Soil nutrient–landscape relationships in a lowland tropical rainforest in Panama

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Abstract

Soils play a crucial role in biogeochemical cycles as spatially distributed sources and sinks of nutrients. Any spatial patterns depend on soil forming processes, our understanding of which is still limited, especially in regards to tropical rainforests. The objective of our study was to investigate the effects of landscape properties, with an emphasis on the geometry of the land surface, on the spatial heterogeneity of soil chemical properties, and to test the suitability of soil–landscape modeling as an appropriate technique to predict the spatial variability of exchangeable K and Mg in a humid tropical forest in Panama. We used a design-based, stratified sampling scheme to collect soil samples at 108 sites on Barro Colorado Island, Panama. Stratifying variables are lithology, vegetation and topography. Topographic variables were generated from high-resolution digital elevation models with a grid size of 5 m. We took samples from five depths down to 1 m, and analyzed for total and exchangeable K and Mg. We used simple explorative data analysis techniques to elucidate the importance of lithology for soil total and exchangeable K and Mg. Classification and Regression Trees (CART) were adopted to investigate importance of topography, lithology and vegetation for the spatial distribution of exchangeable K and Mg and with the intention to develop models that regionalize the point observations using digital terrain data as explanatory variables. Our results suggest that topography and vegetation do not control the spatial distribution of the selected soil chemical properties at a landscape scale and lithology is important to some degree. Exchangeable K is distributed equally across the study area indicating that other than landscape processes, e.g. biogeochemical processes, are responsible for its spatial distribution. Lithology contributes to the spatial variation of exchangeable Mg but controlling variables could not be detected. The spatial variation of soil total K and Mg is mainly influenced by lithology.

Keywords: Soil chemical properties; Lowland tropical rain forest; Soil–landscape relationships

1. Introduction

Soils act as spatially distributed sources and sinks of nutrients, and the concomitant spatial patterns appear to be very variable in forest ecosystems in general and in tropical forests in particular (Silver et al., 1994; Burghouts et al., 1998; Wilcke et al., 2001) and many variables interact and contribute to the spatial distribution of soil chemical properties. Tropical forest soils have been studied for many decades (Milne, 1935; Sánchez, 1976; Baillie, 1989; Richter and Babbar, 1991), but their genesis and functioning have not been fully understood yet. Our understanding of the functioning of tropical forests and of their ecological organization will undoubtedly improve once we identify the environmental factors that control the spatial pattern of soil nutrients.

Various studies investigated relationships between soil chemical properties and landscape features using advances in soil–landscape modeling (e.g., Moore et al., 1993; Gessler et al., 1995; Florinsky et al., 2002; Park and Burt, 2002; Baxter and Oliver, 2005; Henderson et al., 2005), but few dealt with the tropics (e.g., Holmes et al., 2005). Soil–landscape modeling helps to predict the spatial patterns of soil properties and to regionalize point observations by quantifying the relationship between environmental variables and soil properties of interest. It relies on the applicability of Jenny’s (1941) state factor equation:

\[ S = f(cl, o, r, p, t, \ldots) \]

where every soil property (S) is a function of climate (cl), organisms (o), relief (r), parent material (p), time (t) and
possible other variables (…). This equation may be solved by varying one factor while keeping the other factors constant. Soil–landscape modeling focuses on topography as the dominant independent variable that influences the way water moves through and over the land surface, and that can aid tremendously in exploring spatial patterns of soil properties (McKenzie et al., 2000). Digital terrain analysis offers the means to re-express the vague term topography in precise, quantitative variables (Wilson and Gallant, 2000), and various statistical techniques have been developed to quantify the relationships between topography-based environmental variables and soil properties (McBratney et al., 2003). Any spatial patterns derived by these techniques, however, cannot necessarily be generalized or extrapolated geographically.

On Barro Colorado Island, Panama, a remarkably coherent picture of the ecology of a tropical lowland forest emerged thanks to a comprehensive body of work that includes geology (Woodring, 1958), topography, soils and hydrology (Dietrich et al., 1982), long-term rainfall and soil moisture records (Rand and Rand, 1982) soil nutrient dynamics (Yavitt and Wieder, 1988; Yavitt and Wright, 1996; Yavitt, 2000), and forest structure and vegetation history (Foster and Brokaw, 1996). The relationships between landscape features and soil properties have so far received less attention (Johnsson and Stallard, 1989), although a spatially explicit inventory of soil nutrients would further contribute to our understanding of the functioning and the organization of this and other tropical forest ecosystems at a soilscape level.

Hence, our objective was to elucidate the relationships between environmental variables and selected soil chemical properties and to quantify soil nutrient stocks in a spatially explicit manner. We hypothesized that selected soil exchangeable cations (K and Mg) vary with topography, lithology and vegetation, and we used explorative data analysis and Classification and Regression Trees (CART) to understand and quantify the relationships between the landscape features and exchangeable K and Mg.

2. Material and Methods

2.1. Study area

The study area is Barro Colorado Island (BCI), an island which was created when the Panama Canal was flooded, located in the Gatun Lake in the Republic of Panama (9°9′N, 79°51′W) (Fig. 1). The island comprises 1500 ha, which is covered by old growth forest and by low and tall young forest. The forest is classified as a Tropical Moist Forest in the Holdridge system (Holdridge and Budowski, 1956). Mean annual rainfall averages 2600 mm, with a pronounced dry-season between January and April (Dietrich et al., 1982). Mean annual temperature is 27 °C and the climate is classified as Tropical Monsoon [Am] in the Köppen Climate Classification (Croat, 1978). The main soils are Oxisols and Inceptisols (Baillie et al., in preparation, Soil Survey Staff, 2006). The island is formed by two geologic formations of Oligocene age (Woodring, 1958) (Fig. 2). Both formations are of sedimentary origin and subdivided into two facies, volcanic and marine. The two facies of the Bohio formation mainly consist of conglomerate composed of basaltic clasts set in a sandy volcaniclastic matrix (Johnsson and Stallard, 1989), only the volcanic facies is outlined in Fig. 2. The Caimito marine facies is primarily a foraminiferal formation of late Oligocene age (Woodring, 1958) (Fig. 2).
limestone with abundant pelecypods and the Caimito volcanic facies consists of volcaniclastic sandstone (Johnsson and Stallard, 1989). The only non-sedimentary lithology on the island is an andesite flow capping the island (Woodring, 1958). It is not younger than the Caimito formation and represents the episode of volcanic and intrusive activity between Oligocene and early Miocene. It is a non-vesicular, phenocrystic andesite with veins and vugs (Johnsson and Stallard, 1989). The main minerals of the andesite are plagioclase, clinopyroxene, orthopyroxene and magnetite whereas the veins and vugs contain quartz, calcite and zeolite (Johnsson and Stallard, 1989).

The topography on BCI is considerably contrasting and clearly related to the underlying geology (Fig. 2). The topography on the western part of the fault system is cuesta-like with the top corner of the dipslope in the NE of the hilltop, and a general gentle dip to the SW (Fig. 2) (Baillie et al., in preparation). The dipslope, which appears to be structurally controlled by the upper extant surface of the andesite flow, has several subunits, with the large gently dipping upper plateau fringed to the south and west by gently graded treads, which are separated by slightly steeper and moderately bouldery risers (Baillie et al., in preparation). There is a further low rocky riser down to the lowland on the marine sediments in the south and west (Baillie et al., in preparation). The streams are arranged in a radial pattern around the hilltop and are little incised on the andesite and the marine sedimentary dipslope terrains and deeply incised on the Bohio volcanic formation (Woodring, 1958) (Fig. 2). This formation, covering the north, northwest and an area stretching through the centre of the island, also forms the scarp element of the cuesta with steeper terrains (Baillie et al., in preparation) (Fig. 2). The Caimito volcanic formation to the east of the fault system also appears to have a slight cuesta-like form, although this is lower and less pronounced. Its slope dips towards the south and the scarp, which extends down to the lake, has a discontinuous midslope ledge.

2.2. Sampling design

We used a design-based, stratified sampling plan (Brus and DeGrujitter, 1997) with lithology, vegetation and topography as stratifying variables, along the lines of McKenzie et al. (2000). Using spatial data on lithology, vegetation and topography (stored in GIS systems), we created four lithology classes, three vegetation classes and three topography classes. Vegetation is stratifying variables, along the lines of McKenzie et al. (2000).

The density function of the TWI was used to calculate quantiles on an equal area basis, which provided the class boundaries. The combination of forest age and Topographic Wetness Index yielded in nine classes on each lithology or 36 classes for the whole study area. In order to avoid sampling in a wrong class due to dislocation in the field we applied exclusion rules. Areas smaller than 0.01 ha were excluded. This size was chosen because our GPS (Trimble Asset Surveyor v. 5.00, Model TSC1) has an accuracy of 1–10 horizontal meters. Also, a 50 m-wide buffer zone was established along all lithological boundaries, and patches within this buffer zone were excluded. This is because the lines drawn on the geologic map are not based upon visible contacts in the field and also the topography suggests that for example the andesite unit extends much further across its map boundaries on its western side (BCI Soil Survey 2006, personal observations). After application of the exclusion rules three replicates of each class were randomly drawn which resulted in 108 patches. From each patch one sampling site was also randomly selected. The sites provide the exact coordinates for sampling. The locations of the sampling sites are illustrated in Fig. 1.

2.3. Data

We used lithology, vegetation and terrain attributes (Table 1) as predictor variables. The lithology is the ultimate source of cations, the vegetation influences soil chemistry by uptake and release of nutrients, and the topography determines processes that transport nutrients along the surface. A geologic map by Woodring (1958) modified by Johnsson and Stallard (1989) already existed in digital form. Digital data on vegetation included forest age, which was inferred from a color range reflected from an aerial photograph (Svendsen et al., 2004). Topographic information was gained from a digital elevation model (DEM). We generated two sets of the same topographic variables from two different DEMs. One DEM had been generated from a 1:25,000 topographic map with 10 m contour lines by the Defense Mapping Agency on the basis of an aerial photograph. Another DEM was developed from a 1:10,000 topographic map with 6 m contour lines by Miller (1927). Both maps were transformed to DEMs in ArcInfo using the Topogrid algorithm, which is based upon the ANUDEM program by Hutchinson (1989). The selected topographic variables are listed in Table 1 with a description of their generation (software and algorithm) and detailed definitions and significances are provided by Wilson and Gallant (2000).

2.4. Field methods

During the rainy season of 2005, we located sites with a GPS device (Trimble Asset Surveyor v. 5.00, Model TSC1) and sampled five different depths of mineral soil down to 1 m: 0–5 cm, 5–25 cm, 25–50 cm, 50–75 cm and 75–100 cm, unless bedrock was encountered. We used an Eijkelkamp auger with 7 cm in diameter and drilled at three places within the site to obtain a support of 115 cm². Depth to weathered rock was determined in the field. The samples were oven dried at 60 °C.
Bulk density was measured at selected soil pits from the BCI Soil Survey 2006 (Baillie et al., in preparation) in 10 cm increments down to 50 cm and at selected sites measurements were taken in 10 cm intervals down to 1 m. Additional measurements down to 50 cm were also taken at selected sites of the study of Grimm et al. (in preparation). Measurements were conducted after the compliant cavity procedure (4A5) (Soil Survey Staff, 1996). A cylindrical hole was excavated at the zone surface to the desired depth and the excavated soil bagged, oven dried at 105°C in the lab and then weighed in order to obtain a value for the total mass. The dry soil was then wet-sieved through a 2 mm mesh and the obtained fine-earth fraction was again dried at 105°C and then weighed. The resulting hole was lined with thin plastic, water was added to a datum level and the volume of the water was measured. Soil corrections were made for weight and volume of the rock fragments (assuming a rock density of \( \rho = 2.65 \text{ g/cm}^3 \)) and bulk density was calculated as followed:

\[
BD = \frac{W_f}{V_e}
\]

where BD is the bulk density (g cm\(^{-3}\)), W\(_f\) is the oven-dry weight of <2 mm material (g), V\(_e\) is the excavation volume of <2 mm material (g cm\(^{-3}\)).

Stoniness data was taken from two different sources and the information was combined for uncertainty propagation purposes. Field estimates from the BCI Soil Survey 2006 (Baillie et al., in preparation) served as input source as well as lab measurements of rocks larger than 2 mm from the bulk density determination.

2.5. Laboratory methods

2.5.1. Exchangeable cations (K and Mg)

Exchangeable potassium and magnesium were extracted using 1M CaCl\(_2\) (Helmke and Sparks, 1996) and analyzed with an Atomic Absorption Spectrometer. Relative precision of lab methods is 17.6% for K and 19.8% for Mg.

2.5.2. Total elements (K and Mg)

Total concentrations of elements were analyzed with a HF/HClO\(_4\)-digestion method modified after Heinrichs and Hermann (1990). Samples were ground with an agate mortar. Then, between 0.15 g and 0.2 g of soil were weighed and the samples were moistened with H\(_2\)O\(_{\text{MilliQ}}\). Two milliliters of HClO\(_4\) (70%) and 6 ml of HF (40%) were added. The solutions were heated at 85°C over night. Teflon containers were then opened and the solutions were fumed off at 185°C. One milliliter concentrated HCl and 8 ml H\(_2\)O\(_{\text{MilliQ}}\) were added to the residue and the solution was heated again to 85°C over night. The cooled digestion solution was filtered and filled up to 50 ml with H\(_2\)O\(_{\text{MilliQ}}\). Samples were measured using an ICP-OES (Vista-MXP, Varian). For each element, two wavelengths were used and the one providing the better results was used (determined by intensity, symmetry and degree of interference). For K, this was 766.491 nm and for Mg, 279.553 nm. Relative precision of lab methods is 2.2%
for K and 9.4% for Mg (value is based upon three replicates on eight sites (24 samples).

2.5.3. Statistical analysis and modeling

We used the R software (R Development Core Team, 2005) for exploratory data analysis and resistant interval estimation. We used the 95% confidence interval (CI) as a measure of uncertainty in all our analyses. Nutrient stocks on a mass basis were calculated using concentration, bulk density, thickness of the soil layer and stoniness after Ellert and Bettany (1995) and Huntington et al. (1989):

\[
M_{\text{element}} = \frac{C_{\text{element}} \times BD \times T \times 10,000 \text{ m}^2 \text{ ha}^{-1} \times 0.001 \text{ Mg kg}^{-1} \times (1 - S)}{10,000 \text{ m}^2 \text{ ha}^{-1}}
\]

where \( M_{\text{element}} \) is the mass of element per unit area (Mg ha\(^{-1}\)); \( C_{\text{element}} \) is the concentration of element (kg Mg\(^{-1}\)); BD is the bulk density of the soil (Mg m\(^{-3}\)); T is the thickness of the soil layer (m); S is the stoniness of the soil (unitless).

The value for stoniness for each soil type was calculated as the sum of the field estimates from soil survey data and of the measurements from the bulk density survey:

\[
S = S_{\text{FE}} + S_{\text{BD}}
\]

where S is the stoniness (skeletal fraction \( > 2 \text{ mm}\)); \( S_{\text{FE}} \) is the stoniness from field estimations; \( S_{\text{BD}} \) is the stoniness from bulk density measurements (skeletal fraction \( > 2 \text{ mm}\)).

Variables that are a function of other variables contain two different sources of uncertainty: (1) the uncertainty of measurement and (2) the uncertainty due to spatial variation of the individual variables which are in this case stoniness and bulk density. In order to obtain the value of uncertainty due to spatial variation of the soil chemical element mass (in Mg/ha) we performed standard uncertainty propagation (Taylor, 1997) assuming that stoniness and bulk density are independent from each other, due to the fact that the measurements of bulk density did not account for fragments \( > 10 \text{ cm} \) which make up a large component in stoniness quantifications on BCI.

For model building purposes we applied the method of Classification and Regression Trees performed with the rpact-package in R (Therneau and Atkinson, 2005). CART is a non-parametric method used to explore and predict data. CART handles non-linear and non-additive relationships; it uses...
recursive partitioning of the dataset into smaller and successively homogenous subsets. Details are provided in Breiman et al. (1984), Myles et al. (2004), and De’ath and Fabricius (2000).

3. Results

3.1. Potassium

3.1.1. Exchangeable K concentrations

Exchangeable K is almost equally distributed across the whole island. Box plots conditioned by lithology illustrate that values on Andesite and Caimito volcanic are slightly lower than on Bohio volcanic and Caimito marine, but these differences are not significant except for the deepest depth (75–100 cm) where Bohio volcanic (43.9 ± 10.3) (median ± 95% CI) is significantly higher than andesite (21.7 ± 11.9) (Fig. 3).

On all lithologies, the concentration of exchangeable K decreases significantly with increasing depth between the topsoil (0–5 cm) and the mineral soil (>5 cm).

Table 2 compares mean exchangeable K concentrations on BCI with those from other tropical lowland forests across Central and South America and Taiwan. The table shows that the nutrient status on BCI is on the upper end of nutrient concentrations in regard to exchangeable K, similar to the sites in Nicaragua (Blair, 2005), slightly higher than Taiwan (Chen et al., 1997) and much higher than the sites in Paragominas and Belem, Para, Brazil (Mackensen et al., 2000; Markewitz et al., 2001).

3.1.2. Total K concentrations

The total K concentration varies with lithology (Fig. 4), with a concentration almost twice as high on the volcanic facies of the Bohio formation than on the other lithologies. However, the dot plots illustrate that these differences are not significant between the mineral soil (>5 cm) of the Bohio volcanic facies and andesite, between the depth from 5 to 25 cm on Bohio volcanic and Caimito marine and between the deepest depth from 75 to 100 cm on Bohio volcanic and all other lithologies, which is due to the wide confidence intervals of K values on Bohio volcanic (Fig. 4). There is a slight downward trend with decreasing concentrations across the island but this trend is not significant (Fig. 4).

3.1.3. Exchangeable and total K stocks

The mean content of exchangeable K on BCI in the upper 50 cm is 0.25 ± 0.03 Mg/ha (mean ± one-half CI). On all lithologies except on the Caimito volcanic formation, the stocks increase to a depth of 25 cm and then decrease again down to 50 cm (Table 3). The mean content of total K in the upper 50 cm is 5.2 ± 1.0 Mg/ha (mean ± one-half CI). In the uppermost 0.5 m, the total K stock increased with depth in the following intervals: 0–5 cm; 5–25 cm and 25–50 cm (Table 3).

3.1.4. Regression Tree Models

The Regression Tree Models which we developed for every depth with concentration of exchangeable K as response...
variable explained 0, 4, 13, 1 and 8% (for 0–5 cm, 5–25 cm, 25–50 cm, 50–75 cm and 75–100 cm, respectively) of the spatial variability with the soil class being the most important predictor (Table 4). Topography and forest age explained only a negligible fraction and none of the spatial variation, respectively (Table 4).

3.2. Magnesium

3.2.1. Exchangeable Mg concentrations

The concentrations of exchangeable Mg are up to 10 times higher than those of exchangeable K (Figs. 3 and 5), exchangeable Mg, however, is not equally distributed throughout the study area (Fig. 5). Box plots of exchangeable Mg, again conditioned by lithology (Fig. 5), illustrate that in contrast to exchangeable K concentrations there is a large range in measured exchangeable Mg values within each lithology. The lowest concentrations are on andesite and Caimito volcanic, which are alike, and the highest values are on Bohio volcanic and Caimito marine, which are also alike. However, concentrations on Bohio volcanic are significantly higher than on andesite and Caimito volcanic, while concentrations on Caimito marine are only significantly higher than on Caimito volcanic excluding the uppermost 5 cm (Fig. 5).

There is a downward trend with decreasing concentrations but differences are only significant on Caimito volcanic.

Table 5 lists mean exchangeable Mg concentrations of BCI in comparison with mean exchangeable Mg concentrations from other tropical lowland forests across Central and South America, Hawaii and Taiwan. The table shows that exchangeable Mg concentrations on BCI are similar to K at the upper end of the concentration range across the tropics: similar to the sites in Panama and Colombia (Golley, 1986) but exceeding the sites in Hawaii (Scowcroft et al., 2004), and by far those in Brazil (Mackensen et al., 2000; Markewitz et al., 2001) and Taiwan (Chen et al., 1997).

3.2.2. Total Mg concentrations

Values of total Mg concentrations have large ranges on all lithologies except on Caimito volcanic but highest values are found on Bohio volcanic and Caimito marine (Fig. 6). However, the dot plots illustrate that these differences are not significant from the lower values on andesite and Caimito volcanic. Total Mg concentration does not change with depth.

3.2.3. Exchangeable and total Mg stocks

The mean content of exchangeable Mg is 3.0 ± 0.3 Mg/ha (mean ± one-half CI). In contrast to the exchangeable K stocks, exchangeable Mg increases continuously from 0 to 50 cm (Table 6). The mean content of total Mg is 25.8 ± 5.1 Mg/ha (mean ± one-half CI). The total Mg content in the uppermost 0.5 m increases with depth in the following intervals: 0–5 cm; 5–25 cm and 25–50 cm (Table 6).

3.2.4. Regression Tree Models

The Regression Tree Models for exchangeable Mg concentrations yielded slightly better results than for exchangeable K and explained 0, 23, 33, 47 and 33% (for 0–5 cm, 5–25 cm,
25–50 cm, 50–75 cm and 75–100 cm, respectively) of the spatial variability (Table 7). Again, soil class was the most important variable. More importantly, topography and forest age explained only little to none of the spatial variability (Table 7).

4. Discussion

4.1. Differences in exchangeable cation concentrations within the tropics

The soils of BCI are, regarding exchangeable K and Mg, as fertile as other soils in Central America and Taiwan and more fertile than soils in the Amazon basin. This may be accredited to the younger geological history of the Isthmus of Panama, which formed only 3.1–2.8 million years ago (Coates and Obando, 1996) and therefore supports a younger landscape with shallower and presumably less weathered soils than in the continental tropics of the Amazon Basin.

4.2. Exchangeable cations

Exchangeable K is bound to the outer surfaces of clay minerals and humic substances (Helmke and Sparks, 1996). The decreasing exchangeable K concentrations with depth show the same trend as the organic carbon concentrations on BCI (Grimm et al., in preparation). This suggests that exchangeable K is preferentially bound to humic substances. On BCI, exchangeable K resources are limited (S.J. Wright, personal communication). The higher values of exchangeable K in the topsoil than in the subsoil suggest that plants obtain the bulk of their K from the topsoil and that in soils with limited cation concentrations the recycling processes mainly take place in the topsoil.

These results are in line with the exchangeable Mg results. In contrast to K, Mg is not a limited nutrient on BCI. The exchangeable Mg concentrations do not show such a significant trend with increasing depth except on the Caimito volcanic facies. This emphasizes the fact that recycling processes in soils with limited nutrients take place in the topsoil, from which the plants mainly obtain their nutrients.
4.3. Total cations

The total concentration of cations comprises four different forms in which the cations exist: solution, exchangeable, fixed (or non-exchangeable) and mineral (or structural). The fixed form is that portion of K, that is held between adjacent tetrahedral layers of dioctahedral and trioctahedral micas, vermiculites and integrate clay minerals such as chloritized vermiculite whereas the mineral form of K is bonded within the crystal structure of soil mineral particles (Helmke and Sparks, 1996). Helmke and Sparks (1996) mention that 98% of the total concentration belongs to the mineral form. The spatial distribution of total cation concentrations might therefore be closely linked to the underlying lithology and its mineral composition. Table 8 provides a summary of the rock types and their mineral and chemical composition. The abundance of total K in the soils developed on Bohio volcanic results from the mineral composition of this formation, which includes hornblende. Andesite, Caimito volcanic and marine all are made up of minerals that contain only little or no K, which is reflected in the total K concentration of the soils (Fig. 6).

The spatial distribution of total Mg concentrations can also be explained by the mineral composition of the rock types of the different formations. Fig. 6 illustrates that total Mg concentrations are highest on Bohio volcanic and Caimito marine and lowest on Andesite and Caimito volcanic. The magnesium sources for the pool in Bohio volcanic soils are the abundant minerals hornblende and clinopyroxene. On the Caimito marine facies the high Mg concentrations may stem from a magnesium-containing calcite. Although there are no studies on the chemical composition of this mineral on BCI, the age of this formation refers to a time when the Mg$^{2+}$/Ca$^{2+}$-ratio in seawater were high, which is accredited to a change in volume of the mid-Atlantic ridge zone to smaller values, and which led to precipitation of calcite where Mg$^{2+}$ replaces Ca$^{2+}$ in the crystal structure (Stanley, 1999). This mechanism is today expressed in high total Mg concentrations in the soils on the Caimito marine facies.

The slightly higher Mg values on andesite than on Caimito volcanic may be attributed to the andesite containing clinopyroxenes, orthopyroxenes and zeolites (Table 8) whereas the Caimito volcanic facies does not contain any minerals that are made of Mg.

There is abundant evidence that suggests that total nutrient concentrations are controlled by lithology, however, we cannot put any numbers on the chemical composition of the rock types.

4.4. Relationships between soil chemical properties and landscape features

Besides assessing nutrient pools on BCI, the second aim of this study was to investigate the spatial distribution of K and Mg, and to determine the importance of soil–landscape relationships for a lowland tropical rain forest soil chemistry. Johnsson and Stallard (1989) describe the contrasting landscapes on BCI where flat terrains with low landscape gradients are developed on two contrasting lithologies, on the Andesite...
flow and the volcanic sediments of the Caimito volcanic facies, and steeper terrains are developed on Bohio volcanic and Caimito marine facies. They conclude from the composition of stream sediments derived from different terrains that steeper terrains are weathering-limited and support soils that are shallower and richer in cations than soils that are located on the flatter, transport-limited terrains. Our results are not consistent with these conclusions and we need to discuss the two cations of interest separately.

Our exchangeable Mg results (Fig. 5) are in line with the findings of Johnsson and Stallard (1989): Mg concentrations differ according to lithology and values are higher on the deeply dissected terrains of Bohio volcanic and Caimito marine, if only just significantly different from Bohio volcanic. It is therefore surprising that the topography does not emerge as a controlling factor in the regression trees. There are several reasons that might explain the weakness of the relationships between the topography and spatial variation of exchangeable Mg:

First, two different sets of the same terrain attributes were generated from two different DEMs that we used to quantify the relationship between topography and soil chemical properties. Each DEM was developed from a different source of topographic information, and their qualities and potentials in reflecting the true landform vary. One DEM was generated from a 1:25,000 m topographic map by the Defense Mapping Agency that was made from an aerial photograph. Many subtleties of the earth surface are not shown due to the lush vegetation on BCI, which often obscures topographic irregularities (Johnsson and Stallard, 1989). The second DEM was developed from a 1:10,000 m topographic map by Miller (1927). The map is developed on a finer scale but it is hand drawn and can only be as good as the human perception of the environment is. Therefore, not every point in the study area may truly represent the form of the earth surface.

Secondly, processes that are responsible for spatial variation of soil chemical properties might take place on a smaller scale than the one captured with our DEM. Overland flow, which is thought to play an important role in surface processes that erodes and accumulates material, does not occur uniformly across the island (Godsey et al., 2004). In theory, various factors such as rain intensity, depth to an impermeable soil layer and topography influence the generation of overland flow. Topographic variables such as slope, size of catchment area and topographic wetness index, are thought to determine overland

Fig. 5. Grouped boxplots of exchangeable Mg concentration on each of the four lithologies, the notches represent 95% confidence intervals around the median. Sample sizes range from 10 to 27.
flow generation and are used to identify spatial patterns of overland flow. Godsey et al. (2004) though found that overland flow generates already at shallow slopes and small catchment areas, primarily along microtopographic features such as concentrated flow lines and wash areas instead of following topographic gradients outlined by the DEM. Pipeflow mechanisms might be responsible for these spatial variations. If such microtopographic features as concentrated flow lines and wash areas determine the generation of overland flow rather than topographic features such as slope, catchment area and wetness index, then it is also difficult to capture the mechanisms that are responsible for the spatial patterns of exchangeable nutrients. This implies that the resolution of our DEM is too coarse to capture those processes that are controlled by microtopography.

A careful examination of the box plots in Fig. 3 reveals a slight trend with higher values of exchangeable K on the steeper terrains of Bohio volcanic and Caimito marine, but the differences are not significant from the Andesite and Caimito volcanic facies. Therefore, it is not surprising that the Regression Tree Models using lithology and terrain attributes explain only little to none of the variation of exchangeable K. Various factors that may explain the weakness of the relationships between landscape features and exchangeable Mg have been mentioned above and may be true for exchangeable K as well.

A more likely possibility for the explanation of the weak relationships between landscape features and exchangeable K is that biogeochemical processes have a large impact on the distribution of exchangeable K in the soil. Potassium is a very labile element and its biogeochemical cycle has been investigated and described in many studies (Vitousek and Sanford, 1986; Likens et al., 1994; Tobón et al., 2004). Potassium is being leached from green leaves during rainfall (Wilcke et al., 2001; Tobón et al., 2004). However, a larger amount of K is stored in the litter fall and returned to soil via litter leachate (Wilcke et al., 2001; Tobón et al., 2004). Loos et al. (unpublished results) confirm this process for BCI where they found that the amount of K that actually reaches the soil via litter leachate is much larger than what is being leached via through fall. Most of the K that is recycled in the plant-water-soil system and leaves the living plant is accumulated in the litter and returns to the soil. Yavitt et al. (2004) reported that residence time of K is short in the leaf litter and suggest rapid

| Cart results | Exchangeable Mg (mg/kg) in 0–5 cm | – | 1.02 |
| Predictor variables | Exchangeable Mg (mg/kg) in 5–25 cm | Soil type | 0.77 |
| Cross-validated error | Exchangeable Mg (mg/kg) in 25–50 cm | Soil type | 0.67 |
| | Exchangeable Mg (mg/kg) in 50–75 cm | Soil type | 0.53 |
| | Exchangeable Mg (mg/kg) in 75–100 cm | Soil type | 0.67 |

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<tr>
<th>Exchangeable and total Mg stocks (Mg/ha) (mean ± one-half CI)</th>
<th>Depth (cm)</th>
<th>Exchangeable Mg</th>
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<td>Bohio v. Caimito m.</td>
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</tr>
<tr>
<td>0–5</td>
<td>0.55 (0.18)</td>
<td>0.63 (0.27)</td>
<td>0.62 (0.27)</td>
</tr>
<tr>
<td>5–25</td>
<td>1.39 (0.53)</td>
<td>1.20 (0.39)</td>
<td>1.09 (0.32)</td>
</tr>
<tr>
<td>25–50</td>
<td>1.43 (0.58)</td>
<td>1.42 (0.51)</td>
<td>1.22 (0.31)</td>
</tr>
<tr>
<td>0–50</td>
<td>3.06 (0.18)</td>
<td>2.78 (0.26)</td>
<td>2.84 (0.24)</td>
</tr>
</tbody>
</table>

Fig. 6. Dot plots of total Mg distribution on the four lithologies on Barro Colorado Island. The empty circles represent the value of each sample, the filled circles represent the median and the crosses represent the lower and upper 95% confidence limits. Sample sizes range from 9 to 12.

Table 8
Summary of rock types and their mineral and chemical composition of the different formations (compiled from Johnsson and Stallard, 1989)

<table>
<thead>
<tr>
<th>Formation</th>
<th>Rock type</th>
<th>Main minerals</th>
<th>Chemical composition a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andesite</td>
<td>Non-vesicular, phenocrystic andesite with veins and vugs</td>
<td>Plagioclase (feldspar group)</td>
<td>( nNa[AlSi_3O_8] + nCa[Al_2Si_3O_8] )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Clinopyroxene</td>
<td>( (Ca, Mg, Fe, Al)_2(Si, Al)_3O_8 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Orthopyroxene</td>
<td>( (Mg, Fe)SiO_3 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Magnetite</td>
<td>( Fe_3O_4 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Veins and vugs</td>
<td>( SiO_2 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quartz</td>
<td>( CaCO_3 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Calcite</td>
<td>( CaCO_3 )</td>
</tr>
<tr>
<td>Bohio volcanic</td>
<td>Conglomerate with basaltic clasts in a sandy volcaniclastic matrix</td>
<td>Clasts</td>
<td>( nNa[AlSi_3O_8] + nCa[Al_2Si_3O_8] )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plagioclase</td>
<td>( (Ca, Na, K)_{2.5}(Mg, Fe, Al)_3[OH, F]_2(Si, Al)<em>2Si_6O</em>{22} )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hornblende (amphibole group)</td>
<td>( (Ca, Mg, Fe, Al)_2(Si, Al)_3O_8 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Clinopyroxene</td>
<td>( (Ca, Mg, Fe, Al)_2(Si, Al)_3O_8 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Matrix:</td>
<td>( (Na, Ca)[Al_2Si_2O_6] )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Volcanic lithic fragments</td>
<td>( Fe_3O_4 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plagioclase</td>
<td>( CaCO_3 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Amphibole</td>
<td>( CaCO_3 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Magnetite</td>
<td>( CaCO_3 )</td>
</tr>
<tr>
<td>Caimito marine</td>
<td>Foraminiferal limestone with abundant pelecypods</td>
<td>Vitric volcaniclastic debris</td>
<td>( nNa[AlSi_3O_8] + nCa[Al_2Si_3O_8] )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Calcite</td>
<td>( SiO_2 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plagioclase</td>
<td>( SiO_2 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Quartz</td>
<td>( SiO_2 )</td>
</tr>
<tr>
<td>Caimito volcanic</td>
<td>Volcaniclastic sandstone (basaltic agglomerate and tuffaceous graywackes)</td>
<td>Volcanic lithic fragments</td>
<td>( nNa[AlSi_3O_8] + nCa[Al_2Si_3O_8] )</td>
</tr>
</tbody>
</table>

a From Berry et al. (1983).
b \( M \), alkali or alkaline atom; \( n \), charge on that atom; \( x \), a number from 2 to 10; \( y \), a number from 2 to 7.
mineralization. Although plants may take up K directly from leaf litter, the more important mechanism seems to be uptake from the mineral soil after leaching from the litter layer. We conclude that K is recycled fast and efficient in the tropical rain forest ecosystem on BCI and that the importance of topographic processes for its spatial variation is confounded by these biogeochemical processes.

Finally, vegetation features might play a more important role than topography and lithology. We did include forest age as a variable that characterizes differences in species composition due to different stages of forest succession, and in forest structure (Foster and Brokaw, 1996). But these differences are now rather subtle (Foster and Brokaw, 1996) and therefore forest age as a variable characterizing forest structure is too general. For example, Chen et al. (1997) attributed the spatial variation of exchangeable K to variables such as canopy height, average basal area and density. Goodland and Pollard (1973) reported strong correlations between vegetation structure (height, basal area and density) and soil N, P and K contents in the cerrado vegetation of Brazil. This suggests that vegetation features may confound the importance of the topography.

Studies relating topography and nutrient availability often show contradictory results. Although a few studies could establish a link between topography and the spatial pattern of soil exchangeable cations, e.g. Chen et al. (1997) and Silver et al. (1994), others could not, e.g. Johnson et al. (2000), Scowcroft et al. (2004) and Wilcke et al. (2001). Our study belongs to the latter group. The contradictory results may be attributed to different processes in response to specific environmental features discussed in the individual studies. Scale is likely to be another issue. Chen et al. (1997) and Silver et al. (1994) conducted their studies at the hillslope and the catchment scale, with an extent of 10 ha and 12 ha (two catchments), and sample sizes of \( n = 40 \) and \( n = 87 \), respectively. In contrast, Johnson et al. (2000) study was conducted at the catchment scale with an extent of 214 ha and a sample size of \( n = 72 \), and our study was conducted at the landscape scale with an extent of 1500 ha and 108 samples. The ratio of sample size to extent is much larger in the former two studies than in the latter.

Our results clearly show that topography does not control the spatial variation of exchangeable K and Mg in the tropical forest soilscape of Barro Colorado Island at the observed scale. Though, it is not impossible, that microtopography or the topography at a scale smaller than the one we captured with our DEM might be important for the spatial distribution of the observed soil chemical properties.

5. Conclusions

We investigated the spatial distribution of total and exchangeable magnesium and potassium and its relationship to terrain attributes at the landscape scale. This relationship turned out to be weak for various possibilities, such as microtopography (in the case of exchangeable Mg), whose features go undetected at the resolution of our DEM, or biogeochemical processes unrelated to topography (in the case of exchangeable K). Fast nutrient recycling may well mask any effects of topography, which would explain the lack of terrain attributes’ predictive power of spatial patterns. The spatial distribution of total cation concentrations does not depend on the topography, but on lithology only. The apparent lack of a strong relationship between terrain attributes and the selected soil properties suggests that rather simple sampling designs are adequate to estimate the spatial mean of these and related nutrients on Barro Colorado Island and similar soilscales. Our results prompt us to view critically the predictive power of terrain attributes for soil properties at the observed scale.

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References


