

THE UPLIFT OF SOIL NUTRIENTS BY PLANTS: BIOGEOCHEMICAL CONSEQUENCES ACROSS SCALES

ESTEBAN G. JOBBÁGY^{1,2,4} AND ROBERT B. JACKSON^{2,3}

¹CONICET, INTA San Luis—Ruta 7 y Ruta 8, Villa Mercedes, 5730—San Luis, Argentina

²Department of Biology, Duke University, Durham, North Carolina 27708 USA

³Nicholas School of the Environment and Earth Sciences, Duke University, Durham, North Carolina 27708 USA

Abstract. Although the bulk of plant biomass contains relatively light, atmospherically derived elements (C, H, O, N, and S), 5–10% of biomass is composed of heavier elements from soil minerals, such as Ca, Mg, K, and P. Plant uptake and cycling transport these heavier elements to the soil surface, resulting in shallower vertical distributions for strongly cycled elements than for other elements. In this paper, we evaluate the biogeochemical consequences of this process at different spatial and temporal scales based on chronosequence studies and soil database analyses. In the bare coastal dunes of Argentina, the vertical distributions of exchangeable K⁺ (strongly cycled) and Na⁺ (more weakly cycled) were similar initially but diverged 15 years after pine afforestation, with K distributions becoming significantly concentrated in the surface and Na distributions becoming deeper. To evaluate the effects of plant stoichiometry on micronutrient distributions, chronosequences of paired native grasslands (low Mn cycling) and eucalypt plantations (high Mn cycling) in the pampas of Argentina were also used. Within 50 years, eucalypts dramatically redistributed Mn pools toward the soil surface, reducing total pools by half at medium depths (20–60 cm) and increasing concentrations by up to an order of magnitude at the surface. Globally, we used generalized contrasts among exchangeable K, Na, and Mg in 7661 soil profiles to estimate the global magnitude of K uplift due to plant activity. Based on this calculation, the exchangeable K pool in the top 20 cm of soils without plant uplift would be 4–6 × 10¹⁵ g smaller globally, one-third to one-half smaller than its current size. Vegetation change alters the vertical distribution and bioavailability of mineral elements. Understanding how the stoichiometry of plant cycling affects soil nutrient distributions will help refine predictions of the biogeochemical consequences of current vegetation change.

Key words: base cations; biocycling; manganese; nutrient cycling; nutrient pumping; organic cycling; tree plantations; vegetation–soil interactions.

INTRODUCTION

When vascular plants colonized land in the Early Devonian, ~400 million years ago, they transformed the terrestrial environment (Behrensmeyer et al. 1992, Kenrick and Crane 1997). With their vascular systems, extensive root structure, and photosynthetic capacity, these plants captured, transformed, and redistributed materials from the atmosphere and lithosphere at higher rates and across larger volumes than their non-vascular ancestors.

The most significant example of the redistribution of materials by plants is the chemical transformation and movement of relatively light elements (e.g., C, H, O, N, and S) from the atmosphere into the surface of continents. Organic C accumulates in soils after plants grow and senesce, and their residues are transformed to humus. The downward movement of inorganic C (as CO₂ and HCO₃) derived from plant and microbial res-

piration also leaves a unique biotic signature in ground water and pedogenic carbonates (Chebotarev 1955, Van Breemen and Buurman 1998). Similarly, plants transform diatomic N from the atmosphere through symbiotic fixation into inorganic and organic forms (Vitousek et al. 2002). Not surprisingly, plant production and allocation patterns help shape the amount and vertical distribution of these lighter elements in soils (Jobbágy and Jackson 2000, 2001).

Less well understood is the role of plants in redistributing materials derived from the lithosphere. Although most plant biomass contains the relatively light elements that are common in the atmosphere, roughly 5–10% of plant dry mass is composed of heavier elements supplied by minerals (Bowen 1966, 1979, Lambers et al. 1998). Of these elements, Ca and K typically have the highest concentrations in plant tissues, often approaching those of N (Bowen 1966, 1979, Lambers et al. 1998, Gordon and Jackson 2000). Some lithospheric elements, particularly P, limit biological activity in many terrestrial systems and are highly concentrated in plants relative to their abundance in soils and rocks (Bowen 1966, Schlesinger 1997). The weathering of parent material typically supplies these ele-

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⁴ E-mail: egj@duke.edu

ments to plants (Jenny 1980), and plants can in turn dramatically enhance weathering rates (Kelly et al. 1998, Volk 1998), although dust derived from remote rocks and soils and ocean-salt aerosols can be important sources where intensely weathered rocks provide inadequate mineral nutrients (Chadwick et al. 1999).

In this paper, we examine how plant cycling affects the vertical distribution of lithospheric elements at a range of spatial and temporal scales using chronosequence field experiments and soil database analyses. Chronosequences involving plantations established on bare sand dunes and native grasslands in the pampas of Argentina are used to evaluate how vertical nutrient distributions are affected by different plant types and species (and their differing stoichiometries and nutrient requirements). Based on global soil databases, we evaluate the imprint of grasslands (relatively low calcium cycling) and broadleaf forests (higher calcium cycling) on the vertical distribution of base cations in the soil. Finally, we use base cation distributions from 7661 soil profiles to estimate the magnitude of K uplift globally by plants.

NUTRIENT REDISTRIBUTION BY VEGETATION

Decadal time scales

Element cycling by plants results in a net movement of nutrients to the soil surface through transport within the plant and release via litterfall and direct leaching from leaves by throughfall (Stone 1975, Trudgill 1988, Richter and Markewitz 1995). As long as nutrient uptake by plants takes place at greater depth than nutrient return to the soil, a net uplift should be expected as a result of cycling. If the magnitude of plant uplift is large compared to other processes such as leaching, strongly cycled elements will have shallower vertical distribution than less cycled ones. These ideas form what we call the “nutrient uplift hypothesis” (Jobbágy and Jackson 2001). Nutrient uplift could also interact with other influences of plants on the dynamics of lithospheric elements, such as increased nutrient adsorption, through such mechanisms as the build-up of exchange complexes with organic matter additions to the soil (Anderson 1988), enhanced chemical weathering of rocks (Kelly et al. 1998, Volk 1998), and retention of soil/rock particles and the solid products of their weathering as a result of erosion control (Stallard 1992).

Several lines of evidence support the nutrient uplift hypothesis. The vertical distributions of elements derived primarily from the lithosphere show consistent patterns globally that reflect their importance to plants, with greater topsoil concentrations of P and K compared to other less-important plant elements (e.g., Na) across a broad range of ecosystems and soil types (Jobbágy and Jackson 2001). Such patterns are difficult to explain without considering nutrient uplift by plant uptake and cycling.

The stoichiometry of many lithospherically derived elements in plants is relatively conservative and can be used to help infer their imprint on nutrient distributions in the soil. Ratios of K:Na in plants are typically $\gg 1$ and usually higher than ratios observed in rocks and soil minerals. Potassium is important for osmotic regulation in plants, but Na tends to be excluded by plant roots (Marschner 1995). Potassium and Na^+ also have the same monovalent charge, similarly small hydrated radius, and high mobility in plants and soil compared to other cations (Sposito 1989). Because of their contrasting importance to plants, and the fact that both biogeochemical cycles involve no changes in oxidation state, they are a useful comparison for exploring the imprint of plant cycling on soil nutrient distributions. Globally, exchangeable K^+ and Na^+ show the shallowest and deepest vertical distributions, respectively, among base cations (Jobbágy and Jackson 2001).

We used the coastal sand dunes in central Argentina to explore how plant uplift affects nutrient distributions through time. We focused on base cation fluxes along a 55-year chronosequence of *Pinus pinaster* plantations established on bare sand dunes (see Jobbágy and Jackson 2003 for a detailed description of the experimental system). The bare dunes were initially stabilized for three to five years using dead tree branches to arrest sand movement. *P. pinaster* trees were then planted at a density of 800 trees/ha and were never fertilized, irrigated, or harvested. An organic layer of 2–5 cm thickness developed in the surface of the forest stands. Because we wanted to evaluate potential nutrient uplift within the mineral soil we did not consider nutrients held by the organic layer as strictly “uplifted” but as an extension of nutrients sequestered by biomass (Jobbágy and Jackson 2003), and hence focused our observation to the mineral profile.

In the bare dune plots, the vertical distributions of exchangeable K and Na were similar initially (Fig. 1). In contrast, within 15 years, afforested plots had substantially higher concentrations of exchangeable K in the surface mineral soil, and older stands showed even greater topsoil concentrations of K at the surface and Na concentrations at depth (Fig. 1). Maximum K concentrations occurred in the top 20 cm of soil and minimum concentrations between 20 and 80 cm depth; at 1–4 m depths, the concentrations of K were similar and varied little among stands (Fig. 1). Exchangeable Na showed minimal changes in the surface soil after afforestation but large changes at depth, with the oldest afforested stands having three to four times more exchangeable Na than the bare dunes in deeper layers (Fig. 1). This pattern likely reflects the combined effects of water uptake and Na exclusion by trees. In the afforested sites, as water flows downward, root absorption concentrates any solute that is partially or totally excluded by root membranes, resulting in higher contents at depth. In contrast, in the bare dunes where

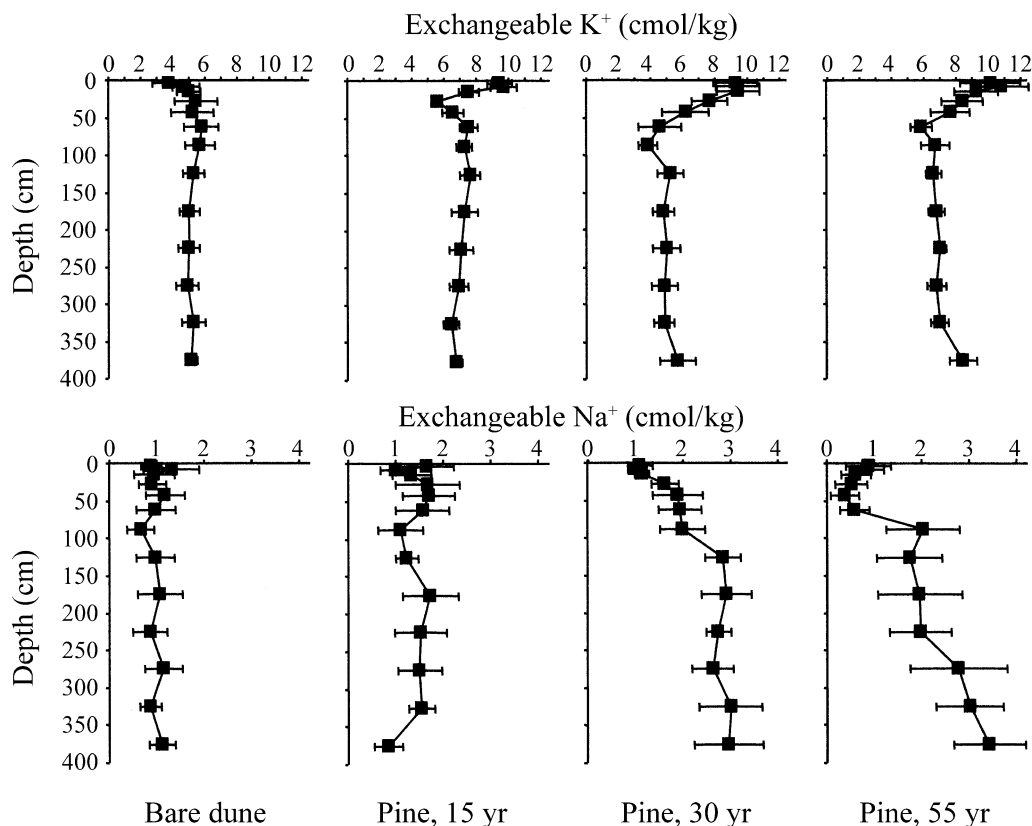


FIG. 1. Vertical distribution of exchangeable base cations (mean $\pm$ 1 SE, $n = 5$ for each point) along a chronosequence (0–55 yr) of *Pinus pinaster* plantations in dunes of coastal Argentina. The bare dunes were stabilized with dry tree branches five years before planting, with measurements obtained at the end of this stabilization period. Concentrations correspond to NH_4OAc (1 mol/L, pH 7) extractions, expressed on a soil gravimetric basis. Bulk density was 1.32 ± 0.45 (mean $\pm$ 1 SD for all samples) and did not vary significantly with depth or across sites.

direct soil evaporation from the top ~ 30 cm is the only evaporative pathway of water loss, concentrations of percolating water remain constant below that depth. Thus, the initially homogeneous K and Na distributions of the bare dunes were transformed to a system in which K was quickly enriched in the surface and Na enriched at depth (as suggested in Jobbágy and Jackson 2001). Lower K concentrations at intermediate soil depths most likely indicate zones of net depletion, and the minimal changes below 1 m may suggest little K uptake below this depth (Fig. 1). Although K has a stronger affinity with the exchange complex than Na, and hence may experience reduced leaching, our results indicate that these two elements were similarly distributed in bare dunes and their divergence was associated with plant establishment.

This sand dune chronosequence shows how vegetation altered the vertical distribution of exchangeable cations in opposite ways within 15 years. While aggrading vegetation can build surface pools of important lithospheric nutrients, biomass harvesting and removal can release the nutrients in a short time. This biotic dependence of surface nutrient pools may be crucial to

manage and sustain soil fertility in areas where base cations or P constrain productivity.

Pedogenic time scales

At even longer time scales, nutrient uplift by aggrading vegetation can help shape soil mineralogy. An extreme example of this pedogenic effect comes from Si dynamics in young soils developed on volcanic ash in Reunion Island which have a 15-cm surface horizon consisting almost entirely of biogenic opal (phytoliths; Meunier et al. 1999). A Si bioaccumulator, the bamboo *Nastus borbonicus*, in a high Si environment is the likely cause of this surface mineral horizon. Through its cycling, *N. borbonicus* sequesters almost all of the Si released by weathering during ~ 3000 years of pedogenesis in the system, preventing Si loss to streams and rivers (Meunier et al. 1999).

Long-term Si uplift is not limited to the bamboos or other strongly Si-cycling *Poaceae*. In tropical Oxisols, millennia of intense weathering and leaching deplete Si, leaving behind less-soluble Al and Fe oxides that give soils their characteristic red color (Van Breemen and Burman 1998). Nonetheless, most Oxisols around

TABLE 1. Manganese and iron concentrations (mg/kg) in the leaves and soil litter of adjacent grasslands and *Eucalyptus camaldulensis* stands and in the shoots of the grass *Cynodon dactylon* growing in each stand.

Nutrient and source	Castelli		Guerrero		América	
	Plantation	Grassland	Plantation	Grassland	Plantation	Grassland
Mn						
Leaves	1276	51*	1062	50*	1256	101*
Litter	1681	77*	1613	65*	2286	123*
<i>Cynodon</i>	160	51*	166	50*	402	101*
Fe						
Leaves	78	281*	71	189*	107	267*
Litter	123	322*	132	271*	188	314*
<i>Cynodon</i>	353	281	209	189	229	267

Notes: Adjacent native grasslands and eucalypt plantations were sampled in three different sites in Argentina. Fully expanded sun leaves of eucalypts were randomly sampled in plantations. Green leaves in grasslands and soil litter in grasslands and plantations were sampled in randomly distributed 0.25×0.25 m quadrats. In both vegetation types, *C. dactylon* shoots from randomly selected individuals were sampled. Concentrations were determined by ICP after Kjeldahl digestion ($N = 5$ individual plants/quadrat for each mean value presented). Asterisks (*) indicate significant differences ($P < 0.05$) between stands at each site.

the world show a surface peak of Si-bearing clays, particularly kaolinite (Lucas et al. 1993). Measurements of ecosystem Si fluxes in Amazonian Oxisols showed that the intense Si uplift exerted by the rain-forest vegetation increased dissolved Si concentration in the surface soil and favored the formation and maintenance of kaolinite, counterbalancing continual weathering and leaching losses (Lucas et al. 1993, Lucas 2001).

NUTRIENT REDISTRIBUTION AFTER VEGETATION CHANGE

Micronutrient and bioaccumulators

The elemental makeup of plant cells constrains stoichiometry across species, with particularly stable ratios among N, P, and K (Bowen 1966, 1979, Lambers et al. 1998, Gordon and Jackson 2000, McGroddy et al. 2004). However, differences due to environment, ontogeny, allocation among woody and herbaceous plants, and specific aspects of plant absorption and metabolism can be large, especially for micronutrients (Lambers et al. 1998). Micronutrient concentrations show large variation among plant species, and individual species and families can behave as “bioaccumulators” of certain metals.

An important example that we examined is Mn in eucalypts, especially species of the *Eucalyptus* subgenus *symphyomyrtus* (Hill et al. 2001). To examine the speed and extent with which accumulator species alter soil nutrient distributions, we used plantations of the Mn accumulator *E. camaldulensis* growing in soils that developed under grasslands with low Mn-cycling capacity. We characterized soil changes with afforestation using a chronsequence of three paired stands of native grasslands and *Eucalyptus* plantations 50–100 years of age in the pampas (see Jobbágy and Jackson 2003 for a description of the experimental system).

Eucalypt leaves at the three sites had Mn concentrations 12–25 times higher than those in pooled leaf samples of grassland species at the sites ($P < 0.05$ in each case; Table 1).

Total Mn concentrations under the youngest plantations were depleted in intermediate soil layers (5–50 cm of depth) but dramatically enriched in the Oh horizon and in the top of the mineral soil (Fig. 2; $P < 0.05$). This ecosystem-scale redistribution of Mn was equally apparent in exchangeable soil Mn concentrations (Fig. 2; 1 mol/L NH_4OAc , pH 7 extraction). Exchangeable Mn values were significantly higher at 0–10 cm depths under eucalypts at all sites ($P < 0.05$ for each). The soil Mn redistribution by *E. camaldulensis* was also accompanied by large changes in Mn bioavailability (Table 1). Total Mn concentrations in tissues of the bioindicator grass *Cynodon dactylon* were three- to fourfold higher when *C. dactylon* was growing in the eucalypt stands vs. the adjacent grasslands (Table 1; $P < 0.05$).

Iron distributions provide a useful “control” for Mn uplift by plants, since Fe and Mn share similar geochemical behavior in soils but Fe is not accumulated by eucalypts (Table 1). Unlike Mn, soil Fe distributions were similar in afforested and native grassland stands (Fig. 2), suggesting that uplift was likely the dominant cause for the soil Mn differences we observed. Other processes such as soil acidification should have affected both elements similarly.

In these systems, the introduction of a species with high Mn demand strongly altered soil Mn pools, with organic and surface mineral soil gaining Mn at the expense of deeper layers in the rooting zone (Fig. 2). These changes occurred within half a century of introduction of the accumulator species. The activity of bioaccumulators can potentially affect other species through the enhancement of total amounts and bio-

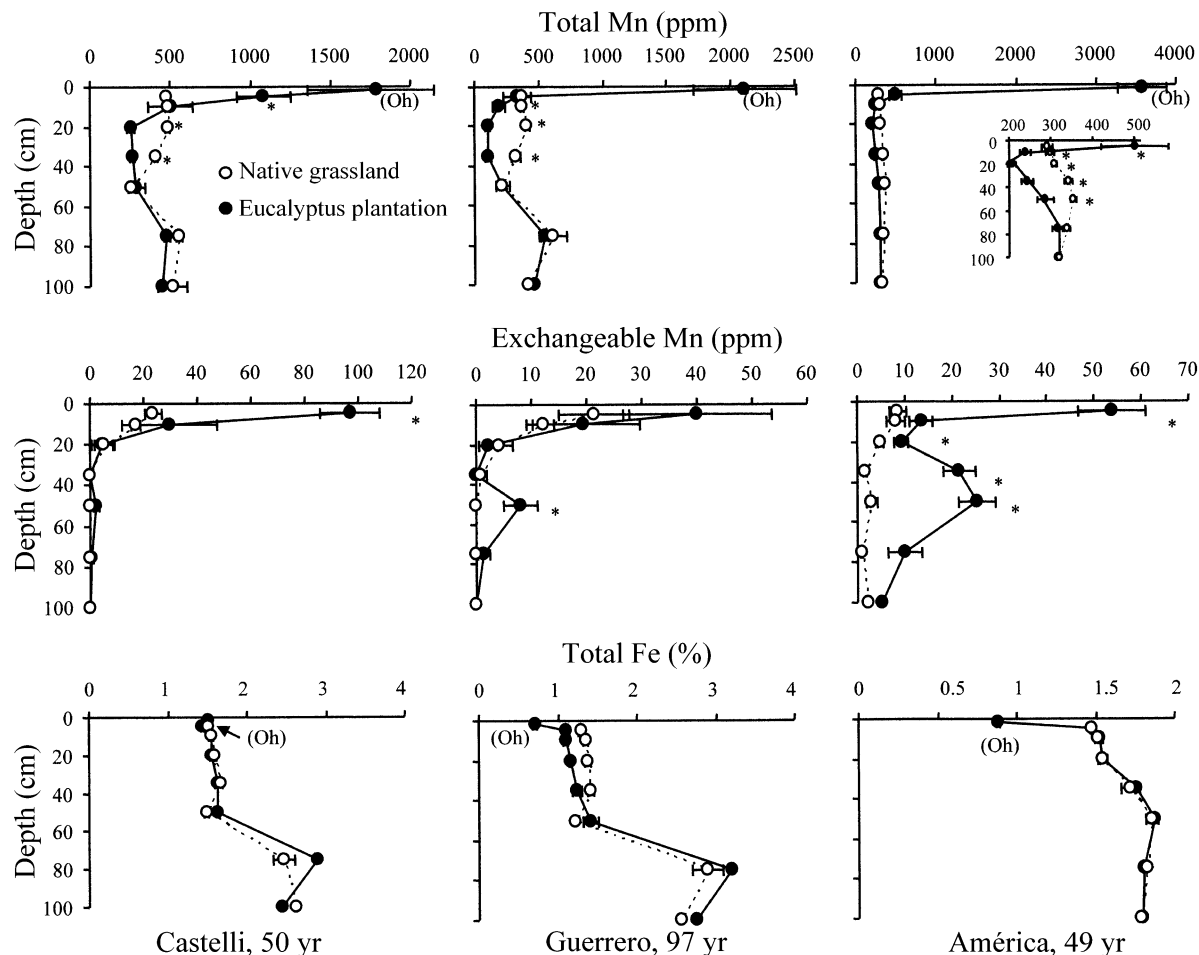


FIG. 2. Vertical soil distributions of total and exchangeable Mn and total Fe (mean $\pm$ 1 SE, $n = 5$ for each point) in adjacent native grassland and *Eucalyptus camaldulensis* stands at three sites in the pampas of Argentina. Asterisks (*) indicate significant differences between native grassland and plantations ($P < 0.05$). The plantations at Castelli, Guerrero, and América are 50, 97, and 49 years old, respectively, grow in a humid to subhumid temperate climate, and have Mollisol soils that were never plowed, fertilized, or irrigated. See Jobbágy and Jackson (2003) for further details on the experimental system. Total Mn and Fe concentrations for the organic horizon (Oh), only present in plantations, are also indicated. The inset in the total Mn plot for the América site shows concentration differences below the organic horizon in greater detail. Total Mn and Fe concentrations were measured by ICP after soil digestion (EPA method 3050-A; Chen and Ma 1998), and exchangeable Mn was extracted with 1 mol/L NH_4OAc at pH 7.

availability of lithospheric elements, potentially beneficial in the case of limiting nutrients but detrimental when toxic levels are approached in the surface soil (Marschner 1995).

Base cations in grassland-forest transitions

Among macronutrients, Ca displays some of the largest variation in foliar concentrations and consistent differences among plant functional types (Thompson et al. 1997), especially compared to another lithospheric macronutrient like K. Broadleaf trees species have three times more Ca (1.8 vs. 0.6 mg/kg) and five times higher Ca:K ratios (1.29 vs. 0.23) in their leaves than grass species have (based on data from Bowen [1966] and Thompson et al. [1997] for trees and grasses, respectively). These contrasts likely result from the larger

exchange capacity and Ca absorption of cell walls in dicots compared with grasses (Meerts 1997). Foliar concentrations do not indicate cycling intensity directly, since reabsorption and litter fall rates also must be considered. Nonetheless, Ca:K ratios suggest that Ca should have a higher cycling intensity compared with other elements under broadleaf forest vegetation than under grasslands. In consequence, soil Ca distributions should be shallower in broadleaf forests than in grasslands.

We explored this prediction by comparing exchangeable Ca distributions from soils of broadleaf forest and grassland vegetation documented in the NSCD database (U.S. Department of Agriculture 1994). We included other base cations in the analysis to assess whether differences in distributions were specific for

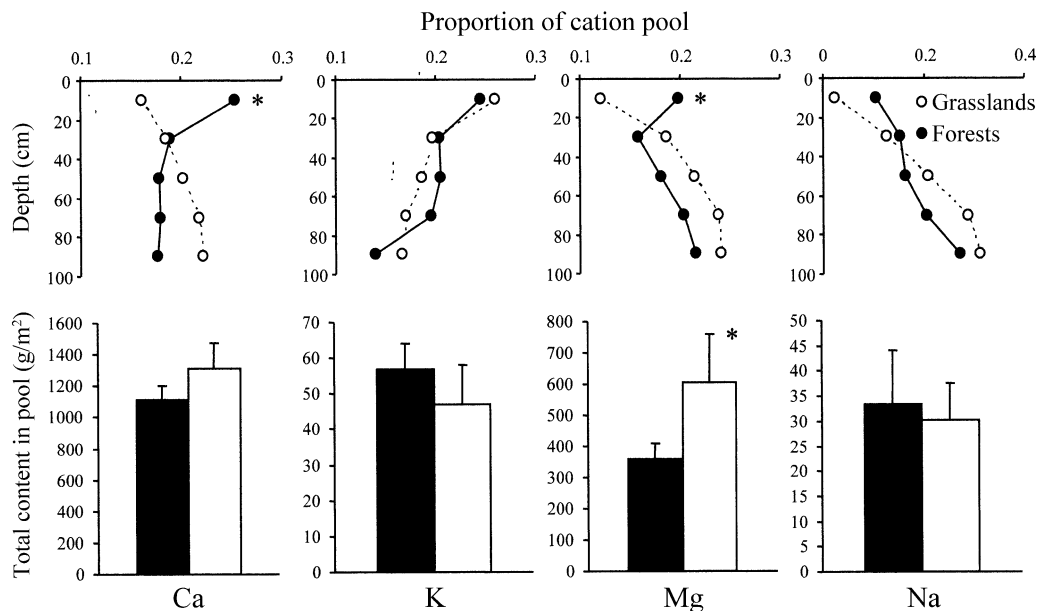


FIG. 3. Vertical distributions of exchangeable base cations in grassland and broadleaf forest soils with high base saturation (75–100%). The top panels show the relative distribution of exchangeable cations in the top 1 m of the soil indicated as the proportion of the pool that is located in each 20-cm layer. Values correspond to the median proportion of each layer calculated across sites. Statistical differences are only indicated for the 0–20 cm layer (t test, $*P < 0.05$). The lower panels show the total contents (mean $\pm$ 1 SE) of exchangeable cations pools in the top 1 m of soils under grasslands and forests ($n = 41$ for forests and 24 for grasslands). All sites used in the analysis were covered by native vegetation. Data were obtained from the NSCD database (U.S. Department of Agriculture 1994).

Ca, as expected from the uplift hypothesis, or involved a broader range of base cations as it would be expected from other mechanisms such as leaching. We constrained the analysis to soils with a high degree of base saturation (75–100% saturation) to remove any bias created by highly leached, base-poor soils, common in humid forests but uncommon in grasslands and to eliminate the potentially confounding effect of soil liming. Soils derived from calcareous parent materials were also excluded from the analysis.

The distribution of exchangeable Ca in the top 1 m of the soil was significantly shallower in forests than in grasslands (Fig. 3). Most forest profiles showed the highest exchangeable Ca concentrations in the top 20 cm of soil (76%), compared with only 29% for grasslands. Exchangeable Mg also showed a shallower profile under forest vegetation. Potassium and Na distributions in the soil did not differ between vegetation types and followed the opposing patterns we observed globally (Jobbágy and Jackson 2001). Total exchangeable pools did not differ between vegetation types, suggesting that the profiles used in the analysis covered similar ranges of nutrient availability for all base cations except Mg, which was higher in forests (Fig. 3). These results suggest that while grasslands enrich surface soil only with K, forests also enrich it with Ca and Mg.

Contrasting soil Ca distributions for grasslands and forests matched the predictions based on differential

Ca cycling for broadleaf trees and grasses. Ca uplift may help explain the acidification of subsurface soil observed after the establishment of high Ca cycling tree species in grassland ecosystems of Australia and Argentina (Noble et al. 1999, Jobbágy and Jackson 2003). The presence of Ca-rich patches of surface soil in temperate North American forests has also been associated with the intense Ca cycling and uplift by individual species such as *Cornus florida* (Thomas 1969), *Picea glauca* and *Populus tremuloides* (Alban 1982) and *Acer saccharum* (Dijkstra and Smits 2002).

In addition to stoichiometric differences across plant species, differences in rooting depth and the vertical pattern of nutrient absorption can play an important role defining nutrient uplift dynamics among plants (Jackson et al. 1999, 2000). For example, the establishment of deep rooted species in systems dominated by shallow rooted plants may bring nutrients from deeper soil layers and even benefit shallower rooted plants. Strontium stable isotope signatures of soils and plants in rangelands of the southwestern United States revealed a substantial shift of base cation absorption towards greater soil depth after native grasslands were encroached by deeper rooted shrubs (Jackson et al. 2002). In shrub wetlands of Alaska, Marsh et al. (2000) showed how horsetails (*Equisetum* spp.), relatively minor components of the plant community, played a key role acquiring large amounts of P, K, and Ca from deep mineral soil and releasing the elements at the surface

TABLE 2. Global estimate of K uplift by plants based on soil types.

Soil order	Global area (millions of km ²)	Amount of K in top 20 cm of soil					
		Per unit area (g/m ²)			Globally (Tg)		
		Actual	Uplifted		Actual	Uplifted	
			Mg-like	Na-like		Mg-like	Na-like
Alfisols	18	45	18	21	820	327	379
Aridisol	32	161	68	109	5121	2155	3471
Entisols	15	112	31	49	1674	460	732
Histosols	2	124	37	18	216	65	31
Inceptisols	24	78	14	21	1887	346	519
Mollisols	5	124	48	75	681	267	412
Oxisols	12	47	10	13	556	120	160
Spodosols	5	28	1	11	138	7	55
Ultisols	11	30	9	11	340	102	127
Vertisols	33	130	40	86	428	131	283
Total	127				11 859	3980	6169

Notes: Estimates are based on the actual vertical distribution of exchangeable K and its difference from sodium (Na-like) and magnesium (Mg-like) distributions in individual soil profiles ($n = 7661$) averaged across soil orders. The area estimates for each soil order were obtained from Eswaran et al. (1993).

through litter fall. Through nutrient uplift, these plants may behave as “ecosystem engineers” (Van Breemen and Finzi 1998).

This synergy of deep and shallow rooted plants has guided the design of agroforestry systems for many years (Young 1997). Traditional agricultural systems in Indonesia alternate two-year periods of agriculture with long fallow cycles of four to five years in which bamboo regrows naturally (Christanty et al. 1996). Nutrient budgets from these systems suggest that the bamboo restores surface nutrient pools through uplift from greater depths (Christanty et al. 1996). Although certain species and their neighbors may benefit from deep nutrient uplift, this is not always the case. Recent isotopic experiments in temperate and tropical forests (Kennedy et al. 2002, Poszwa et al. 2002) suggest actively cycled cation pools in surface soils of these systems and abundant yet poorly cycled pools in deep soil layers.

At pedogenic time scales, the imprint of grasses and trees on soils can extend to Ca mineral pools, as shown by soil observations in the grassland/forest ecotone of central Canada (Fuller and Anderson 1993). In these systems, biogenic particles of calcium carbonate accumulated in surface soils after the invasion of grasslands by aspen trees, which cycled more Ca than the grasses did (Fuller and Anderson 1993, Fuller et al. 1999). The recycling of lithospheric elements by plants strongly influences the net effects of dissolution, leaching and weathering and creates mineral patterns that would otherwise be difficult to explain in the absence of plant activity.

Differences in nutrient uplift among plants are likely to leave distinct imprints on surface soil chemistry and fertility. The stoichiometry of tissues and the vertical rooting patterns of plants are key attributes that can help us understand and predict how vegetation changes

will affect the biogeochemical cycles of lithospheric elements on land.

A GLOBAL ESTIMATE OF POTASSIUM UPLIFT BY PLANTS

To assess the potential importance of plant uplift on biogeochemical cycling at the global scale, we estimated the global magnitude of the exchangeable K pool in the surface soil explained by plant uplift and its significance for nutrient supply. To do this, we evaluated the data for 7661 individual soil profiles across soil orders globally from the National Soil Characterization Database (U.S. Department of Agriculture 1994), using them to estimate the global amount of K that is present in the top 20 cm attributable to plant uplift. We used a conservative estimate of K uplift, accounting only for differences in exchangeable K (as nonexchangeable K can be a significant source for plants in base poor soils; Markewitz and Richter 2000). We also assumed that plant uplift was limited to the top 1 m of soil, a second conservative assumption. We further assumed that in the absence of plant uplift, exchangeable K distributions would fall between (or be bracketed by) Na and Mg distributions (see Jobbágy and Jackson 2001). Exchangeable Na undergoes less cycling by plants and is slightly more mobile in soils than K, so its distribution should be relatively deeper. On the other hand, Mg is slightly less mobile and is subject to some plant uplift, so its distribution should be shallower. In order to discard the possible influence of K fertilization in our uplift estimates, we performed a complimentary analysis based on a subset of soil profiles for which land cover data was available ($n = 1484$ for crops, 322 for deserts, 131 for grasslands, 384 for forests, 8 for tundra). We scaled up our estimates based on the areas of land cover type factoring out the

TABLE 3. Global estimate of K uplift by plants based on land cover types.

Cover type	Global area (millions of km ²)	Amount of K in top 20 cm of soil					
		Per unit area (g/m ²)			Globally (Tg)		
		Actual	Uplifted		Actual	Uplifted	
			Mg-like	Na-like		Mg-like	Na-like
Crops	14	81	29	43	1136	408	603
Deserts	27	146	58	100	3930	1568	2701
Grasslands	24	115	35	72	2771	828	1740
Forests	48	53	13	13	2522	603	643
Tundra	8	32	2	15	255	18	121
Total	121				10 614	3425	5808

Notes: Estimates are based on the actual vertical distribution of exchangeable K and its difference from sodium (Na-like) and magnesium (Mg-like) distributions in individual soil profiles. Data were averaged according to land cover type. Only those soil profiles with records of land cover in the database were considered ($n = 1484$ profiles for crops, 322 for deserts, 131 for grasslands, 384 for forests, 8 for tundra). All cover types other than crops correspond to natural vegetation. The area estimates for each cover type were adapted from Jackson et al. (1997).

contribution of crops, the only land cover that should receive substantial K fertilization.

For each core in the database we calculated exchangeable K in the top 20 cm of each soil profile relative to the first meter of soil under current K distributions and if K behaved as Na and Mg in the profiles. These hypothetical distributions were calculated by applying to K the proportion observed for Na and Mg in the same profile in the top 20 cm of soil relative to the first 1 m. The uplifted pool was calculated as the difference between exchangeable content in the top 20 cm of the profile under current and Na- or Mg-like distributions (Tables 2 and 3). Our analysis by land cover types suggests that any overestimation of K uplift due to fertilization in croplands should be small, since 90% of the global uplifted pool corresponded to the natural vegetation classes (Table 3).

In the absence of plant uplift, the data suggest that the exchangeable K pool in the top 20 cm of soils globally would be $4\text{--}6 \times 10^{15}$ g smaller than its current 1.2×10^{16} g total, or only one-half to two-thirds of its present size (Table 2). This potential reduction is large relative to other global pools and fluxes of K. For example, terrestrial plant biomass stores about 5×10^{17} g of C (Schlesinger 1997). Assuming an average C:K ratio of ~ 250 (estimated from the whole-tree data of Woodwell et al. 1975), the global pool of K in plant biomass is $\sim 2 \times 10^{15}$ g. Annual K requirements by vegetation can be roughly approximated using an annual Global NPP of 6×10^{16} g of C (Schlesinger 1997, 2004) and a C:K of ~ 50 in leaves (Bowen 1966, Thompson et al. 1997), yielding an annual global K requirement of $\sim 1.2 \times 10^{15}$ g/yr.

Plant uplift thus maintains a K pool in the top 20 cm of soil that is roughly four times more than the annual plant growth requirement globally. Such a result demonstrates the importance of plant cycling in maintaining a biologically active nutrient pool that is sub-

stantially larger than the material contained solely in plant biomass.

A LOOK TO THE FUTURE

We have shown how plant uplift can affect the vertical distribution of soil nutrients within decades in newly colonized substrates and after vegetation change. Plant uplift and recycling form the foundation for such applied practices as phytoremediation and heavy metal reclamation (e.g., Keller et al. 2003), where particular plant species are used to accumulate elements in their tissue, as well as in mixed- and inter-cropping systems (Young 1997), where relatively shallow and deep rooted species are grown together. However, nutrient uplift by plants occurs in all terrestrial systems, counterbalancing the downward transport of nutrients by leaching and redistributing elements made available by weathering underground.

Although plants alter nutrient distributions substantially, as shown here by our experiments and global analyses, several questions need to be answered to place the importance of nutrient uplift in the context of other factors. Why are trees in humid forests, often limited by nutrients, sometimes unable to tap and uplift nutrients from deeper sources (Kennedy et al. 2002, Poszwa et al. 2002), as horsetail plants do in the tundra (Marsh et al. 2000) or shrubs do in encroached grasslands (Jackson et al. 2002)? To what extent is plant uplift counterbalanced by surface erosion? If erosion rates are high, uplift may favor nutrient losses by exposing higher amounts of nutrients in the surface soil. The broader issue here is to understand what constrains nutrient losses in terrestrial ecosystems, including the balance of inorganic and organic fluxes (Perakis and Hedin 2002). Such questions may be best approached using ecosystem simulation models that combine plant uplift with other nutrient transport process in a quantitative framework (see Dijkstra and Smits 2002). Mod-

el simulations that examine several nutrients with contrasting influences from plant uplift (e.g., Fe and Mn in our eucalyptus study, or K and Na in general) should be combined with information on stoichiometric ratios in plants, soils, and soil and stream water.

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