



The distribution of soil nutrients with depth: Global patterns and the imprint of plants

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Abstract. To understand the importance of plants in structuring the vertical distributions of soil nutrients, we explored nutrient distributions in the top meter of soil for more than 10,000 profiles across a range of ecological conditions. Hypothesizing that vertical nutrient distributions are dominated by plant cycling relative to leaching, weathering dissolution, and atmospheric deposition, we examined three predictions: (1) that the nutrients that are most limiting for plants would have the shallowest average distributions across ecosystems, (2) that the vertical distribution of a limiting nutrient would be shallower as the nutrient became more scarce, and (3) that along a gradient of soil types with increasing weathering-leaching intensity, limiting nutrients would be relatively more abundant due to preferential cycling by plants. Globally, the ranking of vertical distributions among nutrients was shallowest to deepest in the following order: P > K > Ca > Mg > Na = Cl = SO₄. Nutrients strongly cycled by plants, such as P and K, were more concentrated in the topsoil (upper 20 cm) than were nutrients usually less limiting for plants such as Na and Cl. The topsoil concentrations of all nutrients except Na were higher in the soil profiles where the elements were more scarce. Along a gradient of weathering-leaching intensity (Aridisols to Mollisols to Ultisols), total base saturation decreased but the relative contribution of exchangeable K⁺ to base saturation increased. These patterns are difficult to explain without considering the upward transport of nutrients by plant uptake and cycling. Shallower distributions for P and K, together with negative associations between abundance and topsoil accumulation, support the idea that plant cycling exerts a dominant control on the vertical distribution of the most limiting elements for plants (those required in high amounts in relation to soil supply). Plant characteristics like tissue stoichiometry, biomass cycling rates, above- and belowground allocation, root distributions, and maximum rooting depth may all play an important role in shaping nutrient profiles. Such vertical patterns yield insight into the patterns and processes of nutrient cycling through time.

Introduction

As the interface between the atmosphere, biosphere, and lithosphere, soil undergoes an intense vertical exchange of materials resulting in steep chemical and physical gradients from surface to bedrock. Soil stratification is the most visible result of this exchange, and its extensive observation and synthesis form the basis of pedogenetic and taxonomic study (Hilgard 1906; Jenny 1941; Soil Survey Staff 1975; Buol et al. 1989). The type, thickness, and position of horizons can yield information about soil forming factors such as climate, topography, and vegetation type (Jenny 1941; Marion et al. 1985; Honeycutt et al. 1990). Likewise, the vertical distribution of soil nutrients should yield similar insights into nutrient inputs, outputs, and cycling processes (Smeck 1973; Kirby 1985). The goals of this paper are first to characterize the vertical distribution of nutrients globally and second to evaluate the importance of plant cycling for structuring soil nutrients vertically.

Most knowledge about the role of plant cycling on the distribution of nutrients comes from studies on horizontal nutrient patterns, usually associated with 'islands of fertility' in desert ecosystems (Noy-Meir 1973). Such plants as shrubs in deserts or trees in savannas often accumulate organic matter beneath their canopies, enriching soil nutrient pools as a result of uptake by lateral roots beyond the canopy and subsequent cycling under it (Zinke 1962; Belsky et al. 1989; Jackson & Caldwell 1993; Schlesinger et al. 1996; Burke et al. 1998). These horizontal patterns demonstrate an important imprint of plants on the spatial distribution of nutrients horizontally.

The suite of mechanisms that shape the vertical distribution of soil nutrients can be grouped in at least four major processes: weathering, atmospheric deposition, leaching, and biological cycling (Trudgill 1988). Weathering dissolution and atmospheric deposition affect the depth at which nutrient inputs occur (Kirby 1985). Leaching and biological cycling influence the vertical transport of nutrients in opposite ways. Acting in isolation, leaching moves nutrients downward and may increase nutrient concentrations with depth (Figure 1(a)). In contrast, biological cycling generally moves nutrients upwards because some proportion of the nutrients absorbed by plants are transported aboveground and then recycled to the soil surface by litterfall and throughfall (Trudgill 1988; Stark 1994). Plant cycling should therefore produce nutrient distributions that are shallower or decrease with depth (Figure 1(b)).

The contrasting effects of leaching and biological cycling are apparent from the vertical distribution of K and Cl in arid ecosystems. Chlorine is a relatively mobile element in the soil that does not generally constrain plant growth (Yaalon 1965). The amount of water that leaches salts in arid soils

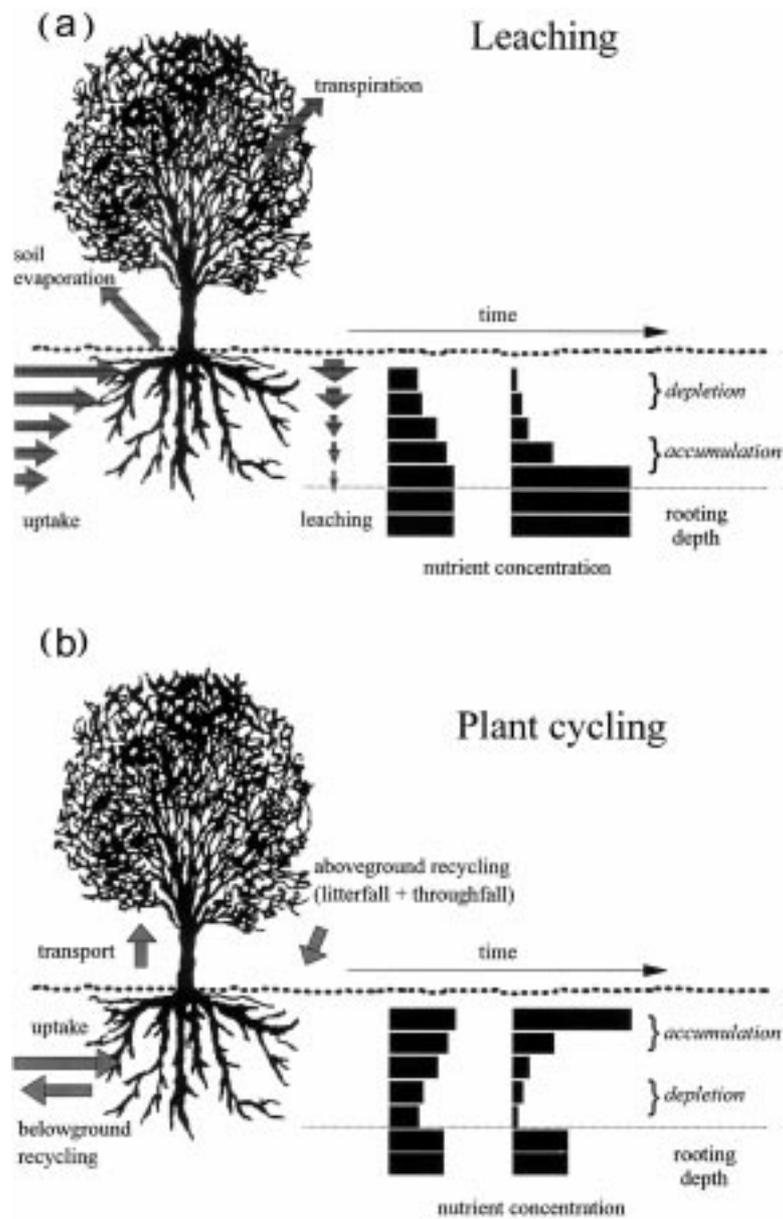


Figure 1. Vertical redistribution of nutrients by leaching and plant cycling. (a) Arrows indicate water inputs and outputs and vertical water fluxes at different depths. Decreasing vertical water flow with depth depletes nutrients from the topsoil and accumulates them in deeper soil layers, producing a peak at the maximum rooting depth. (b) Arrows indicate nutrient uptake, transport, and aboveground cycling via litterfall and throughfall. Plant cycling tends to accumulate nutrients in the topsoil and deplete them in the root zone. Below the rooting depth there is an increase of nutrient concentrations because there is no depletion.

decreases dramatically with depth due to root water uptake, increasing total soil Cl with depth and causing a peak in Cl concentrations that is associated with the maximum rooting depth of the ecosystem (Tyler & Walker 1994; Phillips 1994). In contrast to Cl, K often limits plant growth and is highly concentrated in plant tissues (Bowen 1979). If plant cycling of such a limiting nutrient is important, then K should undergo a net upward transport by plants and the topsoil should be relatively enriched in K. Aridland studies where the vertical distribution of different K forms has been measured support this hypothesis (Juang & Uehera 1967; Rostagno et al. 1991; Schlesinger & Pilmanis 1998). However, there is debate about the potential role of atmospheric deposition of K-rich minerals as an alternative cause of this observed pattern (Singer 1989; Paton et al. 1995). To our knowledge, the generality of these patterns across nutrients and ecosystems has not been examined.

In this paper, we hypothesize that plant cycling exerts the dominant control on the vertical distribution of those elements that most limit plant growth. We consider limiting elements those that are essential and are required by plants in high amounts relative to soil supply. A high ratio of plant uptake to soil supply should result in higher rates a upward transport by plants and, hence, shallower vertical distributions. We focus on nutrients other than N since plants play a clear role in N distribution by controlling most organic additions to the soil. The following predictions, tested with a global soil database, follow from our hypothesis:

- (1) Nutrients that most often limit plant growth (e.g., P and K) will have shallower distributions than nutrients that are less limiting (e.g., Cl, Na, Mg).
- (2) The vertical distribution of soil nutrients will be shallower as nutrients become increasingly scarce.
- (3) Along a gradient of soil types with increasing weathering-leaching intensity, nutrients most limiting to plants will be relatively less depleted due to preferential cycling and retention by plants. We explore this prediction comparing profiles in three soil orders: Aridisols, Mollisols, and Ultisols (USDA 1994).

If these predictions are robust, they will provide an initial step in linking the vertical distribution of nutrients with patterns and processes of nutrient cycling through time. In addition, a better understanding of the vertical distribution of soil nutrients will help us understand the consequences of shifts in resource use and availability with the altered rooting depths that frequently accompanies vegetation change (Jackson et al. 2000).

Materials and methods

The database

To characterize the vertical distribution of nutrients and to evaluate our predictions, we used the National Soil Characterization Database (NSCD) of the United States Department of Agriculture (USDA 1994). We focused on exchangeable K^+ , Ca^{2+} , Mg^{2+} , and Na^+ , and extractable P, NO_3^- , SO_4^{2-} , and Cl^- , for the top meter of the soil. We also compared these nutrient distributions with the distributions of organic C, total N, and cation exchange capacity (CEC) because of their importance for soil fertility. The database includes > 20,000 profiles globally, but approx. 90% of profiles are from U.S. soils (including Alaska, Hawaii, and Puerto Rico). The majority of the non-U.S. profiles are from tropical areas in Central and South America, Africa, and Asia. The analytical methods used for the soil cores in the database were described in Page et al. (1982). They include Walkley-Black for organic C, Kjeldahl for total N, Bray-I and Olsen extractions for P in acidic and alkaline soils, respectively, ammonium acetate extraction at pH 7 for exchangeable base cations and CEC, and distilled water extraction for SO_4^{2-} and Cl^- .

We restricted our analysis to profiles with a complete description of an element to at least one-meter depth. Surface litter layers were not considered in the analyses. Profiles with three or fewer horizons in the top meter were eliminated because there was insufficient detail to characterize vertical distributions. After imposing these restrictions we obtained the following number of profiles for each variable: Exchangeable K^+ , 8955; exchangeable Ca^{2+} , 8236; exchangeable Mg^{2+} , 8694; exchangeable Na^+ , 7773; extractable P, 266; extractable NO_3^- , 327; extractable SO_4^{2-} , 644; and extractable Cl^- , 835; organic C, 10416; total N, 1327; CEC, 8796.

Because soil profiles in the database were described by horizon, depth intervals in the first meter had variable thicknesses. To remove this variation, nutrient concentrations were converted to absolute nutrient contents (g/m^2) using five fixed depth intervals of 20 cm each. When more than one horizon occupied a 20-cm depth interval, the nutrient content of each horizon was estimated with the proportion of the section that each horizon covered.

Gravimetric measurements were transformed to volumetric values using bulk density data. Bulk densities (3706 profiles) were used to adjust nutrient concentrations directly within each horizon. For profiles lacking bulk density data (8513 profiles), we estimated bulk density (BD) using gravimetric carbon content (C%) based on linear regressions adjusted for each 20-cm interval in the top meter ($BD_{0-20cm} = -0.06 C\% + 1.59$, $R^2 = 0.22$; $BD_{20-40cm} = -0.10 C\% + 1.63$, $R^2 = 0.15$; $BD_{40-100cm} = -0.11 C\% + 1.64$, $R^2 = 0.06$; $n = 3706$ and $p < 0.0001$ in all cases). Using these estimates of bulk density for the

entire dataset or just using the subset of 3706 profiles with bulk density data yielded similar results for vertical distribution of nutrients ($\pm 1\%$). Nutrient contents were corrected for gravel content.

The only form of available N present in the database, extractable NO_3^- , had an extremely variable vertical distribution, showing no clear accumulation or depletion patterns in the topsoil. For this reason, general patterns of extractable NO_3^- are presented but comparison with other nutrients are avoided.

The global vertical distribution of nutrients was described on a relative basis within soil profiles. This allowed for a characterization of vertical distributions that was independent of the absolute nutrient contents of each soil. First, we calculated the total content of nutrients in the top meter of the soil per unit area on a volumetric basis. Then, the relative contribution of each 20-cm depth interval was estimated as the ratio of the nutrient content of each layer and the total content in the top meter. These relative values ranged from 0 to 1 and approached 0.2 in all depth intervals when the vertical distribution was homogeneous throughout the soil profile. To summarize the vertical distributions for each nutrient, we obtained the average, median, and quartiles of the relative contribution of each depth interval based on individual profiles. Since the distributions of these relative values were not normally distributed for most of the nutrients (even using logarithmic and angular transformations), we used non-parametric tests to compare them. We evaluated if the vertical patterns were significantly different from random or homogeneous distributions by comparing the relative contributions of depth intervals based on multiple paired comparisons (following a Friedman test; Daniel 1990). Neither homogeneous nor random distributions should display significant differences among soil layers, but variables with a random distribution should have higher variability within soil layers across profiles.

Evaluating the effects of plant cycling

Our second goal was to test the hypothesis that plant cycling is a major control of the vertical distribution of soil nutrients. The first prediction, that the most limiting nutrients for plants (those required by plants in high amounts relative to soil supply) would have the shallowest vertical distributions, was evaluated by comparing the relative surface concentrations of all nutrients. The relative contribution of the 0–20 cm depth interval to the total in the top meter ('topsoil concentration factor') was used as single numeric representation of the distribution's relative depth. This factor increases as the distribution of nutrients becomes shallower. We ranked soil nutrients from shallowest to deepest based on multiple paired comparisons of the topsoil concentration factor using the sign-rank test (Daniel 1990).

To evaluate our second prediction, that the vertical distribution of nutrients would be shallower where they are scarcer, we analyzed the association between the abundance of each nutrient in the first meter and its topsoil concentration factor across profiles grouping them in ranges of increasing nutrient abundance. The abundance of most nutrients followed a log-normal distribution. For this analysis, we used multiple comparisons after a Kruskal-Wallis test (Daniel 1990). We also calculated Spearman correlation coefficient between abundance and topsoil concentration factors for each nutrient. As a complementary way to evaluate our first and second predictions, we explored the association between the relative abundance of nutrient pairs and their relative topsoil concentration using ratios. We focused on exchangeable base cations because they were measured in a large number of soil profiles (Table 1). For every soil profile and nutrient pair we calculated the ratio of abundance in the top meter and the ratio of topsoil concentration factors. We analyzed the relationship between these ratios for individual soils and for the median of soil profiles grouped by soil taxonomic order using non-parametric correlation analysis.

Our third prediction, that along a gradient of soil types with increasing weathering-leaching intensity the most limiting nutrients would be relatively less depleted, was evaluated by comparing broad soil taxonomic units subject to different leaching regimes. About 60% of the soil profiles in the database were classified to order according to the USDA soil classification system (Soil Survey Staff 1975). We focused on Aridisols, Mollisols, and Ultisols. These soil orders represent mature soils developed under desert, grassland, and forest ecosystems, respectively (Soil Survey Staff 1975). The water balance varies drastically across this gradient of soil/ecosystem types, shifting from high water deficits and little drainage below the rooting zone in Aridisols to water excess and intense leaching in Ultisols (see Jenny 1941; Stephenson 1990; Buol et al. 1989).

We compared the abundance and topsoil concentration factors of each nutrient among the three soil orders using multiple comparisons after a Kruskal-Wallis test (Daniel 1990). About 25% of the soil profiles in the database had land-use information, 30% of which were under natural vegetation and 70% under agricultural use. We evaluated differences between profiles under agriculture and natural vegetation using the sign test (Daniel 1990).

Table 1. (A) Number of profiles used to compare the vertical distributions of nutrients and soil variables. (B) Percentage of cases in which the variable in the row had a shallower distribution (lower topsoil concentration factor) than the variable in the column.

	K ⁺	Ca ²⁺	Mg ²⁺	Na ⁺	NO ₃ ⁻	SO ₄ ²⁻	Cl ⁻	P	C	N	CEC
(A)											
K ⁺	x	7564	8457	7661	301	593	775	238	8551	1205	8506
Ca ²⁺		x	8236	6860	250	500	657	251	7881	1113	7739
Mg ²⁺			x	7285	285	575	733	249	8320	1157	8198
Na ⁺				x	300	585	769	196	7413	1043	7438
NO ₃ ⁻					x	326	327	11	311	61	302
SO ₄ ²⁻						x	631	18	604	131	595
Cl ⁻							x	18	774	184	621
P								x	256	44	234
C									x	1271	8411
N										x	1196
CEC											x
(B)											
K ⁺	x	69	84	86	54	84	81	39	20	28	76
Ca ²⁺		x	70	79	47	71	66	25	8	15	47
Mg ²⁺			x	72	49	73	67	16	6	11	23
Na ⁺				x	42	53	50	15	6	8	17
NO ₃ ⁻					x	60	59	9	43	64	50
SO ₄ ²⁻						x	41	0	9	18	24
Cl ⁻							x	0	9	15	23
P								x	53	61	84
C									x	79	98
N										x	96
CEC											x

Results

General patterns and differences among nutrients

In addition to total N, extractable P and exchangeable K⁺ were the only nutrients with consistently higher concentrations in the topsoil, supporting the prediction that the most limiting nutrients for plants would have the shallowest distributions (Figure 2). Exchangeable Ca²⁺ had an intermediate distribution, and exchangeable Mg²⁺ and Na⁺, and extractable Cl⁻ and SO₄²⁻

were depleted from the topsoil and tended to increase steadily with depth (Figure 2). Based on all soil profiles, the depth ranking of nutrients was shallowest for extractable P and organic C (median topsoil concentration factor = 0.43, Figure 3). The vertical distribution of total N was strongly associated with that of organic C but was significantly deeper than organic C (median topsoil concentration = 0.36, $p < 0.001$, Figure 3). Among exchangeable base cations, K^+ had the shallowest distribution (median topsoil concentration = 0.27, $p < 0.001$) and K was the only base cation with a distribution shallower than CEC ($p < 0.001$, Figure 3). Exchangeable K^+ and Na^+ , a useful pair of nutrients for comparing the roles of plant cycling and leaching, showed contrasting vertical distributions with K shallower than Na in 86% of the profiles examined (Table 1).

Nutrient abundance and distribution

In support of the second prediction, we found an inverse relationship between the nutrient abundance in the first meter of soil and relative topsoil concentration factors for many soil nutrients (Figure 4). For all nutrients except exchangeable Na^+ , topsoil concentration was greatest in the lowest abundance ranges. There was a significant and negative correlation between top soil concentration and abundance for exchangeable K^+ , Ca^{2+} , and Mg^{2+} , and extractable P and SO_4^{2-} (Figure 4) ($p < 0.01$). For exchangeable K^+ , Ca^{2+} , and Mg^{2+} , median topsoil concentration values were > 0.75 in profiles where their abundance in the top meter was less than 10 g m^{-2} , compared with values < 0.25 when their abundance was 100 to 1000 g m^{-2} . Extractable P had a relatively high variability within the abundance ranges, but topsoil concentration values still decreased significantly with increasing P abundance; median values shifted from 0.54 in soils with less than 1 g m^{-2} extractable P to 0.32 for the highest abundance ranges ($p < 0.01$; Figure 4). Total N showed a significant but smaller variation, which was closer to the relatively flat response of organic C. The median topsoil concentration of extractable SO_4^{2-} and Cl^- was higher than 0.2 when the abundance was $< 10 \text{ g m}^{-2}$, indicating some degree of concentration in the topsoil when the nutrients were relatively scarce (Figure 4).

To evaluate the relationship between nutrient limitation and vertical distributions among soil profiles and between different nutrients in the same profiles, we compared differences in distributions for selected pairs of nutrients. We expected that as the relative abundance of one of the nutrients in the pair increases, its topsoil concentration would decrease compared to the other nutrient. Among exchangeable cations, we focused on K^+ , Ca^{2+} , and Mg^{2+} , because they showed strong negative abundance-depth relationships when analyzed individually. All three possible pairs showed a significant

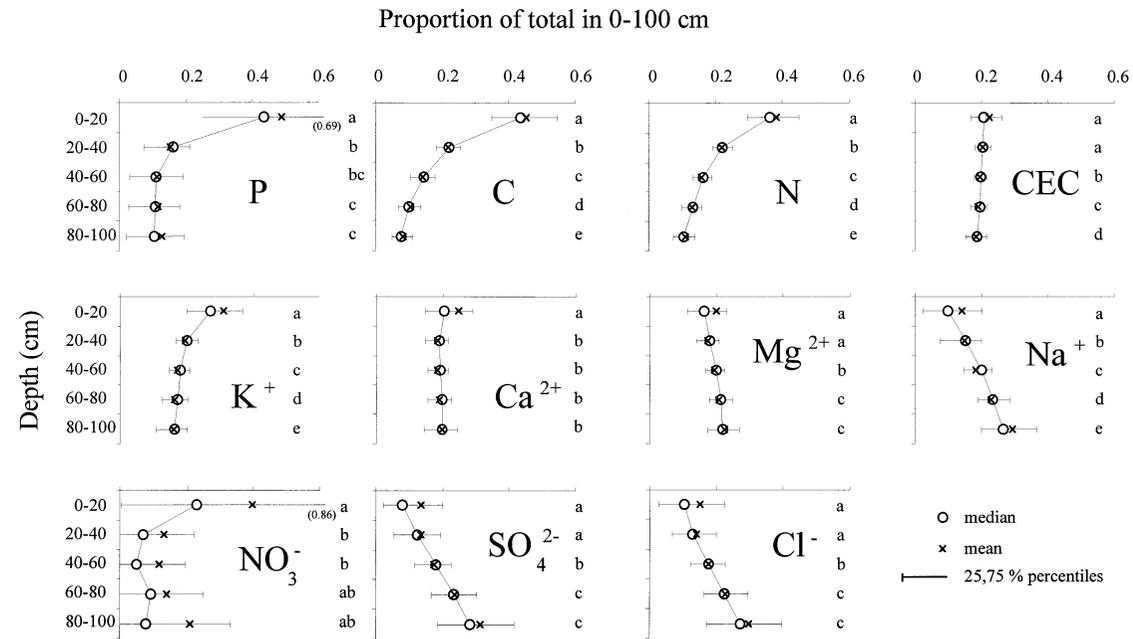


Figure 2. Vertical distribution of nutrients in the first meter of the soil. Curves are based on relative distribution data for individual soil profiles. The mean (crosses), median (circles), and 25 and 75% percentiles (lateral bars) are indicated. Mean contributions sum one for the five depth intervals. Significant differences among the relative contribution of depth intervals are indicated with letters (multiple paired comparisons after Friedman test, $p < 0.01$). All the vertical distributions are significantly different than random or homogeneous (at list one pair of depth intervals shows significant differences). The variables and the number of soil profiles used for the analysis are: Extractable P, 266; organic C, 10416; total N, 1327; CEC, 8796; exchangeable K^+ , 8955; exchangeable Ca^{2+} , 8236; exchangeable Mg^{2+} , 8694; exchangeable Na^+ , 7773; extractable NO_3^- , 327; extractable SO_4^{2-} , 644; and extractable Cl^- , 835.

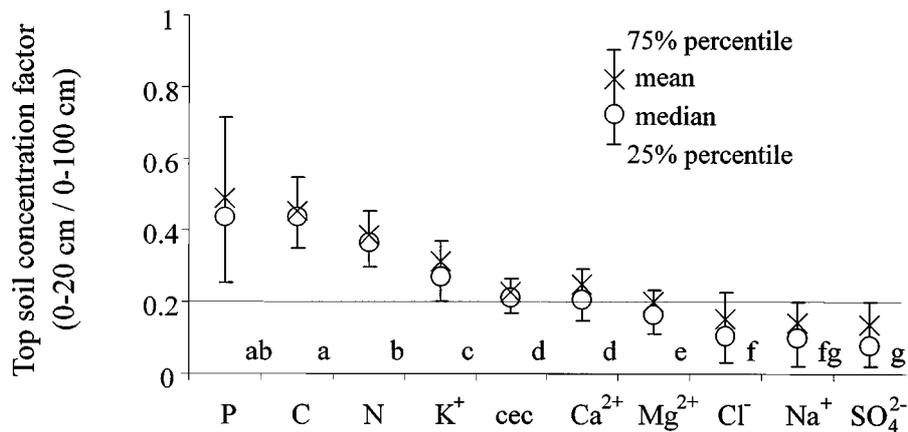


Figure 3. Ranking of soil nutrients according to their vertical distributions, from shallow to deep. The ranking is based on the median topsoil concentration factor (relative contribution of the 0–20 cm depth interval to the total in the first meter). The mean (crosses), median (circles), and 25 and 75% percentiles (error bars) are indicated. The horizontal line indicates a topsoil concentration factor of 0.2, corresponding with a homogeneous or random vertical distribution. Letters indicate significant differences among soil nutrients based on a paired sign test adjusted for multiple comparisons ($p < 0.01$). The number of profiles used for each comparison is indicated in Table 1.

negative correlation between nutrient abundance and the ratios of their topsoil concentration factors (Spearman correlation coefficients were: K:Ca, -0.42 ; K:Mg, -0.36 ; Ca:Mg, -0.51 ; $n = 6860$ to 8457 ; $p < 0.001$ in all cases). These relationships were stronger for soil profiles with base saturation in the top meter < 0.25 (Spearman correlation coefficients were: K:Ca, -0.53 ; K:Mg, -0.56 ; Ca:Mg, -0.65 ; $n = 465$ to 532 and $p < 0.001$ in all cases). Results for the K:Ca comparison are particularly interesting (Figure 5). On average, soil profiles with K:Ca abundance ratios lower than 1:10 tended to have exchangeable K^+ more shallowly distributed than exchangeable Ca^{2+} . In contrast, profiles with K:Ca abundance higher than 1:10 had exchangeable Ca^{2+} more shallowly distributed than exchangeable K^+ . Median values for soils grouped by soil orders displayed the same relationship (Figure 5; $n = 9$, $r = -0.92$, $P < 0.001$) with Aridisols in the high Ca^{2+} extreme and Ultisols in the high K^+ extreme. Vertisols, the only soil order that undergoes intense physical mixing, showed the highest deviation from this relationship, with K:Ca abundance ratios that were close to those of Aridisols but depth ratios that were close to 1:1 and similar to those of Ultisols.

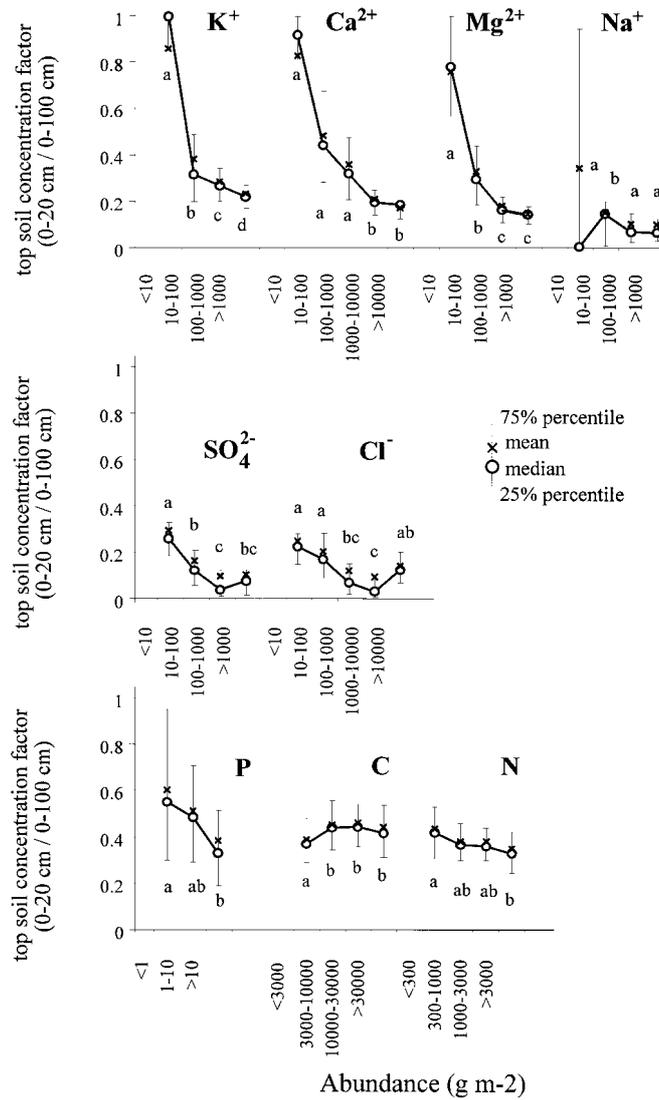


Figure 4. Relationship between the abundance and vertical distribution for different soil nutrients. For each nutrient, soil profiles were grouped according to their total abundance in the first meter and mean (crosses), median (circles), and 25 and 75% percentiles (error bars) for topsoil concentration factors were calculated. The topsoil concentration factor represents the relative contribution of the 0–20 cm depth interval to the total in the first meter. Letters indicate significant differences for topsoil concentration factors among abundance ranges within a given nutrient (multiple comparisons after Kruskal-Wallis test, $p < 0.01$). Spearman correlation coefficients between the topsoil concentration and abundance of individual profiles are: K⁺, -0.21 ; Ca²⁺, -0.25 ; Mg²⁺, -0.27 ; SO₄²⁻, -0.09 ; and P, -0.10 ($p < 0.01$ in all cases). There is no significant association for the rest of the nutrients.

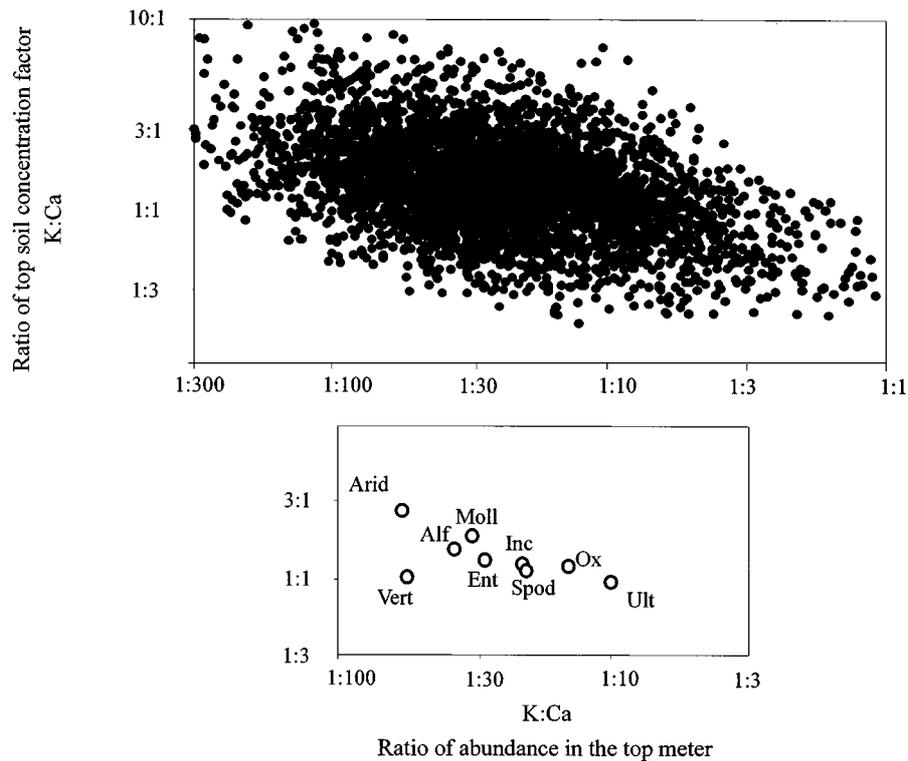


Figure 5. The relationship between nutrient limitation and distribution depth illustrated by changes in the relative depth and abundance of exchangeable K^+ and Ca^{2+} . Each data point represents a single soil profile. The ratio of topsoil concentration factors for exchangeable K^+ and Ca^{2+} is shown as a function of the ratio of exchangeable K^+ and Ca^{2+} abundance in the top meter for the same nutrients. Both axes have a logarithmic scale. The relationship is significant ($n = 7564$, $r = -42$, $p < 0.0001$). As the abundance of K^+ becomes closer to the abundance of Ca^{2+} (1:300 to 1:1), the vertical distribution shifts from K^+ being shallower than Ca^{2+} , to Ca^{2+} being shallower than K^+ . The lower panel shows the median values for soil profiles grouped by soil taxonomic order.

Differences among soil types

Our third prediction was that along a gradient of increased leaching and decreased nutrient supply, the most limiting nutrients would be relatively less depleted due to greater cycling and retention by plants. Along the Aridisol-Mollisol-Ultisol gradient, the abundance of base cations, and extractable SO_4^{2-} and Cl^- decreased (Table 2). In contrast, P was most abundant in Mollisols (Table 2). The relative composition of the exchangeable base cation complex showed important differences among soil orders (Table 3). As total base saturation decreased along the gradient, the vertical distribution of base

Table 2. Nutrient abundance in the top meter of Aridisols, Mollisols, and Ultisols. Values show the median and letters represent significant differences (multiple comparison after a Kruskal-Wallis test, $p < 0.01$).

		Aridisols		Mollisols		Ultisols	
Exchangeable cations							
K ⁺	g/m ²	331	a	342	a	79	b
Ca ²⁺	g/m ²	11691	a	5964	b	408	c
Mg ²⁺	g/m ²	813	a	910	a	121	b
Na ⁺	g/m ²	469	a	63	b	30	c
Extractable anions							
NO ₃ ⁻	g/m ²	19	ab	12	a	23	b
SO ₄ ²⁻	g/m ²	340	a	80	b	7	c
Cl ⁻	g/m ²	131	a	28	b	2	c
Extractable P	mg/m ²	674	a	7429	b	2486	c
Organic C	Kg/m ²	5.8	a	12.5	b	7.0	c
Total N	g/m ²	698	a	1227	b	542	a
CEC	eq ⁺ /m ²	205	c	298	b	105	c

saturation shifted from deeper to shallower distributions. As expected, the relative contribution to base saturation of exchangeable K⁺, usually the most limiting base cation, increased along the gradient of soil orders. Exchangeable Mg²⁺ showed a similar trend. The relative contribution of exchangeable Ca²⁺ decreased along the same gradient. Sodium had its highest relative contribution in both ends of the gradient (Aridisols and Ultisols) and its smallest contribution in Mollisols (Table 3).

The vertical distributions of exchangeable K⁺ was similar among soil orders, with a median topsoil concentration of 0.3 ($p > 0.1$ among orders) (Figure 6). In contrast, exchangeable Ca²⁺ tended to be relatively low in the topsoil of Aridisols and Mollisols (median topsoil concentration factors of 0.14 and 0.17, respectively), but was concentrated in the topsoil of Ultisols (median topsoil concentration factor = 0.29) (Figure 6, $p < 0.01$ among all soil orders). Exchangeable Na⁺ and Mg²⁺ were depleted in the topsoil of the three orders (Figure 6). In contrast with all the other nutrients, the distribution of extractable P was shallowest in Aridisols, where its abundance was lowest, and did not differ significantly between Mollisols and Ultisols (Figure 6).

Table 3. Changes in the relative composition of the base cation exchange complex and base saturation with depth for the soil orders Aridisol, Mollisol, and Ultisol. Proportions of exchangeable K^+ , Ca^{2+} , Mg^{2+} , and Na^+ are shown as percentages of charges or equivalents and sum 100 within each depth interval. Base saturation (Bsat) is the ratio of base cation concentration in equivalents per gram of soil to cation exchange capacity in the same units. Because Ultisols under natural vegetation showed important differences with Ultisols under agriculture we present means for both groups.

Depth interval	Aridisols –all– (<i>n</i> = 527)					Mollisols –all– (<i>n</i> = 1154)					Ultisols –agriculture– (<i>n</i> = 127)					Ultisols –natural veg.– (<i>n</i> = 43)				
	K	Ca	Mg	Na	Bsat	K	Ca	Mg	Na	Bsat	K	Ca	Mg	Na	Bsat	K	Ca	Mg	Na	Bsat
0–20 cm	4.6	78.0	13.2	4.1	2.2	5.0	75.0	18.8	1.3	0.9	6.6	69.8	20.5	3.1	0.6	11.7	60.2	23.7	4.4	0.2
20–40 cm	2.8	77.9	12.9	6.4	2.7	3.5	74.0	20.8	1.8	1.0	5.4	65.5	25.1	4.1	0.5	13.1	43.5	37.6	5.8	0.2
40–60 cm	2.0	78.4	12.2	7.5	3.5	2.9	73.7	21.4	2.1	1.1	5.1	60.8	28.9	5.3	0.4	11.5	35.2	47.7	5.4	0.1
60–80 cm	1.5	78.3	11.9	8.3	3.9	2.5	74.1	21.1	2.4	1.2	5.3	55.5	32.6	6.5	0.4	9.5	32.6	51.9	6.0	0.1
80–100 cm	1.4	77.8	12.1	8.7	4.2	2.2	74.1	20.9	2.8	1.4	5.4	51.7	35.7	7.2	0.3	8.9	29.9	52.2	9.0	0.1

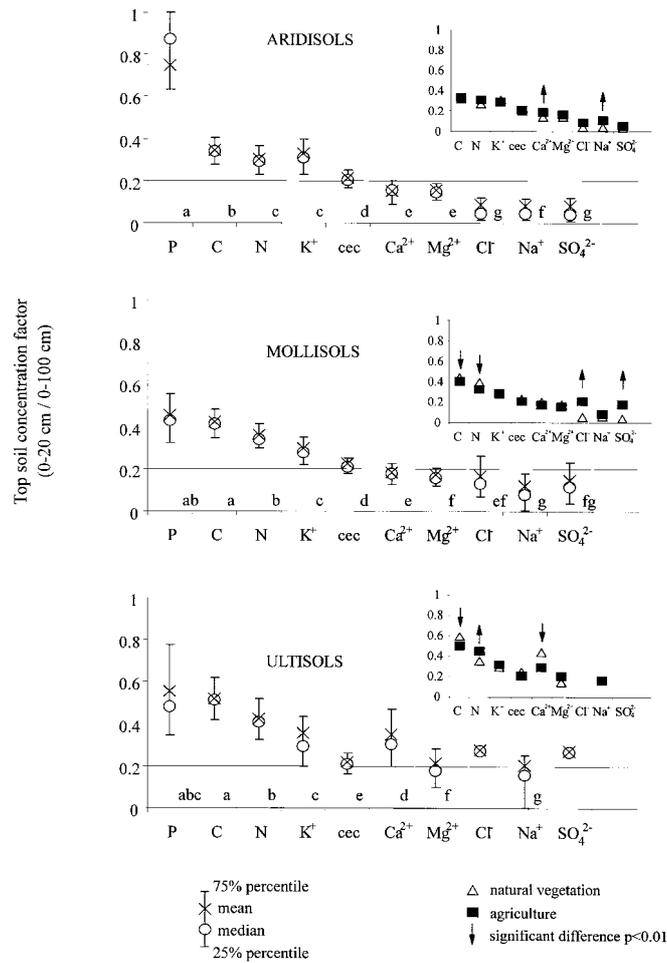


Figure 6. Ranking of soil nutrients according to their vertical distributions, from shallow to deep, for soil profiles in the orders Aridisol, Mollisol, and Ultisol. The ranking is based on the median topsoil concentration factor (relative contribution of the 0–20 cm depth interval to the total in the first meter). The mean (crosses), median (circles), and 25 and 75% percentiles (error bars) are indicated. The horizontal line indicates a topsoil concentration factor of 0.2, corresponding with a homogeneous or random vertical distribution. Letters indicate significant differences among soil nutrients based on a paired sign test corrected for multiple comparisons ($p < 0.01$). Extractable Cl^- and SO_4^{2-} were not compared to the rest of the nutrients in Ultisols because the number of data did not allow critical comparisons. Aridisols are associated with arid climate and desert vegetation, Mollisols with subhumid temperate climate and grassland vegetation, and Ultisols to humid climate and forest vegetation. Insets in the figures show median topsoil concentration values for soil profiles under natural vegetation and agriculture. The arrows indicate significant differences between land use classes ($p < 0.01$) and their position indicates the direction of changes from natural vegetation towards agriculture. Land use comparisons are missing for extractable P in all the cases and extractable anions in Ultisols because the number of soil profiles with land use data did not allow a critical comparison.

Most of the patterns just presented did not differ for agriculture and natural vegetation. The only significant differences were shallower distributions of exchangeable Ca^{2+} and Na^+ under agriculture in Aridisols ($p < 0.01$; Figure 6), slightly deeper organic C and total N and shallower extractable Cl^- and SO_4^{2-} under agriculture in Mollisols ($p < 0.01$), and deeper exchangeable Ca^{2+} and organic C and shallower total N under agriculture in Ultisols ($p < 0.01$). These comparisons were based on the subset of soil profiles that included land-use data (25% of the profiles in the database). Soils sampled under any type of crop, fallow, or cultivated pasture were considered agricultural, and soils under rangeland, woodland, or natural forest, were considered to be under 'natural' vegetation (Figure 6).

Discussion

The role of plant cycling

Our results suggest that plant cycling is a dominant control of nutrient distributions in the soil. Relatively high topsoil concentrations of P and K in most soil profiles support our first prediction, that the most limiting nutrients for plants (those required by plants in high amounts in relation to soil supply) have the shallowest distributions (Figures 2 and 3). This result is a general confirmation of a trend noted earlier at a handful of individual sites (Juang & Uehera 1967; Nettleton et al. 1973; Rostagno et al. 1991; Schlesinger & Pilmanis 1998). P occurs in low amounts in rocks and soils and is often reported to constrain ecosystem productivity (Marschner 1995, Schlesinger 1997). There is a less general picture about the relative limitation imposed by other soil nutrients. K is more abundant in the soil than P but is required in large amounts by plants, being the second most concentrated nutrient in plant leaves and shoots after N (Woodwell et al. 1975; Bowen 1979; Foulds 1993; Thompson et al. 1997). Compared with the rest of the base cations, K has the highest concentration in plant shoots (see Marschner 1995, p. 5) but its concentration in the exchangeable pool of soils is lower than Ca and Mg, and often Na (Tables 2 and 3, see also Bowen 1969). In agricultural systems P and K are second and third after N in terms of global rates of use as fertilizers (FAO 1999). These facts point to K as an element likely to follow N and P in their global limitation to plant production. While topsoil concentration is obvious for total N given its association with the soil organic matter pool, the widespread concentration of limiting mineral-derived nutrients such as P and K in the topsoil gives strong support to the idea that plants control the distribution of these elements. The global ranking of topsoil concentrations for exchangeable base cations ($\text{K}^+ > \text{Ca}^{2+} > \text{Mg}^{2+} > \text{Na}^+$, Figure 3) matched

the ranking of retention observed for these elements throughout succession in temperate and tropical forests, inferred from nutrient outputs in stream and groundwater (Likens et al. 1970; Vitousek 1977; Kellman & Roulet 1990). This provides additional support to the idea that the vertical distribution of nutrients reflects the degree of limitation that they impose on plants.

Supporting our second prediction, that nutrients would have shallower distributions where they are scarcer, nutrients showed a marked increase in topsoil concentration for soil profiles with relatively low nutrient abundance (Figure 4). Na was an exception, as would be predicted from its very low concentration in plant tissues and hence small demand (Bowen 1979; Thompson et al. 1997). The relationship between topsoil concentration and scarcity was confirmed when base cations were analyzed by pairs within individual soil profiles (Figure 5). As one base cation became relatively more abundant, its distribution became relatively deeper compared to the other. This pattern was particularly strong in soils that were poor in total bases.

The composition of the base cations held on the CEC showed important differences along the Aridisol-Mollisol-Ultisol gradient and yielded partial support for our third prediction that the most limiting nutrients are relatively less depleted along a gradient of weathering-leaching intensity (Table 3). From Aridisols to Mollisols to Ultisols base saturation decreased dramatically and shifted from deeper to shallower distributions. Increasing K:Ca abundance ratios and decreasing K:Ca ratios of topsoil concentration towards Ultisols, suggest that along the weathering-leaching gradient of these soil orders, Ca losses are greater than K losses, with Ca becoming a limiting nutrient only in Ultisols (Table 3, Figure 5). These patterns suggest that the retention of K by ecosystems is relatively greater than that of other base cations (see Stone & Kszystyniak 1977; Nowak et al. 1991). These patterns were more evident in Ultisols under natural vegetation (Table 3), perhaps as a consequence of liming practices in agricultural soils. Whereas the relative enrichment of the base cation complex with K was expected as a consequence of high plant cycling and retention, the enrichment of Mg was not. That exchangeable Mg increases with depth in Ultisols suggests that its higher relative contribution is not caused by plant cycling, but by some abiotic process such as the preferential retention of leached Mg over Ca by Al hydroxides in the subsoil (Smeck et al. 1994; Saif et al. 1997).

Another striking pattern along the Aridisol-Mollisol-Ultisol gradient that was not expected from plant cycling is the difference in the relative abundance of exchangeable Na^+ vs. Ca^{2+} . The relative contribution of Na^+ to base saturation was highest in Aridisols, lower in Mollisols, and higher again in Ultisols (Table 3), mirroring the chemical composition of large rivers across a similar gradient of rainfall and weathering (Gibbs 1970; Andrews et al. 1996).

Aridisols, like rivers from arid basins (e.g., Jordan, Pecos), have relatively high Na:Ca ratios as a result of incomplete weathering and leaching of salts and hence a relatively high Na yield. Mollisols, like rivers from basins that are relatively humid but not extremely weathered (e.g., Mississippi, Ganges), have already lost Na from salts by intense leaching but still have primary minerals that provide a low Na:Ca output. Finally Ultisols, like rivers from very humid and highly weathered basins (e.g., Negro in Brasil), have lost most of their primary minerals and their chemistry reflects the dominance of Na atmospheric inputs over Ca from weathering (Gibbs 1970; Andrews et al. 1996; see also Chadwick et al. 1999). Another important difference among soil orders is the extreme topsoil enrichment of extractable P observed in Aridisols, which is especially clear when compared with the other nutrients (Figure 6). High pH and reactions with Ca may reduce extractable P pools to extremely low levels in Aridisols, increasing the potential importance of plant cycling and leading to shallower profiles. Alternatively, the sharp increase of Ca abundance and pH with depth may occlude P with more intensity at depth (Lajtha & Schlesinger 1988; Sposito 1989). Vertisols, the only soil order that experiences a regular vertical mixing as a result of clay expansion and contraction, showed relatively low K:Ca ratios and no differential stratification of exchangeable K^+ and Ca^{2+} , suggesting that this mixing erases any vertical differentiation that may occur (Figure 5).

In contrast with mineral derived elements like P and K, plants play an obvious role in the vertical distribution of organic C and total N by controlling most of the organic additions to the soil (Post et al. 1982; Jackson et al. 1996, 1997; Jobbágy & Jackson 2000). Redistribution by plants does not occur for soil C and may be negligible for total soil N.

Plant cycling vs. other soil processes

Our results and those of many other researchers provide clues to assess the role of plant cycling against other major nutrient transport and input processes: leaching, weathering, and atmospheric deposition (Trudgill 1988). We suggest that the role of leaching for the vertical distribution of essential nutrients is usually subordinate to plant cycling. The adsorption affinity of base cations to the soil exchange complex follows the order $Ca^{2+} > Mg^{2+} > K^+ > Na^+$ (Sposito 1989). Based exclusively on leaching one would expect exchangeable Ca^{2+} and Mg^{2+} to be shallower than K^+ . However, exchangeable Ca^{2+} and Mg^{2+} were shallower than K^+ in only 31 and 17% of the soil profiles, respectively (Table 1). The role of leaching is probably important for exchangeable Na^+ and the anions Cl^- and SO_4^{2-} . It is important to note, however, that Cl^- and SO_4^{2-} were not depleted from the topsoil in Ultisols (Figure 6) and that they display topsoil concentration when their abundance

was low (Figure 4). This could result from Cl and S being more limiting in Ultisols (Ozanne 1958), and hence their vertical distributions dominated by plant cycling, or could be caused by higher anion exchange capacity in these soils (Sposito 1989).

Weathering is the primary source of P and base cations in most soils (Trudgill 1988). Weathering rates can vary with depth because of variation in substrate abundance, abiotic conditions, and root activity (Kelly et al. 1998). However, if we assume a constant stoichiometry of nutrients released after weathering throughout the profile, we should expect topsoil concentration for all nutrients and little differences among their vertical distribution (e.g., K and Na should have similar profiles). Weathering could explain shallower profiles for P and K relative to other nutrients only if the relative weathering rates of their source minerals were higher in the topsoil. Plants could produce this effect if they preferentially enhance the weathering rates of minerals P and K bearing minerals. Plants can mobilize mineral fractions (HCl-soluble) of K and P (e.g., Jungk & Claasen 1986), but we are unaware of reports demonstrating a mechanism of preferential weathering of K- and P-bearing minerals.

Can the vertical patterns that we found be explained by atmospheric deposition? Even though atmospheric inputs occur in the surface of the soil, they should not produce topsoil accumulation under equilibrium conditions. An element like Cl, which in most soils has its only source in atmospheric inputs will accumulate in the soil up to a level at which leaching outputs balance atmospheric inputs. Because leaching intensity decreases with depth in the soil profile as a result of water losses through evaporation and plant water uptake, the concentration of Cl under steady state conditions should increase with depth (Yaalon 1965) (Figure 1(a)). Simulation models of Cl leaching in arid regions support this pattern (Tyler & Walker 1994). Hence, atmospheric deposition under equilibrium conditions is unlikely to explain any shallow distribution of nutrients. However, under transient states in which atmospheric inputs increase and are not being balanced by outputs, soil may undergo a net accumulation, and topsoil accumulation may occur in the absence of plant cycling effects. While this may be possible in some soil profiles, recent regional surveys of wet and dry atmospheric deposition indicate that K has the smallest deposition rates among base cations (Johnson 1992; Erisman & Draaijers 1995). Hence, based only on atmospheric deposition it is not possible to explain the depth ranking of base cations that we observed. Although shallow K in some soil profiles may be caused by atmospheric deposition of illite (Singer 1989; Paton et al. 1995), it is unlikely this would be the primary cause at the global scale.

Volumetric changes associated with the deformation of the soil matrix through soil aging may affect the concentration of nutrients. The most common pattern is the dilation of soil layers with high biological activity and organic matter, usually the topsoil, and the collapse of the subsoil (Brimhall et al. 1991; Jersak et al. 1995). Ignoring other soil processes, this prevalent deformation pattern in soils should cause a dilution of soil nutrients in the topsoil and concentration in deeper soil layers. Since the vertical distribution for the most limiting nutrients showed the opposite trend, it seems unlikely that the deformation process is a dominant determinant of their distribution.

Plant cycling, often overlooked as a transport agent in the soil, should be relatively more important when the amounts cycled by plants are large relative to the soil pool. As nutrients become more limiting, the plant uptake/soil availability ratio should become higher and the upward transport by plants more significant. From a plant perspective we propose that vertical distributions can be used as a relative indicator of nutrient constraints, with abundant nutrients having deeper distributions than scarce ones. The analysis of vertical profiles at remote sites may enable one to predict the nutrient(s) most limiting plant growth in the absence of fertilizer trials. In addition, vertical profiles may help identify limiting nutrients where plant growth will not manifest a rapid response to fertilization (Chapin et al. 1986).

Implications of plant cycling

The upward transport of nutrients by plants depends not just on the ratios of uptake to availability for each nutrient, but also on aboveground allocation (the greater the aboveground allocation by plants, the faster the upward transport). Rooting depth could determine the total pool of nutrients subject to upward transport by plants, with pools below the maximum rooting depth being relatively undepleted (Figure 1(b)). The patterns presented do not show this expected recovery of K or P concentrations at depth. However, they are limited to the first soil meter and evidence suggests that few ecosystems, with the exception of tundra, have maximum rooting depths shallower than one meter (Stone & Kalisz 1991; Canadell et al. 1996). Some studies have shown nutrient concentrations to increase below the first meter, beyond the zone of high depletion by roots (Richter et al. 1994; Jama et al. 1998). We note that under some special conditions plants may redistribute nutrients downward; if nutrient pools are initially concentrated in the surface layers, then root growth and senescence may transport some of these nutrients to deeper layers.

Nutrient distribution patterns resulting from plant activity suggest two opposing strategies for plants to obtain scarce nutrients. The first is to develop a dense root system in the topsoil, exploring the zone of maximum accumulation and intercepting nutrients as they move downward by leaching. An

extreme example of this strategy are apogeotropic roots intercepting stemflow in nutrient-poor tropical forests (Sanford 1987). Alternatively, plants that are able to grow roots below the zone of high depletion may obtain a source of nutrients with relatively little competition (see Lipps & Fox 1956). Root activity and nutrient availability in deep soil layers (>1 meter depth) remains poorly explored and may play an important role in ecosystem functioning (e.g., Richter & Markewitz 1995; Jackson 1999).

There are strong similarities between the nutrient distributions we found in arid soils in the vertical dimension and those observed horizontally between soil patches under shrub canopies and openings in desert ecosystems (Charley & West 1975; Schlesinger et al. 1996; Schlesinger & Pilmanis 1998). The accumulation of extractable N, P, and exchangeable K, and the depletion of exchangeable Ca^{2+} , Mg^{2+} , and Na^{+} found under shrub canopies in arid ecosystems by Schlesinger et al. (1996) and others matches our results for the vertical dimension in Aridisols. This suggests a common imprint of plant cycling in both the horizontal and the vertical dimensions. In humid ecosystems where the canopies of plant individuals overlap, the horizontal manifestation of fertility islands observed in deserts may disappear, but the vertical manifestation apparently remains, as suggested by our global results and results from Mollisols and Ultisols. Extractable SO_4^{2-} and Cl^{-} tend to be horizontally accumulated under shrubs (Schlesinger et al. 1996), but were vertically depleted in the topsoil (Figure 6). This contrast may result from horizontal changes in leaching rates caused by the interception of rainfall by shrub canopies.

The role of plant cycling on vertical distributions of soil properties may be noticeable at various temporal scales. At a pedogenic time scale, plant cycling in acid soils of tropical rainforests has been proposed to cause an upward transport of Si by plants that alters dramatically the mineral composition of the topsoil (Lucas et al. 1993; see also Markewitz & Richter 1998). At the other end of temporal scales, agricultural experiments that compare till and no-till systems show that an upward transport of nutrients can be noticeable in about a decade (Juo & Lal 1979; White 1990; Unger 1991; Edwards et al. 1992; Scheiner & Lavado 1998; Lavado et al. 1999). Soils under conventional tillage are cultivated and mixed every year and usually present a homogeneous distribution of nutrients within the plowing depth (usually 15–30 cm). When these plots shift to no-till management, vertical mixing is interrupted. Experiments that evaluated the vertical distribution of nutrients under this change in tillage with no addition of fertilizers revealed a topsoil accumulation of extractable P, exchangeable K^{+} , and, in some cases, Ca^{2+} after 4 to 20 years (Juo & Lal 1979; White 1990; Unger 1991; Edwards et al. 1992; Scheiner & Lavado 1998). Upward nutrient transport in natural

ecosystems may be slower than in agricultural systems since crops have a relatively higher nutrient uptake and aboveground allocation and all of their biomass usually cycles annually (Chapin et al. 1986; O'Toole & Bland 1987). In contrast, the removal of nutrients by harvests may curtail the upward transport in agricultural ecosystems, particularly in the case of nutrients such as P that are highly retranslocated to seeds or fruits (Marschner 1995).

The control that plants exert on the vertical distribution of limiting nutrients can produce a strong positive feedback for plant productivity by enhancing resource availability (Van Breemen 1993; Van Breemen & Finzi 1998). Soil nutrient pools may represent a potentially large extension of the nutrients sequestered by plant biomass and should be considered in successional models of nutrient dynamics and retention by biota (Vitousek & Reiners 1975; Gorham et al. 1979).

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