	< 0.7 m		No hydromorphy ➤ profile 3 (P 3)	

Figure 8. Topography, soil types, soil profiles location, and leaf Sr isotopic ratios of *Astrocaryum scio-philum* (As), *Eperua falcata* (Ef), *Dicorynia guianensis* (Dg), *Vouacapoua americana* (Va)

(Poszwa 2000). The sharp increase of root $^{87}Sr/^{86}Sr$ ratios within the first 50 cm of all profiles implies that the flux of Sr released by soil mineral weathering was not negligible compared to the flux of Sr entering in the soil with rain and litter leachates. In comparison, the relative stability of root isotopic ratios below the depth of 50 cm in profiles 1, 2 and 3 suggests that weathering does release only
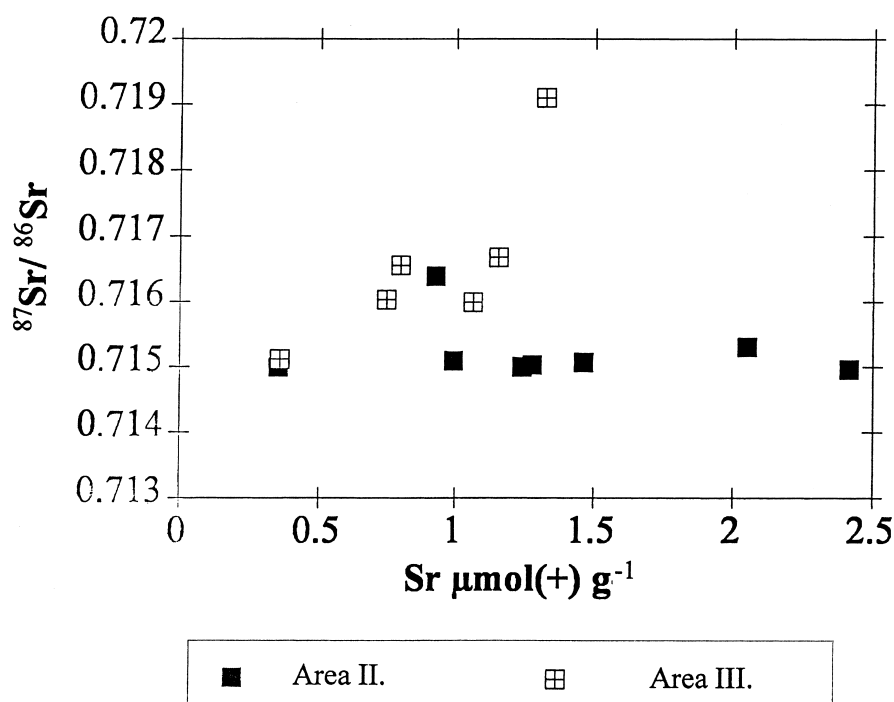
Figure 9. Relation between Sr concentration and $^{87}Sr/^{86}Sr$ isotopic ratio in leaves of *Eperua falcata* on the hillslope.

minor amounts of Sr below this depth. This was obvious in profile 1 because the soil material becomes pure quartz sand at depth, but not in the sandy-clay profile 2. It suggests that weathering was concentrated in upper soil layers, probably in relation to root activity. It is also in agreement with the results of Grimaldi et al. (1994), that almost no weathering occurred in the red saprolite (profile 3), while the white saprolite (profile 4) was submitted to intense weathering.

If the Sr released by weathering was concentrated in upper soil layers, the stability of bulk soil $^{87}Sr/^{86}Sr$ ratio with depth in profile 2, on the detritic cover, could only be explained by the release of Sr with an isotopic ratio similar to that of the bulk soil, that is 0.72. On the hillslope, the isotopic ratio of the Sr released by weathering from upper soil layers should be higher than or close to bulk soil ratios (0.73) but the value cannot be precisely determined from the data in hand, because different mixed materials are present.

Strontium and Calcium cycles and depth of Sr uptake

From the data of Grimaldi (personal communication) and Négrel and Lachassagne (2000), we calculated that about 30 g ha^{-1} of Sr with a mean isotopic ratio of 0.710, and 5 kg ha^{-1} of Ca were annually deposited by rain. Assuming a mean litterfall of

$6 \ 10^3$ kg ha^{-1} yr.$^{-1}$ (Puig and Delobelle 1988) and using the concentrations we measured in litter, we calculated that between 360–760 g ha^{-1} of Sr and 30–61 kg ha^{-1} of Ca return on the soil surface through annual litterfall.

The sharp increase of root $^{87}Sr/^{86}Sr$ ratios within the first 50 cm of all profiles implies also that the flux of Sr deposited with rain and leached from the litter was tightly retained in the upper soil layer, and that the uptake of Sr from deeper layers was not significant. In fact, the drainage of a significant proportion of litter derived Sr and the uptake at depth would have resulted in a smoother isotopic variation with depth. The efficient trapping of Ca deposited on the soil by the superficial root mat was already shown by Stark and Jordan (1978) using a ^{45}Ca addition experiment.

Assuming that the ecosystem was close to equilibrium, the flux of Sr taken up should be equal to that of Sr recycled in the litterfall. Hence, a flux of Sr equivalent to that brought by rain (30 g) and with an isotopic ratio between that of rain and litter, was leached deeper in the soil profiles. The mixture of this Sr with an increasing proportion of Sr released by weathering (which Sr isotopic ratio should be equal or higher than 0.72) explains the variation of the $^{87}Sr/^{86}Sr$ ratio of available Sr with soil depth. Considering that tree Sr was taken up from the upper layer, and that the weathering signature from this layer was equal to the isotopic ratio of the bulk soil, that was 0.72 on the plateau and 0.73 on the hillslope, the contribution of mineral weathering to Sr in trees would be about 50% on the plateau and 35% on the hillslope. Proportions would be much lower for Ca: in fact, as bulk soil Sr and Ca concentrations were close, fluxes of Ca and Sr released by weathering should be of the same order of magnitude. Hence, atmospheric deposition should be the main origin of tree Ca.

For each profile, the litter $^{87}Sr/^{86}Sr$ ratio was surprisingly lower (-2 to $-3 \ 10^{-4}$) than root $^{87}Sr/^{86}Sr$ ratio in the upper layer (0–5 cm). This could indicate that: (1) litter Sr was a mixture of leaf Sr and rain Sr – but given the Sr amount and isotopic signature of litter compared to that of rain, this mechanism would imply a large fixation of rain Sr by litter, which is rather unlikely; or that (2) the signature of plant available Sr vary with the season, ratios being shifted toward higher values during the dry season when the sampling was effected – but this would imply a very high turnover rate of roots; or and more likely that (3) most of the uptake occurred from the litter itself, rather than in the upper mineral soil (0–5 cm) below the litter layer.

Leaf Sr concentrations were not correlated with leaf isotopic $^{87}Sr/^{86}Sr$ ratio, although Sr concentrations and isotopic ratios were higher on the hillslope than on the plateau. We interpret the higher concentrations on the hillslope as the result of the lateral drainage of solutions in the upper sandy layers during the wet season.

Depth of Sr and Ca uptake in relation to rooting patterns and soil types

Leaf isotopic $^{87}Sr/^{86}Sr$ ratios were very close for neighbouring trees, whatever the species and soil type. Several mechanisms are probably involved: (1) the lateral drainage along the slopes; (2) the large area prospected by the surface roots of most

trees (about 300 to 700 m^2); (3) the spreading of falling leaves by wind – it was shown at a similar site (Leroy, unpublished) that less than 30% of litterfall below a tree originates from the tree itself. In spite of these mechanisms, isotopic differences among tree species were found. The isotopic signature of the palm tree *Astrocaryum*, which was rooted in litter accumulations, was slightly lower than that of other species, probably as a result of direct uptake of Sr from rain. Although *Eperua* developed a much deeper rooting system than *Dicorynia*, the isotopic signature of *Dicorynia* was slightly higher, whatever the soil type. This probably results from the fact that the litter layer is more densely prospected by *Eperua* than by *Dicorynia* (Grandval 1993). But it clearly shows that the contribution of deep *Eperua* roots to Sr supply is generally unimportant. However it may be noted that we found one exception: one *Eperua*, close to profile 4, had a much higher isotopic ratio (0.719) than the litter and the neighbouring trees. This tree might provide nutrients from deep horizons to the ecosystem.

Why then was the uptake of Sr and Ca restricted to the upper layers? Several explanations may be given. Reasons might be different on the plateau and on the hillslope. On the plateau, the deep sandy permeable soils are extremely depleted in weatherable minerals. Hence the nutrient source is restricted to the upper organic layer, even if soil water monitoring (Sabatier et al. 1997) showed a deep water uptake during the dry season. On the hillslope, drainage and rooting are mostly lateral in the upper sandy layers. Even if *Eperua* deep roots penetrate in the saprolite, their lateral extension is small in relation to the high density and narrow porosity of the horizon.

Phosphorous, which may be the limiting element in these ecosystems, was mostly available in the upper soil layers, as deep layers were chemically extremely impoverished. Hence, it might be much more valuable for some species to densely prospect upper layers. Recent pot trials in French Guyana showed a strong response of *Dicorynia* growth to phosphorus, but no response of *Eperua* (Montpied, pers. comm.). Besides, uptake in deep soil horizons might be limited by the high levels of exchangeable Al. Studying the distribution of *Eperua* in French Guyana, Barthès (1991) showed that *Eperua* were frequent on soils rich in exchangeable Al. Here experimental evidence is clearly lacking (Cuenca et al. 1990).

Water deficits occurred only during a short period during the year. Soil water and H$_2^{18}$O measurements in the two soil units confirmed large variations in deep soil water content between the wet and the dry season (Bonal et al. 2000). Longer drought periods would have certainly favoured water and possibly nutrient uptake by deep tree roots of *Eperua*. Finally, are deep taproots a competitive advantage for tree species in this environment? Deep water uptake by *Eperua* may explain the spread of *Eperua* on white sand areas in Guyana, but does not seem to justify, from a nutritional point of view, the abundance of *Eperua* on wetter soils. Better anchoring might be another advantage for deep-rooted tree species on wet or poorly penetrable soils. But the abundance of deep rooting tree species in the present forest might also result from their past adaptation to a much dryer climate during the glaciation periods of the late quaternary.

Conclusion

Deep roots in tropical rainforest soils do not seem to play an important role in tree nutrition. This may be explained by two main reasons: 1- Trees superficial root systems are extremely efficient in relation to the major availability of nutrients in litter; 2- hydrological deficits occur only during a short period in a year. Results of this present study confirm the general view that the nutrients cycle in rainforest occurs mostly in upper soil layers. Besides, Sr isotopic ratio measurements appear as a promising tool to study rooting strategies in heterogeneous multispecific tropical forests.

Acknowledgements

References

Åberg G. 1995. The use of natural strontium isotopes as tracers in environmental studies. Water Air Soil Pollut. 79: 309–322.

Austin M.P., Ashton P.S. and Greig-Smith P. 1972. The application of quantitative methods to vegetation survey. III. A re-examination of rain forest data from Brunei. J. Ecol. 60: 305–324.

Bailey S.W., Hornbeck J.W., Driscoll C.T. and Gaudette H.E. 1996. Calcium inputs and transport in a base poor forest ecosystem as interpreted by Sr isotopes. Water Res. Res. 32: 707–719.

Bain D.C. and Bacon J.R. 1994. Strontium isotopes as indicators of mineral weathering in catchments. Catena 22: 201–214.

Bariteau M. 1992. Régénération naturelle de la forêt tropicale humide de Guyane: étude de la répartition spatiale de *Qualea rosea*, Aublet, *Eperua falcata* Aublet er *Symphonia globulifera* Linnaeus f. Ann. For. Sci. 49: 359–382.

Barthès B. 1991. Influence des caractères pédologiques sur la répartition spatiale de deux espèces du genre *Eperua* (Caesalpiniaceae) en forêt guyanaise. Rev. Ecol. (Terre Vie) 46: 303–320.

Bonal D., Atger C., Barigah T.S., Ferhi A., Guehl J.M. and Ferry B. 2000. Water acquisition patterns of two wet tropical canopy tree species of French Guiana as inferred from $H_2^{18}O$ extraction profiles. Ann. For. Sci. 57: 717–724.

Boye M. 1963. La géologie des plaines basses entre Organabo et le Maroni (Guyane française). Paris. Impr. Nat. Mémoires pour servir à l'explication de la carte géologique détaillée de la France Département de la Guyane française.

Bullen T., White A., Blum A., Harden J. and Schulz M. 1997. Chemical weathering of a soil chronosequence on granitoid alluvium: II. Mineralogic and isotopic constraints on the behaviour of strontium. Geochim. Cosmochim. Acta 61: 291–306.

Canadell J., Jackson R.B., Ehleringer J.R., Mooney H.A., Sala O.E. and Schulze E.D. 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108: 583–595.

Capo R.C., Stewart B.W. and Chadwick O.A. 1998. Strontium isotopes as tracers of ecosystem processes: theory and methods. Geoderma 82: 197–225.

Chadwick O.A., Derry L.A., Vitousek P.M., Huebert B.J. and Hedin L.O. 1999. Changing sources of nutrients during four million years of ecosystem development. Nature 397: 491–496.

Clark D.B., Palmer M.W. and Clark D.A. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology 80: 2662–2675.

Collinet F. 1997. Essai de regroupements des principales espèces structurantes d'une forêt dense humide d'après l'analyse de leur répartition spatiale. Thèse Université Claude Bernard.

Cuenca G., Herrera R. and Medina E. 1990. Al tolerance in trees of a tropical cloud forest. Plant and Soil 125: 169–176.

Dambrine E., Loubet M., Vega J.A. and Lissarague A. 1997. Localisation of mineral uptake by roots using Sr isotopes. Plant Soil 192: 129–132.

Elias R.H., Hirao Y. and Patterson C.C. 1982. The circumvention of the natural biopurification of calcium along nutrient pathways by atmospheric inputs of industrial lead. Geochim. Cosmochim. Acta 46: 2561–2580.

Faure G. 1986. Principles of isotopes Geology. 2nd edn. Wiley J and Sons, New-York.

Ferry B., Atger C., Bereau M., Bonal D., Domenach A.M., Fehri A. et al. 2000. Stratégies d'acquisition et d'utilisation des ressources hydriques et minérales dans différents types de sol. Rapport d'étude au Ministère de l'Environnement, programme SOFT.

Grandval A. 1993. Mise en évidence d'une structure spatiale du système de décomposition en relation avec la qualité de la litière en forêt guyanaise. DEA, université Pierre et Marie Currie, Paris VI.

Graustein W.C. and Armstrong R.L. 1983. The use of strontium ^{87}Sr/^{86}Sr ratios to measure atmospheric transport into forested watersheds. Science 219: 289–292.

Graustein W.C. 1989. ^{87}Sr/^{86}Sr ratios measure the source and flow of Sr in terrestrial ecosystems. In: Rundel P., Ehleringer J. and Nagy K. (eds), Stable Isotopes in Ecological Research. Springer Verlag, New York, pp. 491–512.

Grimaldi C. and Pédro G. 1996. Importance de l'hydrolyse acide dans les systèmes pédologiques des régions tropicales humides. Rôle de la forêt et conséquences sur la genèse des sables blancs tropicaux. C.R. Acad. Sci. Paris, t. 323: 483–492.

Grimaldi C., Fritsch E. and Boulet R. 1994. Composition chimique des eaux de nappe et évolution d'un matériau ferrallitique en présence du système muscovite-kaolinite-quartz. C.R. Acad. Sci. Paris, t. 319: 1383–1389.

Grimaldi M. and Boulet R. 1989. Relations entre l'espace poral et le fonctionnement hydrodynamique d'une couverture pédologique sur socle en Guyane française. Cah ORSTOM, sér. Pédol, XXV 3: 263–275.

Gruau G., Martin H., Leveque B. and Capdevila R. 1985. Rb-Sr and Sm-Nd geochronology of lower proterozoic granite-greenstone terrains in French Guyana, South America. Precambrian Research 30: 63–80.

Guehl J.M. 1984. Dynamique de l'eau dans le sol en forêt tropicale humide guyanaise. Influence de la couverture pédologique. Ann. Sci. for. 41: 195–236.

Jacks G., Aberg G. and Hamilton P.J. 1989. Calcium budgets for catchments as interpreted by strontium isotopes. Nordic Hydrology 20: 85–96.

Jordan C.F. 1982. The nutrient balance of an Amazonien rain forest. Ecology 63: 647–654.

Lesack L.F.W. and Melack J.M. 1996. Mass balance of major solutes in a rainforest catchment in the Central Amazon: Implication for nutrient budgets in tropical rainforests. Biogeochemistry 32: 115–142.

Miller E.K., Blum J.D. and Friedland A.J. 1993. Determination of soil exchangeable-cation loss and weathering rates using Sr isotopes. Nature 362: 438–441.

Négrel P. and Lachassagne P. 2000. Geochemistry of the Maroni River (French Guyana) during low water stage: Implications for water rock interaction and groundwater characteristics. J. Hydrol. 237: 212–233.

Nepstad D.C., De Carvalho C.R., Davidson E.A., Jipp P.H., Lefebvre P.A., Negreiros G.H. et al. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372: 666–669.

Poszwa A. 2000. Utilisation des isotopes du strontium pour évaluer la dynamique des éléments minéraux dans des écosystèmes forestiers sous climat boréal, tempéré et tropical. University of Nancy, France.

Poszwa A., Dambrine E., Pollier B. and Atteia O. 2000. A comparison between Ca and Sr cycling in forest ecosystems. Plant Soil 225: 299–310.

Probst A., El Gh'Mari A., Aubert D., Fritz B. and McNutt R. 2000. Strontium as a tracer of weathering processes in a silicate catchment polluted by acid atmospheric inputs, Strengbach, France. Chemical Geology 170: 203–219.

Puig H. and Delobelle J.P. 1988. Litter production, necromass and mineral content of litter in a lowland rain forest of French Guiana. Revue d'Ecologie: La Terre et la Vie 43: 3–22.

Roche M.A. 1982. Evapotranspiration réelle de la forêt amazonienne en Guyane. Cah ORSTOM, sér. Hydrol., XIX, 1: 37–44.

Roggy J.C., Prévost M.F., Gourbiere F., Casabianca H., Garbaye J. and Domenach A.M. 1999. Leaf natural ^{15}N abundance and total N content as potential indicators of plant N nutrition in a rain forest of French Guiana with emphasis on legumes and pioneer species. Oecologia 120: 171–182.

Sabatier D., Grimaldi M., Prévost M.F., Guillaume J., Godron M., Dosso M. et al. 1997. The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. Plant Ecol. 131: 81–108.

Schultz J.P. 1960. Ecological studies on rain forest in Northem Suriname. Verhand. Kon. Ned. Akad. Wetensch. Afd. Natuurk, Amsterdam, ser. 2, 53, 267 pp.

Stark N.M. and Jordan C.F. 1978. Nutrient retention by the root mat of an amazonian rain forest. Ecology 59: 434–437.

Taylor A.S., Blum J.D., Lasaga A.C. and MacInnnis I.N. 2000. Kinetics of dissolution and Sr release during biotite aned phlogopite weathering. Geochim Cosmochim Acta 64: 1191–1208.

Veillon L. 1990. Sols ferrallitiques et podzols en Guyane septentrionale. Relations entre systèmes de transformation pédologiques et évolution historique d'un milieu tropical humide et forestier. Univ. Paris VI, ORSTOM.

Wickman T. and Jacks G. 1991. Strontium isotopes as tools in weathering research. In: Rosen K. (ed.), Chemical weathering under field conditions. Reports in Forest Ecology and Forest soils, Report 63, Swedish University of Agricultural Sciences, Uppsala, pp. 611–614 Rosen K. (ed.) Chemical weathering under field conditions. Reports in Forest Ecology and Forest soils, Report 63, Swedish University of Agricultural Sciences, Uppsala.

Wickman T. and Jacks G. 1992. Sr isotopes as elemental concentrations in tree rings- or mirror of soil acidification? In: Bartholin T.S., Berglund B.E., Eckstein D., Schweingruber F.H. and Eggertsson O. (eds), Tree rings and Environment., pp. 334–337.

Wickman T. and Jacks G. 1993. Base cation nutrition for pine stands on lithic soils near Stockholm, Sweden. Appl. Geochem.: 199–202.

Wickman T. 1996. Weathering Assessment and nutrient availability in Coniferous Forests. Royal Institute of Technology, Stockholm.