Chapter 12
Altitudinal Pattern of Soil Organic Carbon and Nutrients in a Tropical Forest in Puerto Rico

Dingfang Chen, Mei Yu, Grizelle González, and Qiong Gao

12.1 Introduction

Tropical forests have the highest net primary productivity (Chapin et al. 2012) and soil carbon flux (Silver 1998); thus, they play an important role in global C dynamics and changes in climate. Soil physical and chemical properties are essential in influencing soil respiration and plant nutrient status (Valentina et al. 2019), and they vary significantly in tropical forests (Cox et al. 2002; Diekmann et al. 2007; Hutchings et al. 2003; de Souza et al. 2018). Soil age, parent material, disturbance history, vegetation type, and climatic conditions cause considerable temporal and spatial variations in soil physicochemical properties (Augusto et al. 2017; Jackson and Caldwell 1993; Tsui et al. 2004). Such variations in soil properties, especially soil clay content (Müller and Höper 2004), soil organic carbon (SOC), and temperature-moisture conditions (Wan et al. 2007), have been well reported to have significant effects on soil respiration (Chen et al. 2017; Griffiths et al. 2009; Raich and Tufekciogul 2000). Soil texture can affect soil organic matter (SOM) decomposition rate, that is, soil heterotrophic respiration rate, by altering soil water availability, nutrient availability, and surface area (Scott et al. 1996). Using soil laboratory incubations, Scott et al. (1996) concluded that the effects of soil texture combined with soil water pressure influenced decomposition rates significantly. Soil retention characteristics were found to impact the soil microbe respiration (Ghezzehei et al. 2019). From an extensive literature review, Müller and Höper (2004) studied the relationship between soil clay content and SOM turnover rate and concluded that

D. Chen · M. Yu (✉) · Q. Gao
Department of Environmental Sciences, University of Puerto Rico, Río Piedras, San Juan, PR, USA
e-mail: meiyu@ites.upr.edu

G. González
International Institute of Tropical Forestry, USDA Forest Service, San Juan, PR, USA

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soil clay content strongly related to soil respiration rate through soil microbial biomass (Müller and Höper 2004).

Climate change affects SOC (Davidson and Janssens 2006; Kirschbaum 2006), especially in the tropics, although it is still on debate whether tropical soils respond as a carbon sink or source to the increased atmospheric carbon dioxide (CO_2) and global warming (Malhi et al. 2004; Trumbore and Czimczik 2008). Forest soil is also one of the most important sources of nutrients, such as N, P, S, K, Na, Ca, and Mg, for vegetation (Tsui et al. 2004). Therefore, it is ecologically significant to study the patterns of tropical soil properties in the context of global climate change, especially considering that tropics accounts for about 11% of the world's soil C, and contributes 46% of the world's living terrestrial C (Silver 1998).

The Luquillo Experimental Forest (LEF) is a tropical wet montane forest. With the changes in temperature and moisture conditions along the altitudinal gradient, the vegetation displays a distinct distribution pattern from lower altitude to the summit. The altitudinal range in the LEF provides a natural gradient to understand the patterns of soil properties driven by long-term changes in tropical forest ecosystems. In this study, we collected soil samples at a tropical elevation gradient and measured soil physical properties, including soil particle size distribution, bulk density, and moisture content, and soil C, macro- and micronutrients along the elevation gradient. We hypothesized that most of these properties depend significantly on both elevation and vegetation type. We analyzed soil physicochemical characteristics along the altitudinal gradient and then discussed the impacts of climate change on tropical soils, particularly on soil carbon processes.

12.2 Methods and Materials

12.2.1 Field Sites

All the experiment plots were in the Luquillo Experimental Forest (LEF) (18°20′N, 65°49′W), northeastern Puerto Rico (Fig. 12.1). The mean monthly temperature ranges from 23.5 °C in January to 27 °C in September at low elevation, while it ranges from 17 to 20 °C at high elevation (Garcia-Martinó et al. 1996). Rainfall increases with altitude, ranging from an average of 3537 mm per year at low altitude to 4849 mm per year at high altitude (Garcia-Martinó et al. 1996). With the abundant annual rainfalls, moisture is generally not a limiting factor for vegetation growth. The soils in the LEF are mainly derived from volcaniclastic sediments, except for one high-altitude area where the soils are from quartz diorite (Barone et al. 2008). From low to high elevation, four typical forests with distinct dominant species and structures are distributed in LEF: tabonuco forest, palm forest, palo colorado forest, and elfin woodland (Gould et al. 2006; Weaver 2000) (Table 12.1).

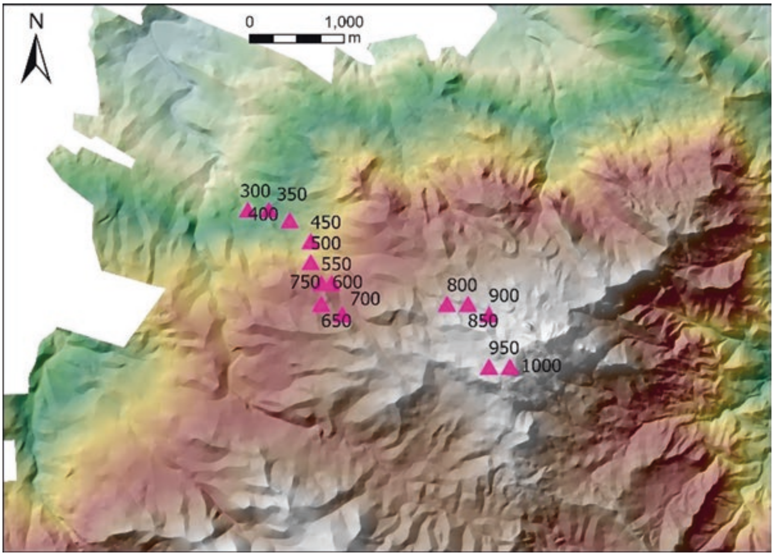

Fig. 12.1 Distribution of the 15 experiment plots along an altitudinal gradient, 300–1000 m, within the Luquillo Experimental Forest in northeast Puerto Rico

12.2.2 Soil Sampling and Lab Analysis

12.2.2.1 Soil Sampling

We collected the soil samples from 15 plots evenly distributed along the altitudinal gradient, that is, 300–1000 m a.s.l., of the LEF in July 2009, and each plot is 20 m by 50 m (Table 12.1). Before collecting soil samples, we removed all the coarse litter debris and organic matters from the surface. For soil extractable nutrients and SOC analyses, we collected for each plot five soil samples, each of which composed of three soil cores of 5 cm in diameter and 15 cm in depth, using a cylindrical soil corer. For soil texture analysis, we collected three soil samples, each separated into two depths of 0–15 cm and 15–30 cm, with a stainless corer (diameter of 1.68 cm) from each plot.

12.2.2.2 Soil Bulk Density (Db) and Soil Water Content (WC)

All the soil samples were oven-drying at 105 °C for 48 h to constant weight. We recorded the weights of both fresh soil samples and oven-drying samples. Soil bulk density (Db, g cm^{-3}) was calculated as the oven-drying soil weight in g divided by the bulk volume of soil solid in cm^3, and soil water content (WC, %) was calculated

Table 12.1 Geographic coordinates of the 15 experiment plots distributed along the altitudinal gradient (from 300 to 1000 m) with three vegetation types in the Luquillo Experimental Forest, Puerto Rico

Plot	Altitude (m)	Latitude	Longitude	Forest type
1	300	18.323	−65.820	Tabonuco
2	350	18.323	−65.818	Tabonuco
3	400	18.322	−65.816	Tabonuco
4	450	18.320	−65.814	Tabonuco
5	500	18.318	−65.814	Tabonuco
6	550	18.316	−65.813	Tabonuco
7	600	18.316	−65.813	Tabonuco/Palo Colorado
8	650	18.314	−65.813	Palo Colorado
9	700	18.313	−65.811	Palo Colorado
10	750	18.316	−65.812	Palo Colorado
11	800	18.314	−65.801	Palo Colorado
12	850	18.314	−65.799	Palo Colorado
13	900	18.313	−65.797	Palo Colorado
14	950	18.308	−65.797	Elfin
15	1000	18.308	−65.795	Elfin

as the difference between fresh weight and oven-drying weight divided by the oven-drying weight.

12.2.2.3 Soil pH and Particle Size

After oven-drying at 105 °C for 24 h to nearly constant weight, the dry soil samples were crushed and sieved with a 10 mesh sieve to remove coarse organic materials and gravels. Then, we measured pH values with an advanced thermo pH meter (Orion 350 PerHect benchtop pH meter with ROSS Micro pH electrode and ATC probe, Thermo Scientific®, Waltham, MA, U.S.A) through a standard procedure (Mclean 1982). We measured the pH values in both water solution and 1 mol L^{-1} potassium chloride solution. The sample preparation for particle size analysis was the same as that for soil pH analysis. The concentration of soil particles with different sizes was measured with a buoyancy soil hydrometer (ASTM 152H, Thermo Scientific ERTCO®, Waltham, MA, U.S.A) through a standard method used by Soil Science Society of America (Dane and Topp 2002). This method is based on the principle that the sedimentation speed in a soil-water suspension varies with different soil particle size and their concentrations (Stokes' law) (Dane and Topp 2002). By calculating the relative solution density at a certain time, the relative proportion of various soil particles can be extrapolated. The proportions of sand, clay, and silt (%) are determined by the following equations:

$$\textbf{sand} = 100 - \left(R_{40\text{s}} - R_{\text{L}1}\right) \times \left(\frac{100}{\text{Sample weight}}\right) \tag{12.1}$$

$$\textbf{clay} = \left(R_{7\text{h}} - R_{\text{L}2}\right) \times \left(\frac{100}{\text{Sample weight}}\right) \tag{12.2}$$

$$\textbf{silt} = 100 - \left(\text{sand} + \text{clay}\right) \tag{12.3}$$

where R_{40s} is hydrometer reading in soil suspension at 40 s in g L^{-1}; $R_{L1,2}$ is hydrometer reading of blank solution at the measurement time in g L^{-1}; R_{7h} is hydrometer reading in soil suspension at 7 h in g L^{-1}; and the unit of sample weight is g.

The buoyancy hydrometer was calibrated at 20 °C. While calculating soil particle proportions, the hydrometer readings were adjusted by adding 0.2 g L^{-1} per degree of the difference in temperature.

12.2.2.4 SOM and Soil Extractable Nutrients

After air-drying for 1 week, the soil samples were oven-drying to constant mass at 50 °C, and then ground and passed through a 20 mesh sieve. We removed stones, coarse root detritus, and other organic materials before further analyses. All the soil physicochemical properties including total organic carbon (*TC*), total nitrogen (*TN*), loss on ignition (*LOI*), and extractable nutrient elements such as aluminum (Al), calcium (Ca), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), and phosphorus (P) were measured at International Institute of Tropical Forestry (IITF), USDA Forest Service, in Río Piedras, Puerto Rico. All the extractable nutrient elements were detected using ICP-Spectro Ciros CCD (Spectro®, SPECTRO Analytical Instruments GmbH, Kleve, Germany). Soil samples to test Ca, Mg, Na, and Al contents were prepared with a standard 1N KCl extraction method of ICP-Spectro Ciros CCD, whereas the samples to test Fe, Mn, K, and P contents were prepared using Olsen-EDTA (NH4-EDTA-NaHCO3) procedure (Anderson and Ingram 1993). Total organic carbon, TN, and LOI were determined using CNS LECO-2000 Analyzer (LECO®, LECO Corporation, Michigan, U.S.A) following the protocol given in a standard procedure.

12.2.3 Statistical Analyses

We first calculated the correlations between all possible pairs of soil properties in the 15 experiment plots. Because the soil properties tend to be highly correlated, we then divided the soil properties into three groups in addition to soil organic carbon, macronutrients that include N, P, K, Ca, and Mg, micronutrients that include Al, Mn, Na, and Fe, and soil physical properties including clay, bulk density, and water content. To explore essential roles of elevation and vegetation in the distribution of soil properties, we regressed the soil physical and chemical properties on the elevation and vegetation types and all variables of soil properties were multiplied by 10 and then log-transformed before regressions. We applied multiple regression to soil C and C:N ratio and multivariate multiple regression to each of the three groups. We then applied multivariate analysis of variance to get a glimpse of the overall response of each group to elevation and vegetation type. We ran all the statistical analyses in R (R Core Team 2020).

12.3 Results

12.3.1 Soil Physical Properties

We plotted soil physical properties including soil texture, bulk density, and soil moisture content against the elevation (Fig. 12.2). Clay contents in both top- and sub-layers decrease, but soil moisture content in the top-layer increases, with the

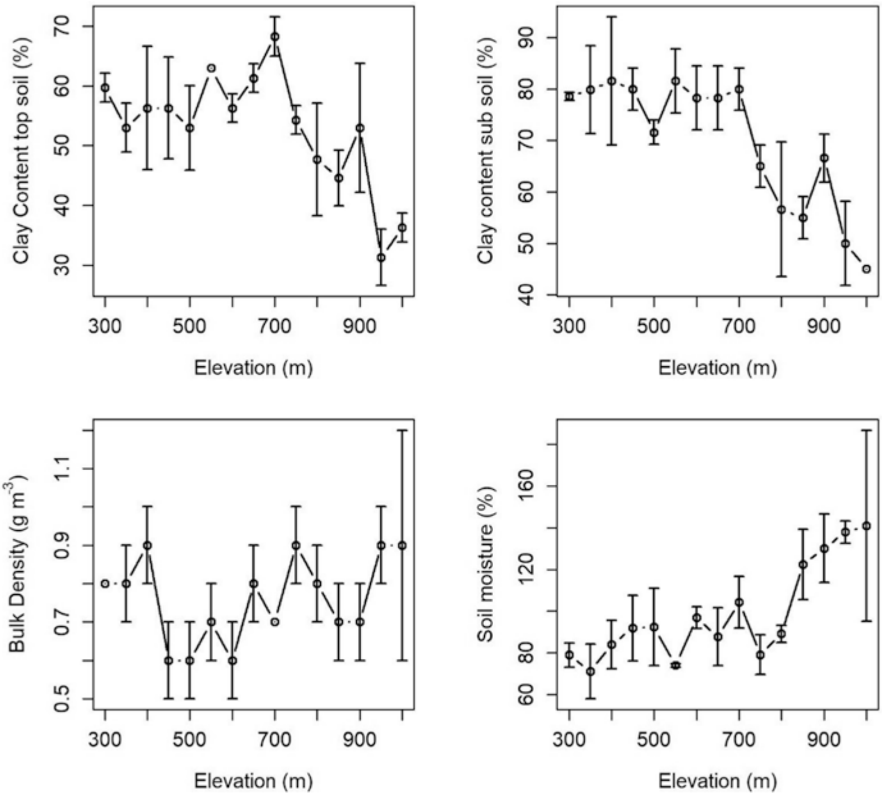

Fig. 12.2 Clay content in both top and sub-soil layers (top panels), and bulk density and soil water content in the top layer (bottom panels) in the 15 plots along the elevation gradient of 300–1000 m

Table 12.2 Multivariate multiple regression of soil physical properties on elevation

	Intercept	Elev	$Elev^2$	R^2
Clay_T	5.67[a]	2.74[a]	−2.57[a]	0.70
Db	2.35[a]	−1.31	1.07	0.17
WC	6.89[a]	−1.10	1.47[b]	0.75
Clay_S	6.48[a]	1.20	−1.54[a]	0.83

Clay_T, Db, and WC are soil clay content, bulk density, and moisture content in top-soil layer, respectively. Clay_S is soil clay in sublayer. Elev is the elevation. We did not find significant relationship between soil physical properties and the vegetation
[a] and [b], significant at 0.05 and 0.1, respectively

elevation. However, there is no obvious pattern in soil bulk density at the top-layer along the elevation gradient. The top layer and sublayer have mean clay contents of 53% and 70%, respectively, and t-test indicated that the clay content in sublayer was significantly higher than that in the top layer ($p < 0.01$, one-tailed). For the top layer, soil clay content is significantly correlated with soil water content (Pearson's correlation coefficient of −0.69). However, the soil texture and soil water content are not significantly correlated with the bulk density.

The multivariate regression showed that the soil clay content and water content significantly depend on elevation (Table 12.2). The multivariate ANOVA showed that the p-value of the Pillai statistics for elevation is 0.0003, and that of the squared elevation is 0.05. Thus, as a whole, the soil physical properties significantly depend on elevation.

12.3.2 Soil Carbon and Macronutrients

Soil carbon and macronutrients in top layer (Fig. 12.3) also showed apparent patterns with respect to elevation gradient. Carbon, nitrogen, and phosphorus tend to increase with the elevation. In contrast, potassium, calcium, and magnesium decrease with the elevation. The Pearson's correlation among the macronutrients showed that carbon was significantly correlated with nitrogen ($r = 0.94$, $p < 0.0001$) and phosphorus ($r = 0.45$, $p = 0.1$), that nitrogen was significantly correlated with phosphorus ($r = 0.54$, $p = 0.04$), and that calcium was correlated with magnesium ($r = 0.44$, $p = 0.1$).

Carbon content is an important indicator of soil carbon storage and the regressions of soil carbon content (C) and C:N ratio resulted in the following equations:

$$C = 1.52 + 1.23N + 1.10 \text{ Elev} + 0.30 \text{ Colorado} + 0.35 \text{ Tabonuco} \qquad R^2 = 0.98 \qquad (12.4)$$

$$\frac{C}{N} = 4.40 + 0.99 \text{ Elev} + 0.19 \text{ Colorado} + 0.16 \text{ Tabonuco} \qquad R^2 = 0.84 \qquad (12.5)$$

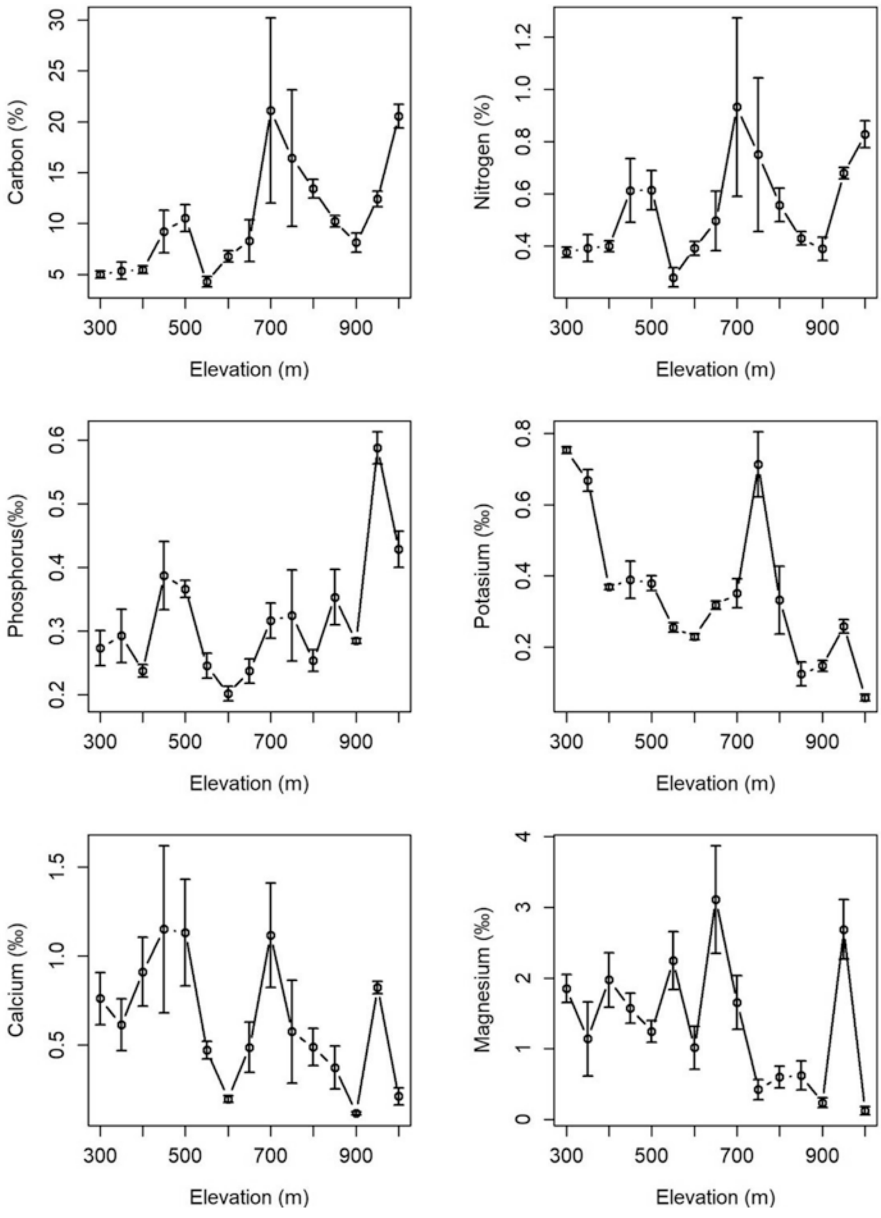

Fig. 12.3 Distribution of soil carbon and macronutrients in top-soil layer along the elevation gradient of 300–1000 m

Table 12.3 Mean and standard deviation of carbon, macronutrient, and micronutrient among different vegetation types

	Tabonuco	Palo Colorado	Elfin
C (%)	6.6 ± 2.4	12.9 ± 5.1	16.5 ± 5.8
N (%)	0.44 ± 0.13	0.59 ± 0.21	0.75 ± 0.10
P (mg g^{-1})	0.29 ± 0.07	0.29 ± 0.04	0.51 ± 0.11
K (mg g^{-1})	0.43 ± 0.20	0.33 ± 0.21	0.16 ± 0.14
Ca (mg g^{-1})	0.75 ± 0.35	0.52 ± 0.33	0.52 ± 0.43
Mg (mg g^{-1})	1.58 ± 0.46	1.11 ± 1.1	1.41 ± 1.81
Al (mg g^{-1})	30.9 ± 2.9	40.7 ± 5.4	50.8 ± 8.8
Fe (mg g^{-1})	64.0 ± 6.7	73.5 ± 21.4	47.9 ± 22.8
Mn (mg g^{-1})	0.41 ± 0.41	0.22 ± 0.19	0.13 ± 0.14
Na (mg g^{-1})	0.094 ± 0.022	0.089 ± 0.035	0.085 ± 0.035

All the coefficients except the one for Tabonuco in $C:N$ ratio (Eq. 12.5) are statistically significant. By including nitrogen as an independent variable, carbon content is significantly dependent on elevation and vegetation types. Hence, both soil carbon content and $C:N$ ratio significantly increase with the elevation.

ANOVA test of soil properties on vegetation showed that only C, N, P, and K differed significantly among the vegetation types. Elfin forest has higher C, N, and P than the palo colorado forest, and palo colorado forest has greater C and N than the tabonuco forest (Table 12.3).

The multivariate regression of macronutrients involving N, P, K, Ca, and Mg showed their great dependence on the vegetation types (Table 12.4). The multivariate ANOVA of the model showed the pillai's statistics had p-values of 0.008, 0.1, and 0.085 for elevation, elevation squared, and vegetation type, respectively.

12.3.3 Soil Micronutrients

The top-layer micronutrients (Fig. 12.4) do not show apparent patterns with respect to the elevation due to the large variations. However, when including vegetation types in the regression, the ANOVA of the model (Table 12.4) still showed significant dependence on elevation and the Pillai statistics had p-value of 0.00005, 0.04, and 0.097 for first- and second-order of elevation and the forest types, respectively. Thus, the micronutrients as a whole significantly responded to both elevation and the forest type.

Table 12.4 Multivariate multiple regressions of macronutrients and micronutrients on elevation and vegetation types

	Intercept	Elev	$Elev^2$	Colorado	Tabonuco	R^2
Macronutrients						
N	2.20[a]	3.34	−3.61	−0.86[a]	−1.49[a]	0.52
P	1.87[a]	−0.54	0.28	−0.56[b]	−0.66	0.53
K	3.88[a]	−0.53	−3.33	−0.42	−1.56[b]	0.70
Ca	4.27[a]	5.73	−8.86[b]	−1.86[a]	−3.09[a]	0.60
Mg	3.33	13.24[b]	−15.23[a]	−2.30[a]	−3.33[a]	0.63
Micronutrients						
Al	5.73[a]	2.64[a]	−2.18[a]	−0.44[a]	−0.72[a]	0.83
Na	0.33	5.57[b]	−6.28[a]	−1.03[a]	−1.58[a]	0.51
Mn	5.16[b]	−16.03[b]	10.92	1.11	0.80	0.41
Fe	6.11[a]	−0.52	0.54	0.53	0.47	0.27

Significance is based on one-tailed *p*-value
[a] and [b], significant at 0.05 and 0.1, respectively

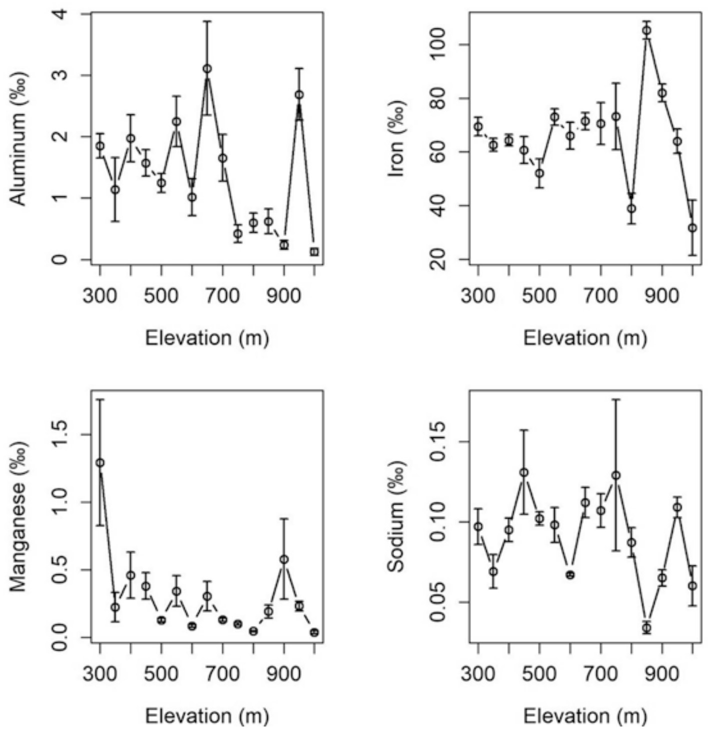

Fig. 12.4 Soil Al, Fe, Mn, and Na in the top layer along the elevation gradient of 300–1000 m

12.4 Discussion

In this study, we characterized soil physicochemical properties along an altitudinal gradient in LEF, which helps understand the interactions among soil patterns, vegetation distribution, and climate changes. Vegetation type and altitude were related to each other, and vegetation type varied significantly with altitude in the tropics (Barone et al. 2008; Gould et al. 2006; Lieberman et al. 1996; Lovett 1996; Weaver 1991; Weaver 2000). Our results on soil physicochemical characteristics were consistent with existing studies in this area. The range of clay content at the depth of 0–15 cm (31.3–68.3%), which is one important factor influencing soil respiration, fell closely within the ranges (22.35–68.25%) reported from long-term soil chemical and physical analyses by IITF, USDA, in Río Piedras, Puerto Rico (Sánchez et al. 1997). Other soil properties (e.g., bulk density and the contents of some extractable nutrient elements such as Al, Ca, Fe, P, Mg, and Na) in this study also had ranges aligned to those reported in existing studies (Sánchez et al. 1997; Soil Survey Staff 1995).

The elevation profile of soil physiochemical properties is the result of long-term balance of interaction with the vegetation, physical and chemical weathering (Bétard 2012), external input, and rainfall-driven leaching gravity. These processes depend on climate, forest type (Zimmermann and Bird 2012), and properties of parent materials (Augusto et al. 2017). According to the recent update, the mean annual rainfall in Luquillo mountain areas was quantified as a quadratic function of elevation so that precipitation increases nonlinearly to about 2000–4000 mm $yr.^{-1}$ (Murphy et al. 2017). The mean annual temperature on the other hand is found to be a linearly decreasing with elevation from 26.9 to 19.4 °C (Waide et al. 2013). The excessive rainfall in the high altitude often saturates the soil, together with the low temperature, suppresses the microbial activities (Cantrell et al. 2013), and brings down the decomposition and ecosystem productivity (Chen et al. 2017). The higher C, N, and P at high elevation found in this study may be a result of long-term accumulation in the soil due to the low decomposition rate.

Leaching driven by rainfall is another strong shaping force of the altitudinal profile of clay and cation in the macronutrients. Leaching contributes to the accumulation of fine particles especially clay in the low altitude. Leaching also tends to reduce K, Ca, and Mg in high altitude but tends to enhance these cations in the low altitude. This trend can also be strengthened by the temperature gradient (White et al. 1999). P, K, and other extractable nutrients such as Ca, Na, and Mg are usually reported as the main limitations to productivity at mountains due to their strong leaching at the high altitude (Diekmann et al. 2007; Tanner et al. 1998; Tsui et al. 2004).

The distribution of forest type along the altitudinal gradient is not only a result of the climate and soil, but also contributes to the formation of the gradient of soil physiochemical properties. Plant growth and productivity decrease at the tops of mountains in the tropics, which are probably caused by lower decomposition rate at higher altitude limited by the lower temperature and more saturated soil (Tanner et al.

1998). The forest in low altitude has thinner leaf with short lifespan and greater nutrient concentration than those growing in higher altitudes (Harris and Medina 2013). On the other hand, the sclerophyllous-leaved species in elfin dwarf forest makes it difficult to decompose. The litter of the tabonuco forest in the low altitude thus is easier to decompose and the nutrient cycling is faster than the elfin dwarf cloud forest in the high altitude, so that the means of the total C, N, P, and *C*:*N* have the following order in our plots: Elfin > Palo Colorado > Tabonuco. Soil *C*:*N* ratio is primarily affected by vegetation type and the *C:N* balance of soil microbes (Cox et al. 2002; Gifford 1994; Rastetter et al. 1991; Schlesinger and Andrews 2000; Silver et al. 1994). Typically, the *C*:*N* ratio in soils is in the range of 8–20 (Gifford 1994), and the maximum can extend to 30 in the acidic and humus-rich soils found in the tropics (Rastetter et al. 1991). Soil *C*:*N* ratio in the LEF increased with altitude from low to top in our study, ranging from 11.9 to 24.9.

Previous experiments at a large scale showed that there were no fixed distribution patterns for most nutrient elements (Appel et al. 2003; Burghouts et al. 1998; Tanner et al. 1998). However, when including both elevation and vegetation types in the regression, we found most nutrients showed significant dependence on elevation and/or vegetation types (Table 12.4).

Spatial heterogeneity of dry and wet depositions might also contribute to the altitudinal gradient of soil chemistry (McClintock 2014). Puerto Rico received great amount of African dust each year (Pett-Ridge 2009). On the other hand, the analysis of rainfall and cloud water chemistry showed that Cl, Na, and Mg with marine origin dominated the deposition. Ca is primarily from the dust, and N is primarily from the anthropogenic activities. McClintock et al. (2019) found that the dry deposition of dust differed by more than two folds in two sites of about 10 km apart, with the east site having higher dry deposition. Our study sites extend from the northwest (low altitude) to the southeast (high altitude) with a horizontal distance of ~3 km. Therefore, the high altitude in the east might receive more dust when compared to the low altitude in the west.

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