Patterns of Soil Texture and Root Biomass along a Humid Tropical Forest Hillslope Catena

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ABSTRACT

Soil texture determines the surface area in a volume of soil, which influences the availability of nutrients, water, and soil organic carbon in an ecosystem. The catena model describes patterns of texture formed in hydrologically connected topography. However, the soil catena model has not been well studied in high rainfall environments (e.g. humid tropical forests). In addition, the influence of soil texture patterns on root biomass distribution in these ecosystems is not clear. I measured the soil texture pattern along four replicate hillslope catenas and examined correlations with root biomass in a Puerto Rican humid tropical forest. One hundred and seventeen soil samples were randomly collected from transects in the Luquillo Experimental Forest (LEF). I measured the percentage of sand, silt, and clay using the hydrometer method and Stoke's Law. I fit linear mixed models to determine the relationship between topography, texture and root biomass. Clay contents in valleys were significantly lower than upper side of catena (ridges and slopes), and sand contents increased from ridges to slopes to valleys. This texture pattern contradicted findings of previous studies in arid areas, and could be explained by increased removal of clays from valleys due to high precipitation. Deeper soil had significantly more clay than surface soil. There was no significant correlation between texture content and root biomass. This relationship between texture and root biomass suggested that humid tropical forests might have patterns of nutrients, water, and primary productivity which are different from drier climate systems.

KEYWORDS

topography, lateral and vertical translocation, clay and sand content, precipitation, Luquillo Experimental Forest

INTRODUCTION

Soil texture determines the total surface area in a volume of soil, which influences the distribution of nutrients and affects the productivity of an ecosystem (Chapin et al. 2002, Hook and Burke 2000). Soil texture is determined by the relative abundance of different particle sizes in a unit volume of soil. As particle size decreases, total surface area per unit volume of soil increases. Small clay particles have high water retention, dissolved nutrients, and soil organic matter due to their large surface area per unit volume (Feller and Beare 1997). Larger sand and silt particles have lower retention of these three biologically important substances (Chapin *et al*. 2002). The particle size of soil constituents therefore significantly influences the fertility of environment.

Flows of water affect soil texture patterns in a hillslope by leaching and accumulating both solutes and particles (Nye 1954, Gressler et al. 2000, Khomo 2011). The patterns of soil characteristics such as soil mobilization, water flux, and nutrient availability across hydrologically connected hillslopes are called catenas (Khomo et al. 2011). The movement of soil particles that creates these patterns is known as translocation (Sommer and Schlichting 1997). The smaller particles are most susceptible to translocation, and they often move vertically and/or laterally (Scatena et al. 1996; Silver et al. 1994). In vertical translocation, clay on the surface is moved to the lower part of the soil and coarse particles tend to be left on the surface (Scatena et al. 1996). Lateral translocation causes downward movement of small soil particles on slopes, and clay tends to be sorted and accumulated downslope (Schimel et al. 1985).

Soil texture patterns along catenas are unique in different climate systems (Sommer and Schichting 1997). Several studies conducted in arid and sub-humid zones with rainfall between 310 mm and 730 mm per year suggest that clay minerals and organic materials accumulate in valleys (Khomo et al. 2011; Schimel et al. 1985). In an arid study area in Colorado, root biomass increased along with clay content from the summit to the footslope, suggesting that lateral translocation accumulates clay particles with nutrients and water to make valleys a more suitable environment for plant to grow (Schimel et al. 1985). The sub-humid area in South Africa also had a downslope shift of clay, but it had evidence of leaching that resulted in a smaller area of clay accumulation in valleys compared to an intermediate rainfall area in Colorado (Khomo et al. 2011). These results suggest that soil texture patterns created by translocation differ among climate systems, and they are likely to influence nutrient distribution and plant growth. However, the soil catena model has not been well studied in high rainfall environments, so soil texture patterns and their relationships with root biomass are not well understood in tropical climate systems.

Humid tropical forests have unique distributions of soil nutrients and plant growth which may be affected by soil texture patterns (Scatena et al. 1996, Silver et al. 1994). In sloped landscapes, smaller particles on the top of catenas (ridges) are removed by lateral translocation, and the soluble nutrients move from ridges to valleys (Silver et al. 1994). However, excessive vertical and lateral translocations caused by high rainfall can cause leaching of soluble nutrients even from valleys (Nye 1954). Moreover, valleys frequently undergo anaerobic conditions which may hinder primary productivity (Silver et al. 1999).

In this study, my objective is to determine how soil texture changes along a hillslope catena and how it affects the root biomass in a Puerto Rican humid tropical forest. The high level of rainfall is likely to create a soil texture pattern that is unique compared with other climate systems. In this case, I hypothesize that clay content is not significantly different along the catena due to the combination of clay loss from ridges by lateral translocation and leaching of clays in valleys (Khomo et al. 2011, Schimel et al. 1985). The soil texture pattern could significantly affect the amount of root biomass by regulating soil nutrient distribution. In this study, I hypothesize higher clay contents should correlate with increased root biomass in the valleys.

METHODS

Site description

The Bisley watershed in the Luquillo Experimental Forest (LEF) of Puerto Rico is in a subtropical wet forest, which has been studied for soil nutrient availability, vegetation characteristics, and geomorphology. The study site is in the tabonuco forest zone (18° 18’N, 65° 50’W) with a mean annual precipitation of about 3500 mm (Scatena et al. 1995). The hillslopes have convex upper slopes and straight middle slopes, and more than half of them have slopes greater than 45% incline. The lower parts of hillslope (toeslopes) are concave, and contain vertical drops where they meet perennial channels (Scatena et al. 1995). In ridges, slopes, and valleys, sediment accumulation is usually faster than removal due to thick soil profiles where sediment accumulation hinders the translocation of soil particles (Scatena et al. 1995). Previous studies have explored the relationships among topographic position, soil nutrients, and vegetation distribution at the same site.

Soil sampling

We (see Acknowledgements for the reason for using “we” instead of “I”) sampled from two different depths in four replicate catenas. In each catena, we sampled five replicate plots from each of three different topographic zones. Topographic zones were categorized as ridge, slope, or valley. Ridges are at the top of the slope, slopes refer to the sloped surface, and valleys are at the bottom of the slope, as defined by a study done by Scatena et al. (1995). We randomly chose four 0.25 m^2 plots located at 5 – 10 m intervals on a linear transect as catena sampling locations. We sampled 6 cm diameter soil cores at 0 – 10 cm and 10 – 20 cm depths. Replicate samples were used to measure root biomass and soil texture.

Soil Texture Analysis

I followed the Gee and Bauder (1986) hydrometer method to measure the soil texture content of each soil sample. First, I sieved each sample to remove all the rocks and roots > 2 mm and homogenize moisture content. I measured the moisture content and calculated the amount of each sample needed for soil texture analysis (50 g in dry mass). Then I soaked the soil samples in sodium - hexametaphosphate (HMP) solution (50 g / L) over-night to chemically disperse soil aggregates and subsequently used an electric mixer to ensure that the aggregates were separated. I then transferred the sample into a graduated cylinder and mixed the solution with a plunger. With a hydrometer calibrated in HMP solution, I recorded the change in liquid density over the following time intervals: 30 seconds, 1 minute, 90 minutes, and 24 hours. I used Stoke’s Law to calculate the fraction of clay, sand, and silt. To quantify texture content, I used the formulas from Gee and Bauder (1986).

Root Biomass Measurement

In order to measure fine root biomass < 2 mm in diameter, we removed the roots from soil samples by wet sieving described by Silver et al. (1993). Then we washed the roots thoroughly to remove any attached soil and dried them at 60° C to constant mass.

Data Analysis

We analyzed variation of texture contents (sand, silt, and clay) between topographical positions (ridge, slope, and valley) and depths (0 – 10 cm and 10 – 20 cm) using mixed models, which account for random effects of blocks and sites within a block (Pinheiro et al. 2010). We tested the following models: Clay=f [positions (3 categorical values), depths (two categorical values), random effects (blocks and sites within a block)], Sand=f [positions, depths, random effects] and Silt = f [positions, depths, random effects]. The optimal random effect structure was selected by likelihood ratio tests using a model with saturated fixed effects. In the models, we considered positions and depth as independent variables, and soil texture as dependent variable. If we found either position or depth to be non-significant, we removed terms until all factors were significant. If the optimal model had position as a significant variable, we tested whether all of three positions were significantly different from each other or not by using the Tukey multiple comparison procedure.

I analyzed correlations between soil texture and the root biomass with a simple linear regression. I tested root biomass as a function of the percentage of sand, silt, or clay and determined if any of these three variables correlated significantly with root biomass. I used the R statistical software package to conduct all of the statistical analysis (Hothorn et al. 2008, Pinheiro et al. 2010, R Development Core Team 2009).

RESULTS

Soil texture and topography

There were significant differences in soil texture contents across topography. The 117 soil texture data met the assumption of normal distribution of residuals in our statistical models. Clay content varied between 10 – 70% and valleys had significantly lower clay contents compared with the upper side of the catena (slopes and ridges) (Fig.1). I found that slope and ridge had no significant difference in clay content. I re-coded the topography to eliminate a redundant category by combining ridge and slope into “upper” and valley as “lower.” The best fit model for estimating clay content had topography and depth as predicting factors, accounted for random effects of blocks and sites within a block. According to the model, ridges and slopes significantly differed from valleys ($p < 0.001$).

Sand content ranged from almost 0% to more than 50% and increased from ridges to slopes to valleys (Fig.1). During the analysis process, I found one obvious outlier whose value was unusually high for its position (ridge). I removed the data point by assuming it was caused by my accidental deviation from the protocol during the experiment. Moreover, I log - transformed the data to satisfy the assumption of normally - distributed residuals. The best model for predicting sand content included topography as a predictive factor and took account of random effects of blocks and sites within a block. The increasing trend from ridge to slope to valley was statistically significant ($p < 0.001$), and multiple comparison of positions in the model showed that each position significantly differed from the others ($p < 0.001$).

Silt content ranged from about 20% to 70%, and there was no clear topographical trend, but the 10 – 20 cm depth tended to have lower values (Fig.1). The best model for predicting silt content had only depth as a predicting factor and accounted for random effects of blocks and sites within a block. Silt content decreased from the surface to deeper soil ($p < 0.01$).

Root biomass and Soil texture

There were 115 root biomass data for the analysis, and they met the assumption of normal distribution of residuals. However, root biomass did not show a significant relationship with soil texture (Fig 2). I constructed three linear models for soil texture data, which had clay, sand and silt contents as independent variables and root biomass as a dependent variable. The explanatory power of the clay-root biomass model, sand-root biomass model and silt-root biomass model was extremely low, and it was not statistically significant ($p > 0.1$).

DISCUSSION

Soil texture patterns strongly influence water and nutrient contents in the soil (Hassink 1997, Laurance et al. 2010, Silver et al. 2000, Telles et al. 2003). My results showed a significant influence of topography on soil texture. In contrast, the relationship between texture and biomass was weak, suggesting that soil texture is not a primary influence on biomass growth in this tropical forest.

Soil Texture and Topography

The decrease of clay content along a gradient from ridges to riparian valleys contrasts with previous studies in arid and moderately wet, mesic areas (Khomo et al. 2011, Schimel et al. 1985). Through gravity and translocation, clay particles are moved down the hillslope and they could be moved from the soil to river channels by occasional flooding events (Scatena et al. 1995). Moreover, the roots from mature trees in ridges might promote clay particles to form soil aggregates (Burri et al. 2009), potentially inhibiting lateral translocation. A previous study at this site found older trees with greater root biomass on ridges that might retain clays better than valley soils (Silver et al. 1994). The accumulation of clays in deeper soil could be explained by vertical translocation, which moves the smaller particles deeper into the soil profile (Dykes and Thornes, 2000). Moreover, shallower soil is less protected from clay loss due to the surface erosion. This process is evident in wetter environment due to its high amount of precipitation.

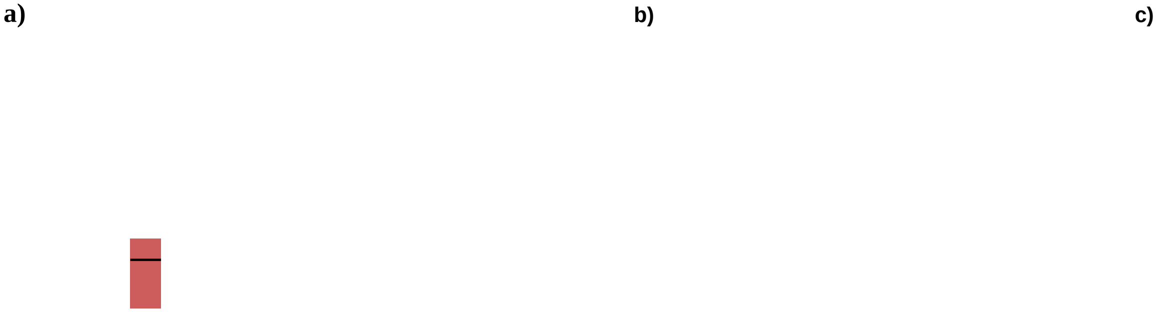

Fig. 1. Texture contents of soil samples in different topographic areas. Box-and-whisker plot comparisons of three particle sizes between three positions, ridge, slope and valley: (a) % clay, (b) % sand, and (c) % silt contents. The line on a box indicate the median of the data, and the top and bottom of the box indicate upper and lower 25% of the data respectively. The whisker is calculated by 1.5 * IQR, where IQR = top 25% quartile (the top of box) – bottom 25 % quartile (the bottom of box). The red boxes represent shallower soil samples (0 – 10 cm) and blue boxes represent deeper soil samples (10 – 20 cm). Empty circles are potential outliers or data points which are not in the range of whiskers. n = 117, except (a), which has n = 116 due to one obvious outlier.

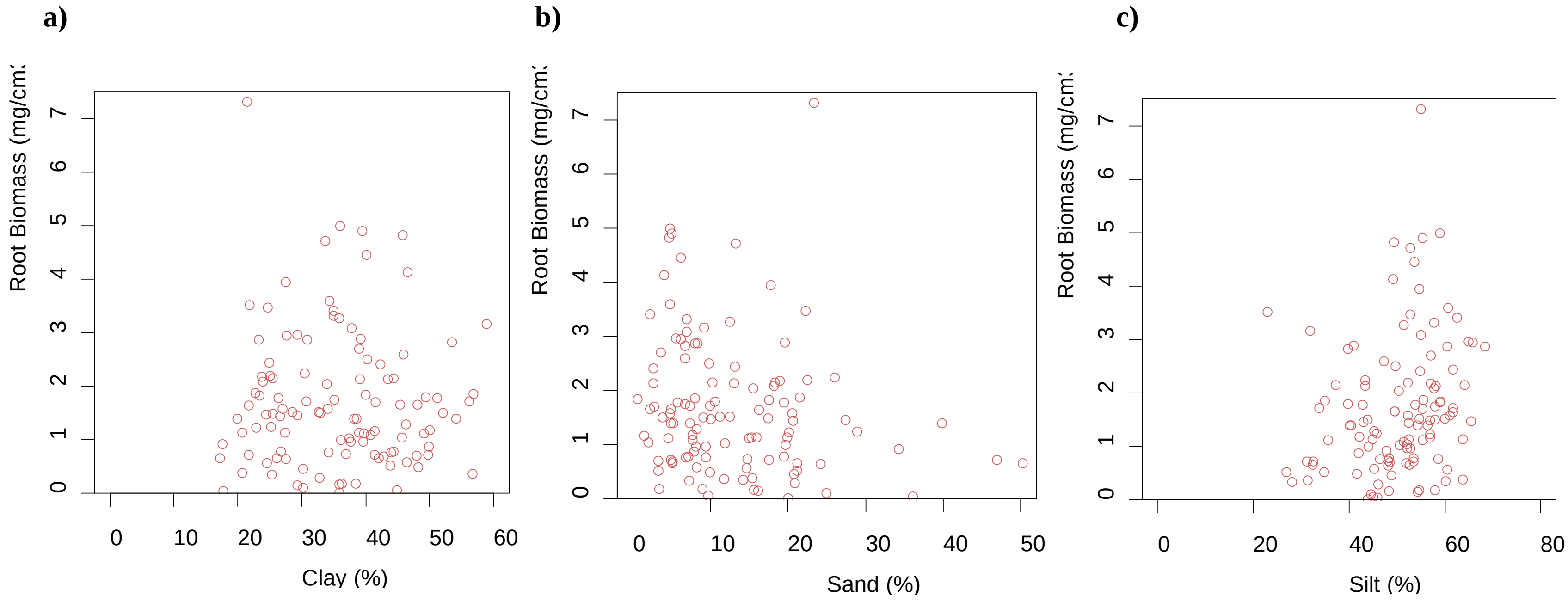

Fig2. Root biomass in soil samples with different texture contents. Scatter plot comparisons of root biomass amount distribution along contents of three texture types: (a) % clay, (b) % sand, (c) % silt. n = 115.

Soil texture and root biomass

Among the soil samples from Puerto Rico, there was no relationship between soil texture and underground biomass. The scattered relationship between texture and root biomass might be due to the high degree of spatial heterogeneity of texture and root biomass even among replicates sampled in close proximity. The mean of both clay content and root biomass along the hillslope from valley to ridge increased, so there was an indirect relationship between texture and plant biomass at this broader spatial scale. Nonetheless, the weak correlation is intriguing because other studies found positive correlations between clay content, and soil fertility and above ground biomass in a lowland tropical forest (Laurance et al. 1999, Laurance et al. 2011).The study site had a similar amount of annual precipitation to my study site, but it has dry and wet seasons. Because smaller particles retain water more effectively than larger particles, clay may positively affect plant growth in relatively dry seasons whereas vegetation in my study area was not likely limited by water due to abundant year-round rainfall. Moreover, the excess water can cause anaerobic conditions which are not favorable for plants (Kozlowski 1986, Silver et al. 1994), and clay particles may have negative effects on plants by accumulation of excess water.

In terms of nutrient availability, clay-rich soils tend to have more free cations and exchangeable bases which are necessary nutrients for plants (Chapin et al. 2002, Scatena et al. 1996). However, sandy soils potentially have more exchangeable phosphorus, which is often considered a limiting factor for biomass growth in humid tropical forests (Silver et al. 2000). Phosphorus can be adsorbed on clay particles and protected against uptake from plant roots (Olsen and Watanabe 1957). Those findings suggest that clay content can cause both positive and negative effects on plant growth, and a recent study showed a weak correlation between soil texture and plant growth compared to bulk density and the depth of organic matter abundant soil profiles (A-horizon) (Pangous et al. 2011). Additionally, frequent disturbances in tropical forests such as hurricanes and landslides may prevent plants from establishing clear patterns over topographical zones (Scatena et al. 1996). These findings suggest that tropical plant distribution is influenced by multiple environmental factors, and is hard to predict solely by soil texture patterns.

Limitations and Further Studies

We could not evaluate the role of clay aggregation in this study. In the protocol of the soil texture analysis, I dispersed the clay aggregates by using the phosphate solution (HMP) to determine soil particle size. However, other studies suggest that aggregates of clay might behave as larger particles in actual tropical environments (Endara and Jaramillo 2011). It could be necessary to analyze the effects of aggregation to capture a more accurate picture of how texture influences root biomass.

Root biomass had high degree of spatial heterogeneity in this experiment (standard deviation was 1.28 while mean was 1.69 mg / cm^3). Even though it was not feasible to process a larger number of sample in this experiment, the lack of correlation between texture and root biomass might be resolved by increasing the sample size.

Conclusions

In this study, soil texture was correlated with varying topographical positions in humid tropical forest catenas. The loss of clay particles in valleys has not been observed in other climate systems (Khomo et al. 2011, Schimel et al. 1985), suggesting that soil particle distribution could be influenced by climatic factors, especially precipitation. The soil texture pattern may result in a unique topographical distribution of nutrients and soil carbon in humid tropical forests. The weak correlation between soil texture and underground biomass was also a significant contrast with other study results in arid areas (Schimel et al. 1985). This difference indicated that the retention of water caused by clay particles is not likely to be a significant factor for biomass growth in tropical forests. Further investigations on potential positive effects such as nutrient retention and negative effects such as excess water retention and increased bulk density will deepen the understanding of the relationship of soil texture and primary productivity.

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