

PATTERNS OF SOIL PROPERTIES AND RESPIRATION ALONG AN ELEVATION  
GRADIENT IN THE LUQUILLO MOUNTAINS, NORTHEASTERN PUERTO RICO

By

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## ABSTRACT

Soil respiration is one of the most important components in the global carbon cycle. It is also one of the primary paths to release carbon fixed by vegetation to the atmosphere.

Climate change has direct impacts on soil respiration, and the responses of soil respiration also have important feedback to future climate change. Tropical forests store about 11% of the global soil carbon pool. The amount of carbon stored in soils is twice of that in either the atmosphere or terrestrial vegetation. Thus, understanding how soil respiration responds to climate change in tropical forest ecosystems has profound ecological significance.

Soil temperature, moisture, and carbon substrate are three main factors influencing soil respiration. Soil carbon substrate is significantly correlated to the distribution of vegetation and soil fauna. Abiotic factors such as solar radiation, topography, parent material, soil temperature and moisture also partly determine the spatial variation in soil carbon. This thesis was developed to study the variation in soil organic matter (SOM) and respiration rate as responses to environmental changes in a tropical wet montane forest. In general, microclimate conditions, vegetation, and SOM vary with elevation. We hypothesized that SOM increase with elevation from low to upper, whereas soil respiration rate decreases due to the limitation of low temperature. To test these two hypotheses, we analyzed soil properties including texture, SOM, and other physicochemical properties along an elevation gradient in the Luquillo Experimental Forest (LEF), northeastern Puerto Rico. We then conducted a soil translocation experiment and measured monthly soil respiration rate to investigate the impacts of environmental changes on soil respiration, as well as the responses in soil carbon.

As the results showed, soil properties were strongly related to the elevation gradient in the LEF. Especially, SOM content increased significantly along the elevation gradient with altered temperature and precipitation. The soil translocation experiment indicated that soil carbon processes were affected by climate change, especially the variation in temperature and moisture. Soil cores translocated from the plots with high elevation to the plots with lower elevation showed increased soil respiration rates and decreased soil C content at the end of the experiment, mainly because of the increased temperature. Soil cores translocated from the low elevation to the top also showed increased soil respiration rates and decreased soil C content, which might have been related to the increased soil moisture and altered soil microbes at the top. The experiment indicated that both soil respiration rate and soil C content changed with altered climate. Therefore, the predicted climate change in the Caribbean region, warmer and drier, might bring significant impacts on C sequestration in tropical forests.



## **CHAPTER I**

### **INTRODUCTION: THE ROLE OF TROPICAL FOREST IN GLOBAL CARBON CYCLE AND CLIMATE CHANGE**

## **Carbon cycle and climate change**

Atmospheric carbon dioxide (CO<sub>2</sub>) concentration has increased significantly due to anthropogenic activities, such as fossil fuel combustion, deforestation, and other land use changes (IPCC 2010). These anthropogenic activities are the principal climate driven factors at a global scale in the industrial and post-industrial eras (Gifford 1994, Cramer *et al.* 2004, Angeles *et al.* 2007, Taylor *et al.* 2007). According to the Intergovernmental Panel on Climate Change report (IPCC 2010), the global average temperature increases in response to the accumulation of greenhouse gases such as CO<sub>2</sub>, methane (CH<sub>4</sub>) and nitrous oxide (NO) in the atmosphere. Other long-term changes in climate such as precipitation and extreme weather (e.g., drought) have also been observed (IPCC 2010). Particularly, the Small Island Developing States (SIDS) is one of the most seriously impacted regions due to global climate change on Earth (Angeles *et al.* 2007). For example, the Caribbean region is predicted to be between 1°C and 5°C warmer in annual mean temperature by 2080, and drier, with a reduction of 10 % to 50% in its annual rainfall (Angeles *et al.* 2007, Taylor *et al.* 2007).

It is important to understand the impacts of current global warming on carbon cycle, as well as the feedbacks of the carbon cycle to future climate. Most research indicated that the global warming and other climate change have significant negative effects on ecosystem, for example, the potentially increased droughts and hurricanes might increase damage to biodiversity and ecosystem productivity (Markham 1996, Silver 1998, Cramer *et al.* 2004). There is a general concern that increased temperature accelerates soil carbon decomposition and enhances carbon release to the atmosphere (Raich & Schlesinger 1992, Kirschbaum 1995, Kirschbaum 2000). However, the carbon cycle is composed of a series of complex

biogeochemical processes, and its responses to climate change are still controversial (Jones *et al.* 2003, Trumbore & Czimczik 2008).

The carbon cycle includes the fluxes of carbon among four main reservoirs: fossils, the atmosphere, oceans, and the terrestrial biosphere. As the second largest flux between the atmosphere and the terrestrial biosphere, soil respiration (i.e. the total emissions of CO<sub>2</sub> from the soils) is the primary component in the carbon cycle that responds to climate change (Schlesinger & Andrews 2000, Jones *et al.* 2003, Trumbore & Czimczik 2008). Experiments have demonstrated that soil respiration is mainly affected by climate conditions and carbon substrate (which is related to vegetation) (Atkin *et al.* 2000, Cramer *et al.* 2001, Conant *et al.* 2004, Zimmermann *et al.* 2009). The effects of elevated CO<sub>2</sub>, increased temperature, and variation in precipitation or soil water availability on soil respiration have been well studied (Rustad *et al.* 2001, Sjögersten & Wookey 2002, Davidson *et al.* 2006, Wan *et al.* 2007). However, it is still unclear how the responses of soil respiration will affect the global carbon cycle and future climates (Clark 2004, Wan *et al.* 2007). Considering the magnitude of carbon stored in the soils, any small changes in soil respiration could have significant effects on the concentration of CO<sub>2</sub> in the atmosphere (Kirschbaum 2000, Schlesinger & Andrews 2000, Wan *et al.* 2007). Future climate change, therefore, depend critically on the sensitivity of soil respiration to temperature (Jones *et al.* 2003, Davidson & Janssens 2006, Kirschbaum 2006, Trumbore & Czimczik 2008).

### **The role of tropical forests**

Tropical biosphere stores 46% of the world's living terrestrial carbon and 11% of the world's soil carbon (Brown & Lugo 1982, Pan *et al.* 2011). It accounts for an estimated 43% of global net primary productivity (NPP) (Silver 1998, Clark 2004). "The tropical biosphere

plays an important role in global climate change and the global carbon cycle” (Cleveland & Sullivan 2012). Understanding whether the tropical biosphere responds to global climate change by either releasing or sequestering more carbon is crucial to evaluate the future global carbon balance (Foster 2001, Cramer *et al.* 2004, Clark 2004).

Many studies have demonstrated that the tropical biosphere could become an unexpected carbon source with a warmer climate due to human-induced greenhouse effect (Foster 2001, Cramer *et al.* 2004, Sayer *et al.* 2011). By modeling the effects of increased temperature on the potential sensitivity of carbon at the ecosystem level, Townsend *et al.* (1992) investigated the interactions between carbon turnover rate and temperature changes in the major biomes of the world, including boreal, tundra, and equatorial tropical areas. The results showed that although the high-latitude biomes such as boreal and tundra may result in carbon storage over some limited range of temperature increases, equatorial tropical areas, where the relatively high soil respiration rate is highly sensitive to temperature changes, are very likely to release large amounts of carbon to the atmosphere (Townsend *et al.* 1992). This conclusion was further fortified by Cramer *et al.* (2004). By constructing a dynamic global vegetation model, Cramer *et al.* (2004) used multiple scenarios of tropical deforestation and climate change to identify the relative roles of climate change, CO<sub>2</sub> increases and exacerbated anthropogenic activities, and their impacts on atmospheric CO<sub>2</sub> concentrations. Their results explicitly indicated that the tropical carbon stocks were at severe risk because of the large carbon fluxes to the atmosphere induced by climate change (mainly referring to increased temperature and decreased rainfall.) and anthropogenic activities such as deforestation. Their estimates of carbon emissions during the twenty- first century resulted from climate change and deforestation range from 101 to 367 Gt C (Cramer

*et al.* 2004). In a recent study, using a large-scale litterfall controlled experiment with carbon isotope measurements in a tropical forest, the authors found that soil carbon release could be enhanced by increased litterfall due to temperature increases, which indicated that tropical forest could respond positively to climate warming by releasing more C to the atmosphere (Sayer *et al.* 2011).

Nevertheless, some researchers argue that how tropical forests respond to the current global changes in atmospheric CO<sub>2</sub> and climate is little studied and understood (Clark 2003). Long-term monitoring of ecosystem functions and intensified experiments are required to evaluate the role of tropical forests in future global climate and carbon balance (Clark 2004). As a main factor determining future atmospheric CO<sub>2</sub> concentration, tropical forests release CO<sub>2</sub> due to deforestation and other land use changes, meanwhile, tropical forests also function as C sink due to high production and increased biomass storage (Malhi *et al.* 1999, Malhi *et al.* 2000, Clark 2004). The C balance then depends on the difference between the responses in net primary productivity and those in heterotrophic respiration. CO<sub>2</sub>-stimulated photosynthesis increases forest productivity, which usually produces more litter to the forest floor (Gifford 1994, Sayer *et al.* 2011). As a result of temperature increases, the increased SOM decomposition provides more mineralized N, which would be largely taken up by vegetation, this would cause a much higher carbon to nitrogen ratio in soil than that in vegetation. Thus, the amount of carbon fixed by the N-stimulated productivity will exceed greatly the amount of carbon released by SOM decomposition (Rastetter *et al.* 1991, Gifford 1994, Yang *et al.* 2011). As a result, the carbon storages in vegetation and soils are likely to increase in response to the increases in global temperature and atmospheric CO<sub>2</sub> concentration (Rastetter *et al.* 1991, Gifford 1994). Furthermore, long-term studies indicated

that carbon decomposition rate in forest soils was remarkably constant within a gradient in mean annual temperature at a global scale (Giardina & Ryan 2000). The decomposition rate was not controlled by temperature alone, which mainly affected decomposition processes through limiting microbial activities (Giardina & Ryan 2000). In a recent study to investigate the effects of drought on trace gas fluxes and nutrient availability in humid tropical forests in Puerto Rico, Wood & Silver (2012) suggested that drought has the potential to decrease net trace gas emissions in tropical forest soils. These findings implied that drought-induced decreases in such greenhouse-gas emissions could counter climate change (Wood & Silver 2012, Cleveland & Sullivan 2012). Therefore, it is not certain that temperature increases will accelerate SOM decomposition rate in the long term, and that global warming will definitely stimulate carbon effluxes from soils to the atmosphere (Malhi *et al.* 2000, Clark 2004, Wood & Silver 2012).

### **Objectives and hypotheses**

This thesis was designed to improve our understanding of the impacts of climate change on soil carbon process in a tropical montane forest. Climate change was simulated by an elevation gradient instead of a temporal scale. Specifically, we asked two scientific questions: 1) How tropical soils, especially soil organic carbon (SOC) and soil organic matter (SOM), vary along the elevation gradient, whereas temperature decreases and moisture increases from the low to high elevation? And 2) How soil respiration rates in tropical forests respond to climate change? In order to answer these questions, we proposed two hypotheses: 1) the stocks of SOC and SOM increase with elevation from low to top; and 2) soil respiration rates decrease in high elevation due to low temperature. We tested these hypotheses along an elevation gradient in the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico.

“Gradient analysis with the changes in a variety of ecosystem parameters provides a very useful insight to study complex ecosystem interactions and patterns” (Beck *et al.* 2008).

Along the elevation gradient, we analyzed the variation in different soil properties, such as SOC, SOM, texture and other physic-chemical characteristics. We also conducted a soil translocation experiment to measure the responses of soil respiration to climate change.

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## **CHAPTER II**

### **PATTERNS OF SOIL ORGANIC CARBON AND OTHER SOIL PROPERTIES ALONG AN ELEVATION GRADIENT IN THE LUQUILLO EXPERIMENTAL FOREST, PUERTO RICO**

To better understand the responses of tropical soil carbon to global climate change, we analyzed the distribution patterns of soil organic matter (SOM) and other soil properties along an elevation gradient in the Luquillo Experimental Forest (LEF), northeastern Puerto Rico. Soil properties at two depths (0-15 and 15-30 cm, respectively) including soil organic carbon (SOC), nitrogen (N), particle distribution, pH, extractable nutrient elements (Ca, K, Fe, P, Na, Mg, and Mn), water content, and bulk density were measured and analyzed in 15 plots along the elevation gradient from 300 m to 1000 m in the LEF, with an interval of 50 m. Soil clay content at the depth of 0-15 cm was significantly related to both elevation and vegetation type (Pearson correlation coefficient for the clay and elevation  $r=-0.56$ ,  $P<0.003$ ,  $0.007$ , respectively). Soil clay content at the depth of 15-30cm was also significantly correlated to elevation ( $r=-0.61$ ,  $P<0.01$ ), but the effect of vegetation on soil clay content at the depth of 15-30 cm was not as significant as that on the soils at the depth of 0-15 cm. Soil clay contents both at the depth of 0-15 cm and 15-30 cm tended to decrease with increased elevation ( $P<0.03$ ,  $0.02$ , respectively), from 68.3% to 31.3%, and from 79.9% to 45.0%, respectively. Most of the soil properties measured (e.g., SOC, SOM, and some extractable nutrient elements) showed high spatial variation along the elevation gradient, and were highly correlated among one another. For example, the correlations between total organic carbon (TC) and total nitrogen (TN) ( $r=0.92$ ), between clay and loss-on-ignition (LOI) ( $r=-0.50$ ), between C to N ratio and Mg ( $r=-0.69$ ), between Al, P, and clay ( $r=-0.54$ ,  $-0.68$ , respectively) were significant. Water content (WC), TC, LOI, and C to N ratio significantly increased with elevation from low to top (linear regression,  $P<0.001$ ), whereas K decreased ( $P<0.001$ ). In summary, soil properties, especially SOC, and clay content showed significant

elevation patterns in the LEF. The current changes in temperature and precipitation may bring significant impacts on tropical C redistribution.

## **Introduction**

As important factors influencing soil respiration, soil properties vary significantly in tropical forests (Silver *et al.* 1994, Cox *et al.* 2002, Wang *et al.* 2002, Hutchings *et al.* 2003). The considerable temporal and spatial variation in soil physicochemical properties primarily results from soil age, parent material, disturbance history, vegetation type, and climatic conditions (Hook *et al.* 1991, Jackson & Caldwell 1993). Such variation in soil properties has been reported to affect plant species compositions, and plant functions such as productivity (Hutchings *et al.* 2003, Venterink *et al.* 2003, Mazzoleni *et al.* 2007, Wood & Silver 2012).

Soil properties, especially clay content, SOC, and temperature-moisture conditions have been well documented to have significant effects on soil respiration (Trumbore 1997, Raich & Tufekcioglu 2000, Cramer *et al.* 2001, Müller & Höper 2004). Soil texture can affect SOM decomposition rate (i.e., 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. In a study on the relationship between soil microbial biomass and SOM turnover, based on an extensive literature review, Müller & Höper (2004) suggested SOM turnover rate as a function of soil clay content, and soil clay content strongly related to soil respiration through soil microbial biomass.

Many studies indicated that SOC, especially tropical SOC, is affected by climate change, although whether tropical soils respond primarily as a carbon sink or source to the increased atmospheric CO<sub>2</sub> and global warming is still on debate (Jones *et al.* 2003, Davidson &

Janssens 2006, Kirschbaum 2006, Trumbore & Czimczik 2008). “High latitude soils are usually more vulnerable and sensitive to climate change” (Sjogersten & Wookey 2002). However, tropical soils are also important in the debate of the potential impacts of climate change on global C cycle (Malhi *et al.* 2000, Clark 2004, Sayer *et al.* 2011). Considering “tropics account for about 11% of the world’s soil C, and contribute 46% of the world’s living terrestrial C” (Silver 1998), it is important to study the patterns of tropical soil properties in the context of global climate change.

In this study, we analyzed soil physicochemical characteristics along an elevation gradient with remarkable alteration in temperature, moisture, and other environmental conditions in the LEF, Puerto Rico, and then discussed the impacts of climate change on tropical soils, particularly on soil carbon processes.

## **Study area**

All the experiment plots were located in the Luquillo Experimental Forest (LEF) (18°20'N, 65°49'W), northeastern Puerto Rico (Figure 2.1). The LEF is a tropical wet montane forest. “The mean monthly temperature ranges from 23.5°C in January to 27°C in September at the lowest elevation, while it ranges from 17°C to 20°C in January and September at the highest elevation” (Garcia-Martinó *et al.* 1996). “Rainfall increases with elevation, ranging from an average of 3,537 mm per year at low elevation to 4,849 mm per year at high elevation” (Garcia-Martinó *et al.* 1996). The soils in the LEF are mainly derived from volcaniclastic sediments, except for one high- elevation area where the soil are from quartz diorite (Sieders 1971, Barone *et al.* 2008) (Figure. 2.1). Four typical forest types with different dominant species and forest structure are represented in the LEF: tabonuco forest, palm forest, palo colorado forest, and elfin woodland (Weaver 2000, Gould *et al.* 2006).

## Soil sampling

All the soil samples were collected along the elevation gradient at the LEF. The elevation rises from 300 m to 1000 m above sea level. According to the elevation, fifteen twenty-by-fifty-meter plots were established, at intervals of 50 m along the elevation gradient (Table 2.1). For soil extractable nutrients and SOC analyses, five soil samples (each composed of three soil cores with 5 cm in diameter, and 15 cm in depth) were collected with a specific cylindrical soil corer (with diameter of 4.3 cm, and length of 5.0 cm) from each plot (total  $5 \times 15 = 75$  soil samples). For soil texture analysis, three soil samples, which were separated into two depths of 0-15cm and 15-30 cm, were collected with a stainless corer (diameter: 1.68 cm) from each plot (Total  $3 \times 15 \times 2 = 90$  soil samples). Before collecting soil samples, all the coarse litter debris and organic matters were removed from the soil surface. All soil samples were collected in July, 2009.

## Soil analyses

### *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. The weights of both fresh soil samples and oven-drying samples were recorded. To calculate soil bulk density (Db, g/cm<sup>3</sup>) and soil water content (WC, %), the following formulas were used:

$$Db = \text{oven-drying soil weight (g)} / \text{bulk volume of soil solid (cm}^3\text{)} \quad (\text{Eqn. 1})$$

$$WC = [(\text{fresh weight (g)} - \text{oven-drying weight (g)}) / \text{oven-drying weight (g)}] \times 100 \quad (\text{Eqn. 2})$$

### *Soil pH and particle size analyses*

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, pH values were measured with an advanced thermo pH meter (Orion 350 PerHect benchtop pH meter with ROSS Micro pH electrode and ATC probe, Thermo Scientific<sup>®</sup>, Waltham, MA, U.S.A) through a standard procedure (Mc Lean 1982). The pH values in both water solution and 1 mol/L potassium chloride solution were measured.

The sample preparation for particle size analysis was as the same as that for soil pH analysis. The concentrations of soil particles with different size were measured with a buoyancy soil hydrometer (ASTM 152H, Thermo Scientific ERTCO<sup>®</sup>, Waltham, MA, U.S.A) through a standard method used by Soil Science Society of America (SSSA) (Dane & 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 & Topp 2002). By calculating the relative solution density at a certain time, the relative proportion of various soil particles can be extrapolated. The following formulas were used to determine the proportions of sand, clay, and silt (%):

$$\text{sand} = 100 - (R_{40s} - R_{L1}) \times (100 / \text{sample weight}) \quad (\text{Eqn. 3})$$

$$\text{clay} = (R_{7h} - R_{L2}) \times (100 / \text{sample weight}) \quad (\text{Eqn. 4})$$

$$\text{silt} = 100 - (\text{sand} + \text{clay}) \quad (\text{Eqn. 5})$$

where

$R_{40s}$  is hydrometer reading in soil suspension at 40s in g/L;

$R_{L1,2}$  is hydrometer reading of blank solution at the measurement time in g/L;

$R_{7h}$  is hydrometer reading in soil suspension at 7h in g/L; and the unit of sample weight is g.



Because the Buoyancy hydrometer was calibrated at 20°C, when calculating soil particle proportions, if the temperature of soil suspension and blank solution was above 20°C, the hydrometer readings were adjusted by adding 0.2 g/L per degree of the difference in temperature. If the temperature of soil suspension and blank solution was below 20°C, 0.2 g/L per degree of the difference was subtracted from the hydrometer readings.

Soil wilting coefficient (WP) and soil field capacity (FC) were then calculated based on the soil particle proportions using the following equations (Blackman 1914, Saxton *et al.* 1986):

$$WP = \text{sand} + \text{silt} + \text{clay} \times 0.57 \quad (\text{Eqn. 6})$$

$$FC = fc_{\text{raw}} + (0.07 \times fc_{\text{raw}}) \quad (\text{Eqn. 7})$$

where

$$fc_{\text{raw}} = (0.333/a)^{(1.0/b)}$$

$$a = \exp(-4.396 - 0.0715 \times \text{clay} - 4.88 \times 10^{-4} \times (\text{sand})^2 - 4.28 \times 10^{-5} \times (\text{sand})^2 \times \text{clay})$$

$$b = -3.14 - 2.22 \times 10^{-3} \times (\text{clay})^2 - 3.48 \times 10^{-5} \times (\text{sand})^2 \times \text{clay}$$

#### *SOM and soil extractable nutrients analyses*

After air-drying for one week, the soil samples were oven-drying to constant mass at 50°C, and then ground and passed through a 20 mesh sieve. Stones, coarse root detritus, and other organic materials were removed before further experiment. All the soil physicochemical properties including total organic carbon (TC), total nitrogen (TN), loss on ignition (LOI), and extractable elements such as aluminum (Al), calcium (Ca), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), and phosphorus (P) were

measured at the International Institute of Tropical Forestry (IITF), USDA Forest Service, in Río Piedras, Puerto Rico. All the extractable elements were detected using ICP-Spectro Ciros CCD (Spectro<sup>®</sup>, 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 (NH<sub>4</sub>-EDTA-NaHCO<sub>3</sub>) procedure (Anderson 1993). Total organic carbon, TN and LOI were determined using CNS LECO-2000 Analyzer (LECO<sup>®</sup>, LECO Corporation, Michigan, U. S. A) with a standard procedure.

### **Statistical analyses**

Correlations between all possible pairs of soil properties in the 15 plots, and between soil properties and elevation were analyzed by Pearson product-moment correlation coefficients. Two-way analysis of variance (ANOVA) was used to test the impacts of vegetation, elevation, and their interaction on soil properties. Where the test of two-way ANOVA indicated significant impacts of elevation on soil properties, we further used linear regression analysis to identify the patterns of these soil properties along the elevation gradient. Statistical analyses were run in R software (R 2.15.1, R Development Core Team 2010).

### **Results**

#### *Soil texture*

Soil texture varied greatly along the elevation gradient (Figure 2.2). Both the correlation analysis and two-way ANOVA showed that soil clay content at the depth of 0-15 cm was

significantly related to both elevation and vegetation type (the Pearson correlation coefficient for soil clay content at the depth of 0-15 cm and elevation  $r=-0.56$ ,  $P<0.003$ ,  $0.007$ , respectively) (Tables 2.2 and 2.3). However, the interaction between vegetation type and elevation on soil clay content at the depth of 0-15 cm was not significant (Table 2.3). Soil clay content at the depth of 15-30 cm was also significantly correlated with elevation ( $r=-0.61$ ,  $P<0.01$ ) (Tables 2.2 and 2.3). Soil clay contents both at the depth of 0-15 cm, and 15-30 cm tended to decrease with elevation from low to top ( $P<0.03$ ,  $0.02$ , respectively), from 68.3% to 31.3%, and from 79.9% to 45.0%, respectively (Figure 2.2). According to the soil texture classification defined by the USDA (Schoeneberger *et al.* 2002) (Appendix 2.1), the soils in all the 15 experiment plots can be classified as “clay”, except for the soils at the depth of 0-15 cm from the two highest plots (with elevations at 950 m, and 1000 m, respectively). These soils belong to “clay loam” with relatively lower clay.

Soil wilting point (WP) and field capacity (FC) were estimated based on the proportions of sand, clay and silt (Eqns. (6) and (7)). The water contents at both wilting point and field capacity of the soils at the depth of 15-30 cm were higher than those of the soils at the depth of 0-15 cm (Table 2.4). However, there were no significant patterns of these water characteristics in the 15 plots in the LEF (Table 2.4).

### *SOC and other properties*

The descriptions of soil physicochemical properties in all the 15 experiment plots were given in Table 2.5. The variation in soil properties along the elevation gradient were showed in Figures 2.3-2.6. Correlations between soil properties and elevation, and possible correlations among all the soil properties in the LEF, were analyzed. Most of the soil properties (e.g., TC, TN, and some extractable nutrient elements) measured showed high

spatial variability along the elevation gradient (Table 2.2). Soil moisture (WC), TC, TN, C to N ratio, and LOI significantly correlated with elevation ( $r=0.83, 0.75, 0.55, 0.89,$  and  $0.79,$  respectively). The Pearson correlation coefficients between some extractable elements and elevation were also relatively high (e.g., the  $r$  value was  $0.76, -0.73, -0.57, -0.52,$  and  $-0.55,$  respectively, for Al, K, Ca, Mg, and Mn). Some soil properties were positively correlated among one another (Table 2.2). For example, the correlations between TC and TN ( $r=0.92$ ), between TC, TN, LOI and Al ( $r=0.55, 0.51,$  and  $0.64,$  respectively), between Ca, K and Mg ( $r=0.74, 0.52,$  respectively) were significant. There were also strong negative correlations among soil properties, such as the correlations between Mg and TC, C to N ratio, LOI ( $r=-0.52, -0.69,$  and  $-0.51,$  respectively), between Fe and TN ( $r=-0.51$ ), between Ca and C to N ratio ( $r=-0.51$ ).

To further compare the interaction between elevation and vegetation type on soil properties, we used two-way ANOVA. The results were closely consistent with the correlation analysis (Table 2.3). Soil WC, TC, TN, C to N ratio, LOI, and some extractable elements, such as Al, K, and Mg, showed significant elevation distribution patterns along the gradient in the LEF ( $p=0.0009, 0.0009, 0.03, 0.0001, 0.0004, 0.0002, 0.0008,$  and  $0.03,$  respectively). However, the interaction between elevation and vegetation type on soil properties was not significant (Table 2.3). A linear regression model was used to identify the elevation patterns of these soil properties. Soil WC, TC, LOI, Al, C to N ratio, and TN significantly increased with elevation from low to top ( $P<0.0001, 0.001, 0.0003, 0.001, 0.0001,$  and  $0.01,$  respectively) (Table 2.6), whereas, the content of K decreased with elevation from low to top ( $P<0.002$ ) (Table 2.6, Figure 2.6).

## Discussion

Few studies have examined the spatial variation in soil properties at such continuous scale along the elevation gradient in the LEF. Our understanding of spatial variation of soil properties usually came either from site-specific studies undertaken for different research purposes, or from studies limited in only one or two vegetation types, or from laboratory modeling work (Silver *et al.* 1994, Cox *et al.* 2002, Wang *et al.* 2003, Wang *et al.* 2004). In this study, we characterized various soil properties along an elevation gradient in the LEF. Vegetation type and elevation were related to each other. Vegetation type varied significantly with elevation in the tropics (Lieberman *et al.* 1996, Lovett 1996, Weaver 2000, Gould *et al.* 2006, Barone *et al.* 2008). In this study, vegetation type and elevation were used as two different treatments. As our results showed the clay contents both at the depth 0-15 cm and 15-30 cm were affected by vegetation type. However, the effect of vegetation on the soils at the depth of 15-30 cm was not as significant as that on the soils at the depth of 0-15 cm, partly because the quality and quantity of litter fall from vegetation have more direct impacts on soil clay at the depth of 0-15 cm than those at 15-30 cm.

Soil wilting point and field capacity are soil moisture characteristics that are closely related to plant growth and nutrient transportation. Soil wilting point and field capacity are determined by soil texture and structure. Usually the field capacity and wilting point of sands are much lower than those of clay soil. Neither of wilting point and field capacity showed significant patterns along the elevation gradient in the LEF in this study.

Our results on soil physicochemical characteristics were consistent with other studies in this area. The range of clay content at the depth of 0-15cm (31.3%-68.3%) fell closely within the range (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., pH, Db, and the content of some extractable elements such as Al, Ca, Fe, P, Mg, and Na) also had ranges similar to those reported in other studies (Soil Survey Staff 1995, Sánchez *et al.* 1997).

Plant growth and productivity decrease at the tops of mountains in the tropics, which are probably caused by lower nutrient supply and other environmental conditions such as soil saturation (Tanner *et al.* 1998). For example, 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 elevation (Tanner *et al.* 1998, Diekmann *et al.* 2007, Tsui *et al.* 2004). However, the results of experiments at a large scale showed that there were no fixed distribution patterns for most nutrient elements (Burghouts *et al.* 1998, Tanner *et al.* 1998, Appel *et al.* 2003). One possible explanation is that the distribution of nutrient elements is primarily influenced by environmental conditions, such as quantity and quality of litterfall (vegetation type), topography (slopes), soil pH, and other aspects of soil and vegetation development (Burghouts *et al.* 1998, Tanner *et al.* 1998, Appel *et al.* 2003). In our study, the soil K content decreased significantly with the increased elevation, which can be explicitly explained by the strong leaching at the high elevation. However, the patterns of some other nutrient elements were noteworthy. For example, Al distinctly increased with the increased elevation. “Aluminum is not essential to vegetation nutrition and its movement in the soils is geochemically controlled” (Diekmann *et al.* 2007). Therefore, the distribution pattern of Al should be either random or markedly different from other soil properties strongly affected by biotic processes (Diekmann *et al.* 2007). Further studies are needed to interpret the strong correlations between Al, Ca, Mg and elevation.

As one of the main factors influencing soil respiration, SOM turnover-rate decreased with decreased clay content, partly due to the impacts of clay on microbial biomass (Müller & Höper 2004). This interpretation was enhanced by our experiment. The stocks of SOM, estimated by LOI percent (21.3-48.2), increased significantly along the elevation gradient in the LEF, while clay content decreased with elevation from low to top. The significant decreases in clay content with elevation from low to top can be attributed to the variation in vegetation type, the complex topography, and soil parent material (Silver *et al.* 1994, Soil Survey Staff 1995, Wang *et al.* 2002). SOC increased approximately linearly along the elevation gradient in the LEF. Both the increases in SOM and SOC with elevation from low to top can be partially explained by the lower decomposition rate at higher elevation caused by lower temperature. In general, our results supported the hypothesis that SOM stocks increased with elevation from low to upper.

C to N ratio is another important factor influencing soil respiration (Rastetter *et al.* 1991, Gifford 1994, Schlesinger & Andrews 2000). Soil C to N ratio is primarily affected by vegetation type and the C-N balance of soil microbes (Rastetter *et al.* 1992, Gifford 1994, Silver *et al.* 1994, Schlesinger & Andrews 2000, Cox *et al.* 2002). Typically the C to 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 to N ratio in the LEF increased with elevation from low to top in our study, ranging from 11.8 to 24.8.

Soil respiration rate was reported to increase with SOM and soil moisture conditions, but decrease with clay content and C to N ratio (Gifford 1994, Coûteaux *et al.* 1995, Raich & Tufekcioglu 2000). In our study, SOM, WC, and C to N ratio were positively correlated to elevation, whereas the clay content was negatively correlated. Soil respiration rates, therefore,

tend to depend on the interaction among soil properties, vegetation type, and other environmental factors such as soil temperature.



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## TABLES

Table 2.1 Geographic coordinates of the 15 experiment plots distributed along the elevation gradient (from 300 m to 1000 m) with different vegetation types in the Luquillo Experimental Forest, Puerto Rico.

<b>Plot</b>	<b>Elevation (m)</b>	<b>Latitude</b>	<b>Longitude</b>	<b>Forest Type</b>
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

Table 2.2 Pearson product-moment correlations among soil properties along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. Ele, Db, WC, TC, TN, and LOI stand for elevation, bulk density, water content, total organic carbon, total nitrogen, and loss-on-ignition, respectively. TClay and SClay stand for clay content at the depth of 0-15cm, and 15-30 cm, respectively. n=15.

	<b>Ele</b>	<b>SClay</b>	<b>pH</b>	<b>Db</b>	<b>WC</b>	<b>TClay</b>	<b>TC</b>	<b>TN</b>	<b>C:N</b>	<b>LOI</b>
<b>Ele</b>		-0.61*	-0.04	0.31	0.83*	-0.56*	0.75*	0.55*	0.89*	0.79*
<b>pH</b>				0.06	-0.04	-0.15	-0.13	-0.17	-0.06	-0.08
<b>Db</b>					0.20	-0.41	0.42	0.38	0.22	0.41
<b>WC</b>						-0.66*	0.58*	0.46	0.65*	0.59*
<b>TClay</b>							-0.49	-0.45	-0.42	-0.50*
<b>TC</b>								0.92*	0.83	0.99*
<b>TN</b>									0.58	0.90*
<b>C:N</b>										0.85*
<b>Al</b>	0.76*		0.21	0.43	0.67*	-0.54*	0.55*	0.51*	0.51*	0.64*
<b>Fe</b>	-0.06		0.31	-0.23	-0.03	0.25	-0.44	-0.51*	-0.12	-0.31
<b>Ca</b>	-0.57*		0.66*	-0.12	-0.38	0.14	-0.29	-0.11	-0.51	-0.33
<b>K</b>	-0.73*		0.38	0.08	-0.71*	0.31	-0.37	-0.20	-0.60*	-0.40
<b>Mg</b>	-0.52*		0.58*	-0.02	-0.38	0.23	-0.52*	-0.33	-0.69*	-0.51*
<b>Mn</b>	-0.55*		0.73*	-0.05	-0.33	0.10	-0.46	-0.38	-0.54*	-0.48
<b>Na</b>	-0.35		0.17	-0.01	-0.45	0.35	-0.04	0.23	-0.41	-0.07
<b>P</b>	0.30		0.29	0.24	0.52*	-0.68*	0.41	0.56*	0.12	0.41

Table 2.3 Results (*P*-values) of two-way ANOVA assessing the impacts of vegetation types and elevation on soil properties along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. Ele., Veg., Ele.+Veg., Db, WC, TClay, SClay, TC, TN, and LOI stand for elevation, vegetation type, the interaction between elevation and vegetation type, bulk density, water content, soil clay content at the depth of 0-15 cm, soil clay content at the depth of 15-30 cm, total organic carbon, total nitrogen, and loss-on-ignition, respectively.

	<b>Ele.</b>	<b>Veg.</b>	<b>Ele.+Veg.</b>
	df=1	df=1	df=2
<b>pH</b>	0.9021	0.5433	0.5304
<b>Db</b>	0.1555	0.0190*	0.7554
<b>WC</b>	0.0001***	0.1301	0.3394
<b>TClay</b>	0.0024**	0.0066**	0.05567
<b>SClay</b>	0.0093**	0.2011	0.1963
<b>TC</b>	0.0009***	0.3152	0.1502
<b>TN</b>	0.0256*	0.1976	0.3660
<b>C:N</b>	0.0000***	0.1047	0.07453
<b>LOI</b>	0.0004***	0.3497	0.1668
<b>Al</b>	0.0001***	0.0317*	0.0658
<b>Fe</b>	0.7955	0.1858	0.2419
<b>Ca</b>	0.0282*	0.2413	0.7321
<b>K</b>	0.0007**	0.0390*	0.5129
<b>Mg</b>	0.0206*	0.0965	0.1630
<b>Mn</b>	0.0225*	0.2715	0.1808
<b>Na</b>	0.1594	0.3715	0.1755
<b>P</b>	0.1174	0.0096**	0.2234

Significant codes:  $P < 0.001$ \*\*\*,  $P < 0.01$ \*\* ,  $P < 0.05$ \*.



Table 2.4 Soil wilting point (WP) and field capacity (FC) in the 15 experiment plots along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. The formulas to calculate WP and FC were cited from Blackman 1914, and Saxton *et al.* 1986, respectively. n=3.

Plot (m)	WP (%)		FC (%)	
	0-15 (cm)	15-30 (cm)	0-15 (cm)	15-30 (cm)
<b>300</b>	37.418	47.15	52.65	63.02
<b>350</b>	33.49	54.12	47.27	67.44
<b>400</b>	34.82	48.66	48.59	64.30
<b>450</b>	35.33	47.39	49.77	63.36
<b>500</b>	33.45	42.59	47.19	58.09
<b>550</b>	39.57	48.77	55.30	64.30
<b>600</b>	36.09	46.38	51.17	62.39
<b>650</b>	37.64	46.31	52.49	62.30
<b>700</b>	41.78	47.61	57.73	63.51
<b>750</b>	33.69	38.59	47.01	52.53
<b>800</b>	30.21	34.99	42.46	48.82
<b>850</b>	26.58	33.18	35.94	45.25
<b>900</b>	32.72	41.03	45.42	56.92
<b>950</b>	22.42	31.74	33.56	44.77
<b>1000</b>	23.21	27.07	33.12	36.77

Table 2.5 Soil physicochemical properties in the 15 experiment plots along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. Except for the soils to measure clay content at the depth of 15-30 cm, all the other soil samples were collected at the depth of 0-15 cm. All the soil samples were collected in July, 2009. Standard deviations are in parentheses. pH (H<sub>2</sub>O), pH (KCl), Db, WC, TC, TN, and LOI stand for pH measured in water solution, pH measured in 1 mol/L KCl solution, bulk density, water content, total organic carbon, total nitrogen, and loss-on-ignition, respectively.

Plot (m)	pH (H <sub>2</sub> O)	pH (KCl)	Db (g/cm <sup>3</sup> )	WC (%)	Clay (%) 0-15 cm	Clay (%) 15-30 cm	TC (%)	TN (%)	C:N
<b>300</b>	4.4	3.7	0.8	79.0	59.7	78.6	4.9	0.4	12.9
	(0.4)	(0.4)	(0.0)	(5.8)	(2.4)	(0.8)	(0.6)	(0.0)	
<b>350</b>	4.2	3.4	0.8	71.1	53.0	79.9	5.4	0.4	13.6
	(0.2)	(0.1)	(0.1)	(13.2)	(4.1)	(8.5)	(1.6)	(0.1)	
<b>400</b>	4.6	3.8	0.9	84.0	56.3	81.6	5.5	0.4	13.7
	(0.2)	(0.3)	(0.1)	(11.6)	(10.3)	(12.5)	(0.8)	(0.0)	
<b>450</b>	4.3	3.7	0.6	91.8	56.3	80.0	9.3	0.6	15.1
	(0.2)	(0.2)	(0.1)	(15.7)	(8.5)	(4.1)	(4.4)	(0.3)	
<b>500</b>	4.3	3.7	0.6	92.3	53.0	71.6	10.5	0.6	17.1
	(0.3)	(0.2)	(0.1)	(18.6)	(7.1)	(2.4)	(2.6)	(0.2)	
<b>550</b>	4.6	3.6	0.7	74.0	63.0	81.6	4.3	0.3	15.2
	(0.2)	(0.1)	(0.1)	(0.9)	(0.0)	(6.2)	(0.1)	(0.1)	
<b>600</b>	4.6	3.9	0.6	96.9	56.3	78.3	6.8	0.4	17.2
	(0.1)	(0.1)	(0.1)	(5.2)	(2.4)	(6.2)	(1.1)	(0.1)	
<b>650</b>	4.6	3.8	0.8	87.7	61.3	78.3	8.3	0.5	16.7
	(0.2)	(0.1)	(0.1)	(13.9)	(2.4)	(6.2)	(4.1)	(2.0)	
<b>700</b>	4.6	3.9	0.7	104.3	68.3	80.0	13.1	0.6	20.7
	(0.2)	(0.1)	(0.0)	(12.4)	(3.3)	(4.1)	(0.4)	(0.1)	
<b>750</b>	4.7	4.0	0.9	79.1	54.3	65.0	16.4	0.8	21.9
	(0.3)	(0.2)	(0.1)	(9.6)	(2.4)	(4.1)	(13.4)	(0.6)	
<b>800</b>	4.7	3.9	0.8	89.1	47.7	56.6	13.4	0.6	24.1
	(0.2)	(0.2)	(0.1)	(4.1)	(9.4)	(13.1)	(1.8)	(0.1)	
<b>850</b>	4.9	4.1	0.7	122.3	44.6	55.0	10.2	0.4	23.8
	(0.1)	(0.1)	(0.1)	(16.8)	(4.7)	(4.1)	(1.1)	(0.1)	
<b>900</b>	4.5	3.8	0.7	130.1	53.0	66.6	8.1	0.4	20.8
	(0.1)	(0.0)	(0.1)	(16.5)	(10.8)	(4.7)	(1.9)	(0.1)	
<b>950</b>	4.9	4.1	0.9	137.9	31.3	50.0	12.4	6.8	18.2
	(0.2)	(0.1)	(0.1)	(5.3)	(4.7)	(8.2)	(1.6)	(0.0)	
<b>1000</b>	4.4	3.7	0.9	141	36.3	45.0	20.5	8.3	24.8
	(0.1)	(0.1)	(0.3)	(45.9)	(2.4)	(0.0)	(2.4)	(0.0)	

Table 2.5 (cont.)

<b>Plot</b>	<b>LOI</b>	<b>Al</b>	<b>Ca</b>	<b>Fe</b>	<b>K</b>	<b>Mg</b>	<b>Mn</b>	<b>Na</b>	<b>P</b>
<b>(m)</b>	<b>(%)</b>	<b>(mg/g)</b>	<b>(mg/g)</b>	<b>(mg/g)</b>	<b>(mg/g)</b>	<b>(mg/g)</b>	<b>(mg/g)</b>	<b>(mg/g)</b>	<b>(mg/g)</b>
<b>300</b>	21.4	2.8	0.8	69.4	0.8	1.9	1.3	0.1	2.7
	(0.2)	(3.2)	(0.3)	(6.9)	(0.0)	(0.4)	(0.9)	(0.0)	(0.1)
<b>350</b>	22.6	27.9	0.6	62.6	0.7	1.1	0.2	0.1	0.3
	(4.1)	(2.1)	(0.3)	(4.9)	(0.1)	(0.1)	(0.2)	(0.0)	(0.1)
<b>400</b>	23.1	30.5	0.9	64.3	0.4	2.0	0.5	0.1	0.2
	(2.1)	(4.8)	(0.4)	(4.3)	(0.0)	(0.8)	(0.3)	(0.0)	(0.0)
<b>450</b>	30.3	33.2	1.2	60.7	0.4	1.6	0.4	0.1	3.9
	(6.2)	(4.2)	(0.9)	(9.9)	(0.1)	(0.4)	(0.2)	(0.1)	(0.1)
<b>500</b>	30.5	30.8	1.1	5.2	0.4	1.3	0.1	0.1	0.4
	(4.3)	(4.3)	(0.6)	(10.9)	(0.0)	(0.3)	(0.0)	(0.0)	(0.0)
<b>550</b>	22.3	35.4	0.5	7.3	0.3	2.3	0.3	0.1	0.3
	(1.9)	(6.3)	(0.1)	(0.6)	(0.0)	(0.8)	(0.2)	(0.0)	(0.0)
<b>600</b>	26.4	31.3	0.2	6.6	0.2	1.0	0.1	0.1	0.2
	(1.7)	(3.1)	(0.0)	(1.0)	(0.0)	(0.6)	(0.0)	(0.0)	(0.0)
<b>650</b>	30.2	46.8	0.5	7.1	0.3	3.1	0.3	0.1	0.2
	(0.5)	(8.8)	(0.3)	(6.4)	(0.0)	(1.5)	(0.2)	(0.0)	(0.0)
<b>700</b>	35.6	38.8	1.3	6.7	0.4	1.9	0.2	0.1	0.3
	(5.2)	(4.6)	(0.5)	(13.8)	(0.1)	(0.7)	(0.0)	(0.0)	(0.0)
<b>750</b>	43.9	42.3	0.6	7.3	0.7	0.4	0.1	0.1	0.3
	(19.5)	(10.6)	(0.6)	(24.8)	(0.2)	(0.3)	(0.0)	(0.1)	(0.1)
<b>800</b>	35.7	32.5	0.5	3.9	0.3	0.6	0.0	0.1	0.3
	(3.7)	(2.5)	(0.2)	(11.4)	(0.2)	(0.3)	(0.0)	(0.0)	(0.0)
<b>850</b>	35.0	45.5	0.4	10.5	0.1	0.6	0.2	0.0	0.4
	(1.8)	(14.5)	(0.2)	(6.5)	(0.1)	(0.4)	(0.1)	(0.0)	(0.1)
<b>900</b>	28.0	36.8	0.1	8.2	0.2	0.2	0.6	0.1	0.3
	(3.4)	(2.4)	(0.0)	(6.5)	(0.0)	(0.1)	(0.6)	(0.0)	(0.0)
<b>950</b>	36.0	57.0	0.8	6.4	0.3	2.7	0.2	0.1	0.6
	(2.3)	(5.9)	(0.1)	(8.9)	(0.0)	(0.8)	(0.1)	(0.0)	(0.1)
<b>1000</b>	48.3	44.6	0.2	3.2	0.1	0.1	0.0	0.1	0.4
	(2.7)	(3.7)	(0.1)	(20.7)	(0.0)	(0.1)	(0.0)	(0.0)	(0.1)

Table 2.6 Results (*P*-values) of linear regression between soil properties and elevation (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. pH (H<sub>2</sub>O), Db, WC, TClay, SClay, TC, TN, and LOI stand for pH measured in water solution, bulk density, water content, soil clay content at the depth 0-15 cm, soil clay content at the depth 15-30 cm, total organic carbon, total nitrogen, and loss-on-ignition, respectively.

<b>pH (H<sub>2</sub>O)</b>	<b>Db</b>	<b>WC</b>	<b>TClay</b>	<b>SClay</b>	<b>TC</b>	<b>TN</b>	<b>C:N</b>	<b>LOI</b>
0.8960	0.2470	<0.0001	0.0232	0.0125	<0.001	0.0282	<0.00001	<0.0003
		***	*	*	***	*	***	***
<b>Al</b>	<b>Fe</b>	<b>Ca</b>	<b>K</b>	<b>Mg</b>	<b>Mn</b>	<b>Na</b>	<b>P</b>	
0.00066	0.8140	0.0222	0.0015	0.0389	0.0284	0.1810	0.2521	
***		*	**	*	*			

Significant codes: *P*<0.0001<sup>\*\*\*</sup>, *P*<0.01<sup>\*\*</sup>, *P*< 0.05<sup>\*</sup>.

## FIGURES CAPTIONS

Figure 2.1 All the 15 experiment plots were located along the elevation gradient (from 300 m to 1000 m) with different vegetation types in the Luquillo Experimental Forest, northeastern Puerto Rico.

Figure 2.2 Variation in soil clay contents both at the depth of 0-15 cm and 15-30 cm in the 15 experiment plots along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. Bars stand for standard errors (n=3).

Figure 2.3 Soil pH at the depth of 0-15cm in the 15 experiment plots along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. pH values were measured in both H<sub>2</sub>O and 1 mol/L KCl solution. Bars stand for standard errors (n=3).

Figure 2.4 Variation in extractable mineral elements of the soils at the depth of 0-15 cm in the 15 experiment plots along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. Bars stand for standard errors (n=3). The units for all the 8 mineral elements are mg/g. a). Aluminium (Al). b). Potassium (K). c). Magnesium (Mg). d). Manganese (Mn). e). Iron (Fe). f). Sodium (Na). g). Phosphorus (P). h). Calcium (Ca).

Figure 2.5 Variation in total organic carbon, total nitrogen, loss-on-ignition, and C to N ratio of the soils at the depth of 0-15 cm in the 15 experiment plots along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico. Bars stand for

standard errors (n=3). a). Total organic carbon (%). b). Total nitrogen (%). c). Loss-on-ignition percentage (%). d). C to N ratio.

Figure 2.6 Linear regressions of water content, total organic carbon, Al, K, loss-on-ignition and C to N ratio of the soils at the depth of 0-15 cm in the 15 experiment plots along the elevation gradient (from 300 m to 1000 m) in the Luquillo Experimental Forest, Puerto Rico.

a). Water content (%). b). Loss-on-ignition percentage (%). c). Total organic carbon (%). d). C to N ratio. e). Al (mg/g). f). K (mg/g).

Figure 2. 1

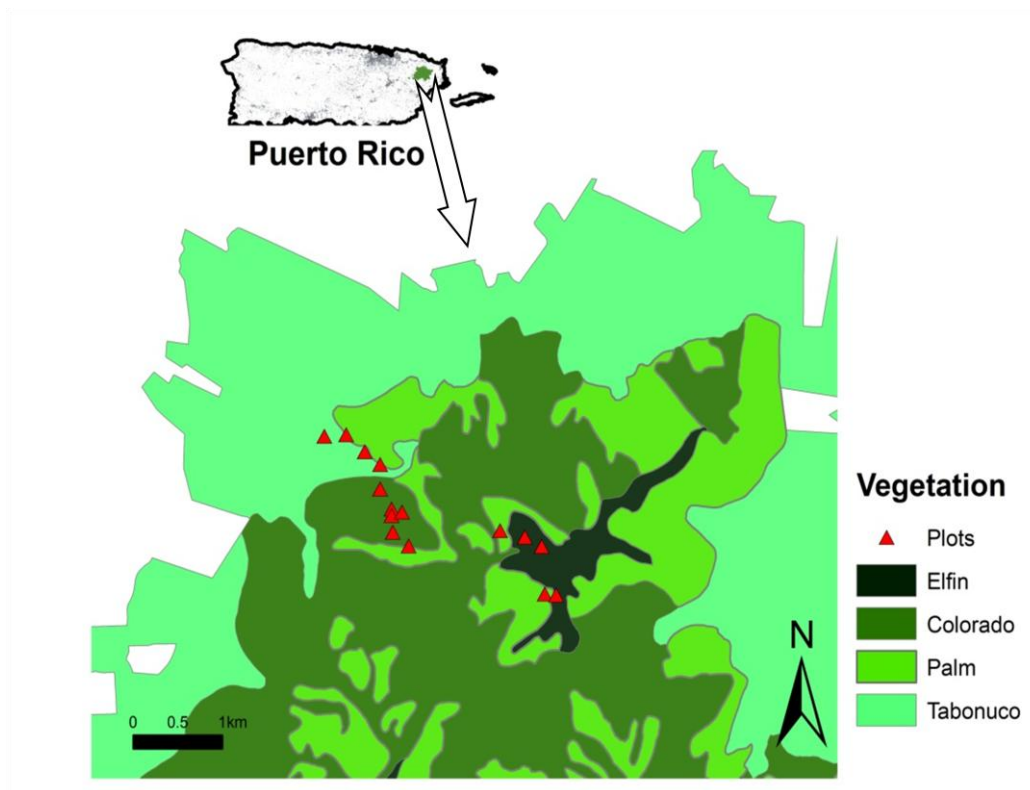


Figure 2.2

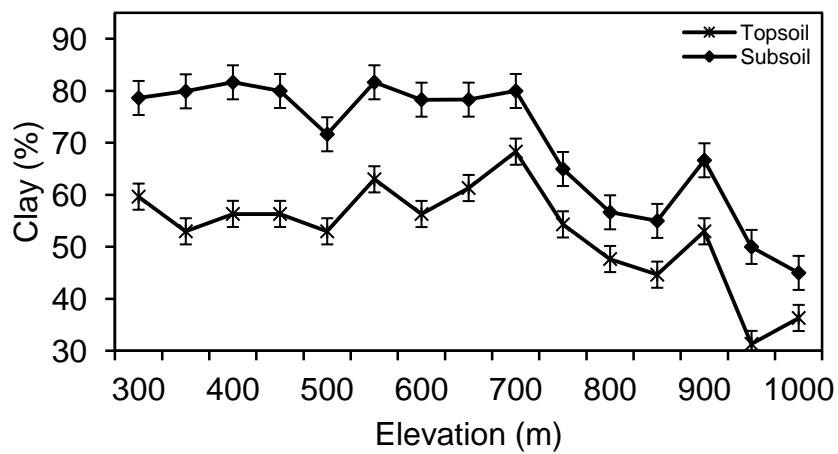




Figure 2.3

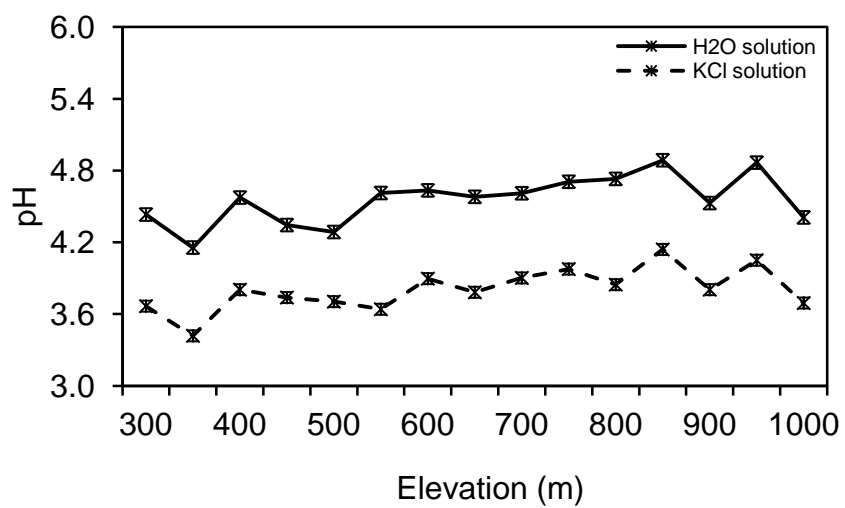


Figure 2.4

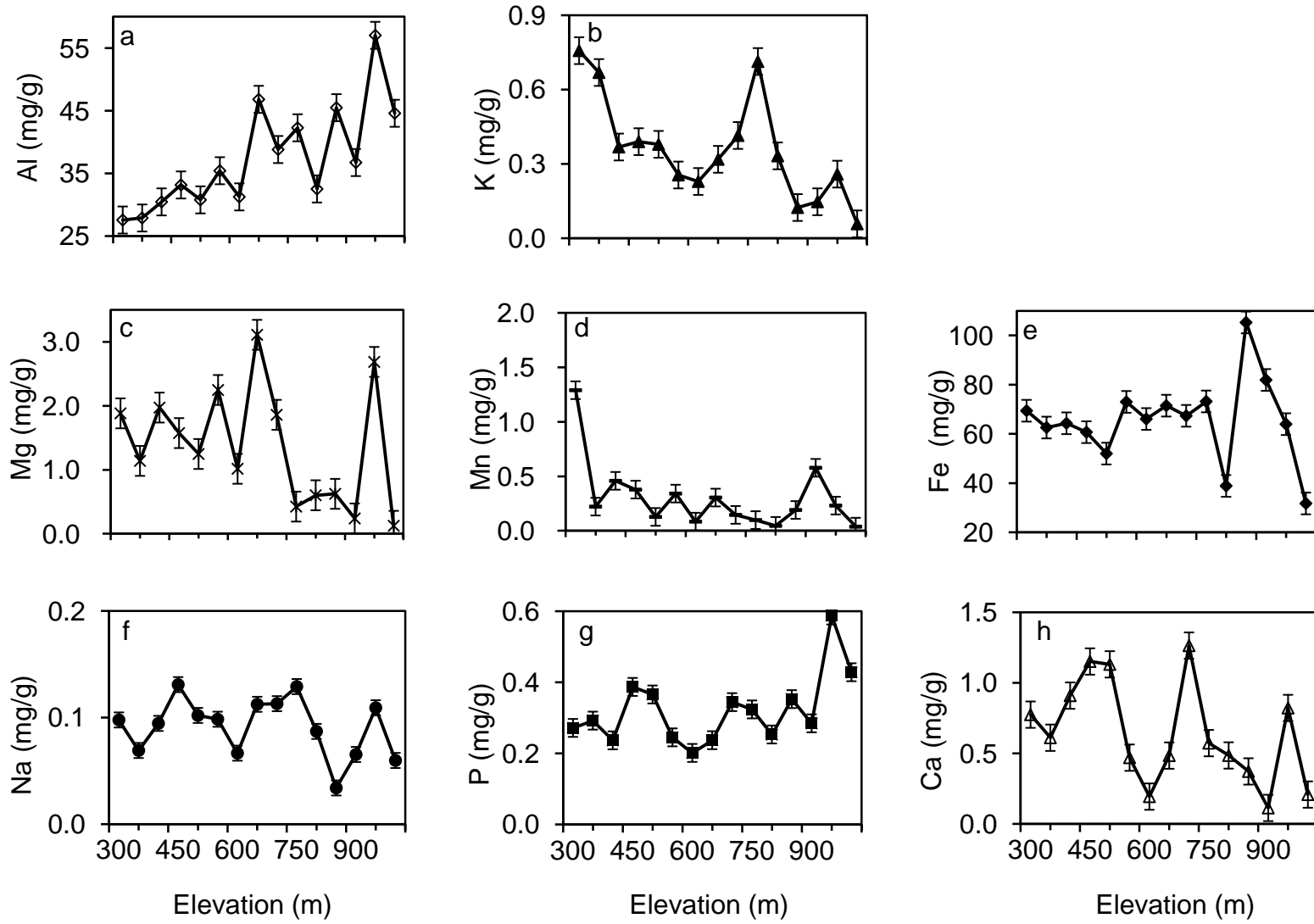


Figure 2.5

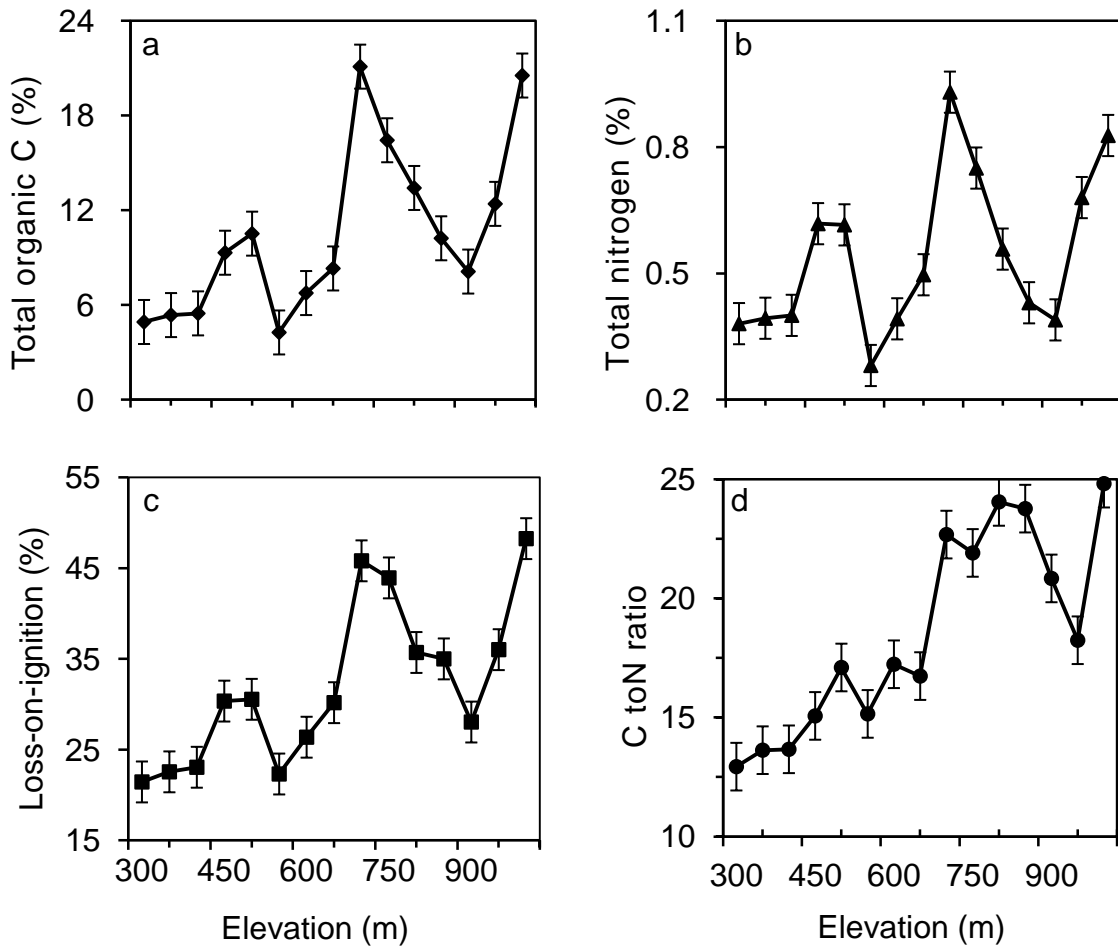
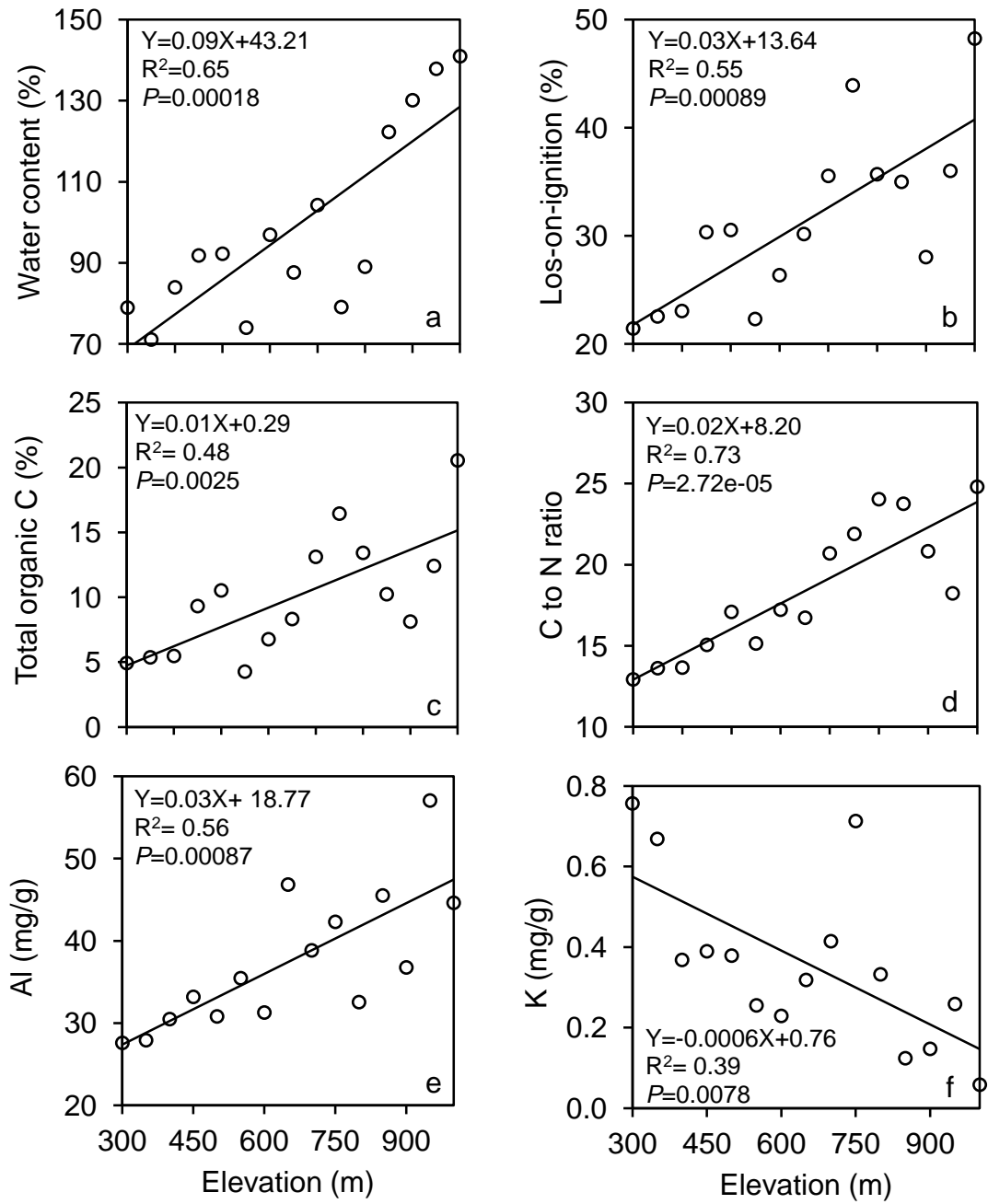
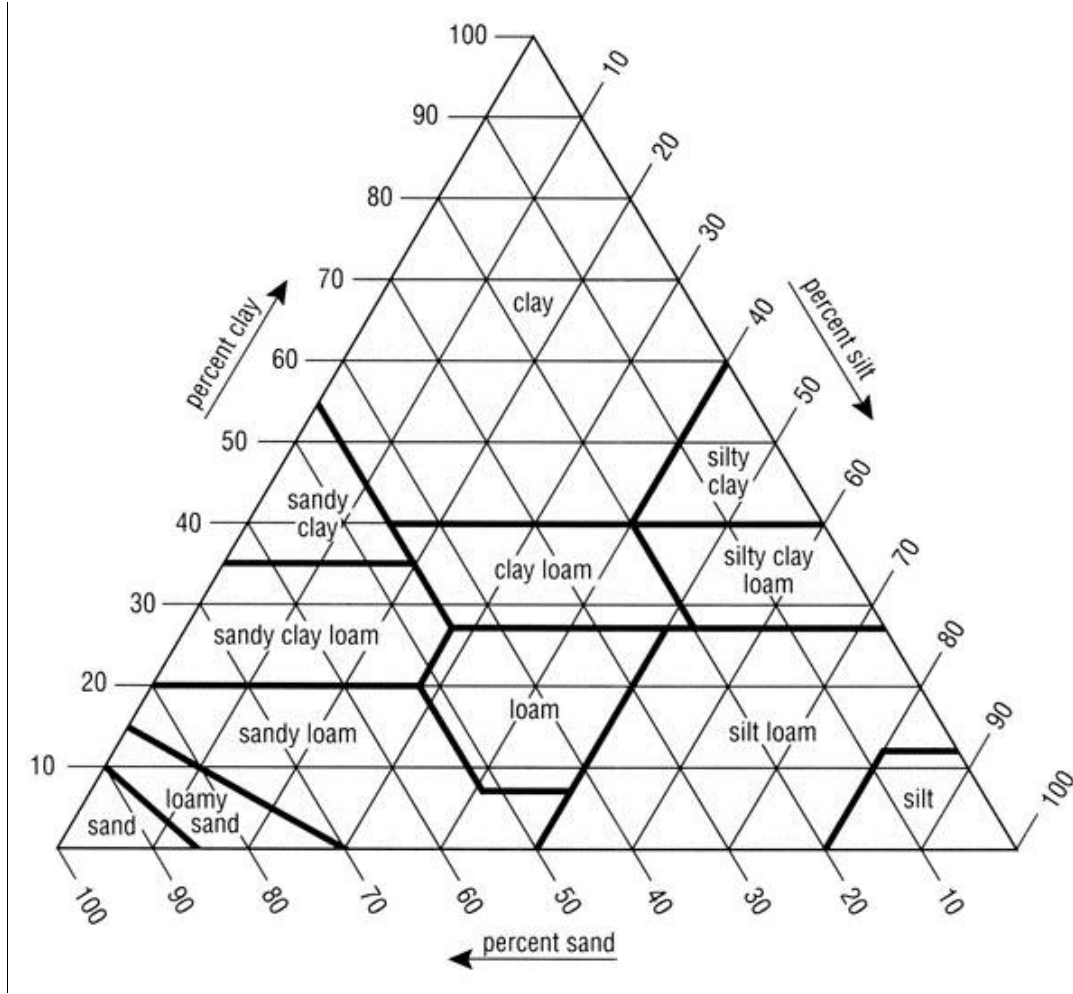


Figure 2.6



Appendix 2.1 Soil texture classification by USDA (Schoeneberger *et al.* 2002).



## **CHAPTER III**

### **CLIMATE IMPACTS ON SOIL CARBON PROCESSES ALONG AN ELEVATION GRADIENT IN THE LUQUILLO EXPERIMENTAL FOREST, PUERTO RICO**

The Luquillo Experimental Forest (LEF) is a tropical wet montane forest. With the altered temperature and moisture conditions along the elevation gradient, the vegetation displays a distinct altitudinal pattern from lower elevation to the summit. The elevation range in the LEF provides a natural gradient to understand factors driving long-term changes in tropical forest ecosystems. In this study, we conducted a soil translocation experiment along an elevation gradient to study the impacts of climate change on soil organic matter (SOM) and soil respiration.

As the results showed, both soil carbon and respiration rate were influenced by climate change, specifically by variation in temperature and moisture. Soils translocated from the high elevation to the low elevation showed increased respiration rate with lower SOC content at the end of experiment, which indicated the increased temperature at low elevation enhanced decomposition rate. Soils translocated from the low elevation to the high elevation also showed increased respiration rate with decreased soil organic carbon (SOC) content at the end of experiment, which might be related to the increased soil moisture and altered soil microbes. With the predicted warmer climate in the Caribbean areas, the tropical soils in high elevation forests are under risk to release sequestered carbon to the atmosphere.

## **Introduction**

Soil respiration, defined as CO<sub>2</sub> emissions from the soil surface through the activities of soil microbes, plant roots and other organisms, is one of the main pathways to release carbon fixed by vegetation to the atmosphere (Townsend *et al.* 1995, Schlesinger & Andrews 2000). Because the quantity of carbon stored in soils is double of that stored in either the atmosphere or the terrestrial vegetation, soil respiration is a critical component in the global carbon cycle (Townsend *et al.* 1995, Silver 1998). At steady state, the carbon emissions from

soil, as the second largest carbon flux between the atmosphere and the terrestrial biomes, can be balanced by CO<sub>2</sub> net uptake by plants (net primary productivity, i.e., NPP) (Townsend *et al.* 1995, Wan *et al.* 2007). However, any small changes in soil respiration caused by climate change could have huge impacts on global carbon cycle and future global climate (Schlesinger & Andrews 2000, Wan *et al.* 2007). Especially, with current rapid climate change due to the greenhouse effects, the variation in soil respiration rate alters soil carbon storage patterns progressively, and eventually soils may exhibit a positive response to global climate change by releasing more carbon to the atmosphere (Atkin *et al.* 2000, Cramer *et al.* 2001, Conant *et al.* 2004, Wan *et al.* 2007).

Soil respiration involves the interactions among plant roots, rhizosphere, soil microbes, soil fauna and other physicochemical conditions (Baggs, 2006). It mainly consists of two parts (autotrophic respiration and heterotrophic respiration) and three processes: biotic, chemical, and physical processes (Baggs, 2006). Experiments indicated that changes in environmental conditions, especially climate, will affect soil respiration rate, which eventually bring a significant impact on global carbon cycle (Cramer *et al.* 2001, Kane *et al.* 2003, Wan *et al.* 2007). Many important hypotheses on soil respiration have been proposed in the early studies, which focused on the influencing factors, and the relations with terrestrial ecosystem structure and function such as productivity (Raich & Tufekcioglu 2000, Qi *et al.* 2002, Conant *et al.* 2004, Müller & Höper 2004, Li *et al.* 2006). The interaction between soil respiration and global carbon cycle, and future climate have also been well studied (Markham 1996, Cramer *et al.* 2001, Foster 2001, Rustad 2008). According to these studies, soil temperature, moisture, and carbon substrate for microorganisms (which is



related to vegetation type) are three main factors influencing soil respiration rate (Atkin *et al.* 2000, Cramer *et al.* 2001, Conant *et al.* 2004, Zimmermann *et al.* 2009).

Temperature influences almost all the aspects of soil respiration. Soil respiration generally increases exponentially with temperature (Raich & Tufekcioglu 2000, Qi *et al.* 2002, Kane *et al.* 2003, Li *et al.* 2005). Temperature mainly functions by affecting the soil fauna and microbial activities and controlling decomposition rate (Heneghan *et al.* 1999, González & Seastedt, 2001, Li *et al.* 2006, Dechaine *et al.* 2005). When temperature reaches a certain maximum point, most of the enzymatic activity involved in the respiration processes will be inhibited due to enzyme malfunction and soil respiration stops to increase (Sjögerstern & Wookey 2002, Lawrence *et al.* 2009). The behavior and function of soil fauna and microbes are partially dependent on temperature, too. While temperature is beyond their tolerance, their activities and then litter decomposition will be inhibited correspondingly (Mikan *et al.* 2002). For example, “cryophile functions ideally at temperature below 20°C, while mesophile functions optimally at temperature between 20°C and 40°C, and thermophile functions best at over 40°C” (Mikan *et al.* 2002). In a study on the response of root respiration to changes in temperature, root respiration tended to shut down completely at temperature above 35°C (Atkin *et al.* 2000). It is widely accepted that temperature is one of the main factors to affect soil respiration, whereas soil respiration usually increases with temperature (Raich & Schlesinger 1992, Lloyd & Taylor 1994, Kirschbaum 1995, Silver 1998, Knorr *et al.* 2005).

Soil moisture is another important factor influencing soil respiration rate and is generally considered to positively correlate with soil respiration (Raich & Tufekcioglu 2000, Sjögersten & Wookey 2002, Kane *et al.* 2003, Li *et al.* 2005). Soil respiration, especially root

respiration accounting for almost half of soil respiration, is relatively low in dry conditions, and increases to a maximum at intermediate moisture conditions (Sjögersten & Wookey 2002, Kane *et al.* 2003, Zimmerman *et al.* 2009). Lacking of water can limit root respiration, as well as the activities of soil fauna and soil microbes, although some microorganisms develop strategies to survive and grow under low soil moisture conditions (Xu *et al.* 2004, Lawrence *et al.* 2009). Moreover, under certain soil humidity, some soil bacteria and fungi may take in too much water via diffusion, or other transporting processes through cell membrane, which may cause cell membranes to lyse, or some other physiological damages. This broken-to-dead microorganism debris provides rapid available decomposing substrates, which actually can temporally increase heterotrophic respiration (Xu *et al.* 2004, Li *et al.* 2005 & 2006, Lawrence *et al.* 2009). On the other hand, when soil is saturated, oxygen can be excluded. Anaerobic conditions can depress aerobic microbial activities which ultimately results in a limited soil respiration (Sjögersten & Wookey 2002, Li *et al.* 2005, Lawrence *et al.* 2009). Another mechanism of the effects of soil moisture on soil respiration rate is related to the availability of soil nutrients (Qi *et al.* 2002, Kane *et al.* 2003, Li *et al.* 2005, Lawrence *et al.* 2009). Some of the nutrients available to plants and soil microorganisms need to be dissolved in water solution (e.g., N) (Rastetter *et al.* 1991, Gifford 1994, Raich & Schlesinger 1992, Raich & Tufekcioglu 2000).

The influencing of soil moisture on soil respiration differs from site to site. “Soil moisture can have a significant influence in semiarid ecosystems, particularly during the dry and warm seasons of the year” (Conant *et al.* 2004). But in some ecosystems with relatively high humidity, soil moisture may not significantly affect soil respiration (Kane *et al.* 2003). “Partially because of the similar relative high soil moisture of all the sites, the soil moisture

was only important during warm and dry periods” (Kane *et al.* 2003). Furthermore, the effects of moisture combined with temperature were suggested experimentally to be more reliable (Kane *et al.* 2003, Conant *et al.* 2004, Li *et al.* 2006, Wan *et al.* 2007).

The availability of soil carbon substrate to microorganisms and vegetation type are the other two factors influencing soil respiration, especially heterotrophic respiration (Raich & Tufekcioglu 2000, Wang *et al.* 2003, Vance & Chapin III 2001, Blagodatsky *et al.* 2010). Heterotrophic respiration (i.e., CO<sub>2</sub> emissions produced through SOM decomposition) is primarily driven by the activities of soil microorganisms and fauna, and their richness and abundance primarily control the decomposition rate of SOM (Heneghan *et al.* 1999, González & Seastedt 2001, Dechaine *et al.* 2005, Li *et al.* 2006). The spatial distribution of soil microbes, to a great extent, is affected by the availability of carbon substrate (Rastetter *et al.* 1991, Gifford 1994, Schlesinger & Andrews 2000, Vance & Chapin III 2001). Moreover, soil microbes themselves have particular C:N balance needs (Vance & Chapin III 2001, Blagodatsky *et al.* 2010). Therefore, soil carbon substrate affects soil respiration by controlling the distribution and activities of soil fauna and microbes.

Soil respiration rate varies with vegetation type (Raich & Tufekcioglu 2000, Smith & Johnson 2004, Li *et al.* 2005). The global mean soil respiration rates varied widely among major vegetation biomes (Raich & Tufekcioglu 2000). “The lowest rates occurred in tundra and northern bogs, while the highest rates occurred in tropical moist forests” (Raich & Tufekcioglu 2000). Although the distribution patterns of soil respiration rates in these biomes may be partially affected by temperature and moisture, these results still exemplified that there was a close relation between soil respiration rate and vegetation type (Raich & Tufekcioglu 2000). The difference in soil CO<sub>2</sub> emission rates between a secondary forest and

a pine plantation was reported in the Luquillo Experimental Forest in Puerto Rico (Li *et al.* 2005). The impacts of vegetation on soil respiration were mainly through affecting soil microclimate and forest structure, the quantity and quality of detritus supplied to the soils, and by changing the rate of plant root respiration (Kleb *et al.* 1997, Raich & Tufekcioglu 2000, Smith & Johnson 2004).

Almost all the environmental conditions influencing soil respiration rate (e.g., forest type, solar radiation, temperature & moisture, and soil fauna such as earthworms) have distinct elevation patterns in the LEF. Usually temperature, NPP, and plant species richness and abundance decrease with elevation from low to high, whereas SOM, SOC, precipitation and soil moisture increase (Lovett 1996, Bruijnzeel & Veneklaas 1998, Vazquez G & Givnish 1998, Gould *et al.* 2006, Barone *et al.* 2008). “The number of earthworm species also significantly increased along elevation from low to top” (González *et al.* 2007). The elevation gradient provides a natural *in situ* simulation of climate change (Townsend *et al.* 1995, Kane *et al.* 2003, Zimmermann *et al.* 2009 & 2010). Therefore, to study the variation in soil carbon along an elevation gradient in the LEF is an ideal approach to estimate the impacts of climate change on carbon processes and their responses. The elevation gradient approach has been experimentally proved to be very practical (Kane *et al.* 2003, Zimmermann *et al.* 2009). In this study, we conducted a soil translocation experiment along the elevation gradient in the LEF to study the impacts of climate change on SOC and soil respiration.

## Methods and Materials

### *Study area*

All the experiment plots were located in the same elevation gradient as the soil properties experiment in the LEF (18°20'N, 65°49'W), northeastern Puerto Rico (Figure 2.1 in Chapter II). The LEF is a tropical wet montane forest. “Rainfall ranges from an average of 3,537 mm per year at low elevation to 4,849 mm per year at high elevation” (Garcia-Martinó *et al.* 1996). Moisture is generally not a limiting factor with such high annual rainfalls in the LEF. The soils in the LEF are mainly derived from volcaniclastic sediments, which can be classified as “Clay” according to their particles proportion, except for one high-elevation area where the soil are derived from quartz diorite with lower clay content (Sieders 1971, Barone *et al.* 2008). The distribution of vegetation in the LEF exhibits distinct elevation pattern. Four typical forest types with different dominant species and forest structure distribute along the elevation gradient: tabonuco forest, palm forest, palo colorado forest, and elfin woodland, respectively (Weaver 1991 & 2000, Gould *et al.* 2006).

### *Soil translocation experiment*

A soil translocation experiment was performed among three plots along the elevation gradient in the LEF, with their elevations at 350 m, 600 m, and 1000 m, respectively. The typical forest types in the three soil translocation plots change from tabonuco to palo colorado. Nine soil cores were excavated from each plot, six of them were translocated to the other two plots (three for each), and three soil cores remained at the source plot but different places. Before collecting the samples, all the aboveground litters were removed. The organic-rich soils (0-5 cm) were collected separately and later put back on the top of soil cores after

reinstalled in the destination plots. The soil cores were taken by a polystyrene tube with 10 cm in diameter and 15 cm in length. When excavating the soil cores, the tubes were inserted vertically into subsoil to take an intact soil monolith with a depth of 15 cm. When reinstalling soil cores, the bottom of coring tube was covered with iron mesh (63- $\mu\text{m}$ ) to prevent large roots to grow in and to balance the effects of temperature and moisture on the soil within and outside the tubes.

In each of the three soil translocation plots, one soil temperature and one moisture probe were installed at both surface and 15 cm deep in a undisturbed place and connected to a data logger (HOBO<sup>®</sup> Micro station, ONSET Computer Corporation, Bourne, MA, USA). Soil temperature and moisture were recorded every 30 minutes. The soil translocation experiment lasted 11 months from July 2011 to May 2012.

Soil respiration rates ( $R_s$  rates) were measured monthly with a portable Infra Red Gas Analyser (EMG4, PP Systems, Amesbury, MA, USA), with a cylindrical cuvette (CPY-2) inserted in soil cores. The soil respiration fluxes were recorded for 2-3 min after the  $\text{CO}_2$  concentration in the closed chamber increased steadily. Soil respiration fluxes were estimated by linear regression of  $\text{CO}_2$  concentration versus time with air temperature, adjusted chamber volume and pressure. The real-time temperature and moisture for both soil and air were measured with external sensors or thermometer. All the measurements were repeated three times. At the end of the soil translocation experiment, SOC and SOM contents of all the soil cores were measured (Chemistry Laboratory, International Institute of tropical Forestry (IITF), USDA, Forest Service, Río Piedras, Puerto Rico). The methods of soil sampling, sample preparation and lab analyses were as the same as the ones used in the soil properties study (see Chapter II).

## *Statistical analyses*

Pearson product-moment correlation coefficients were used to test the correlations between Rs rate and soil temperature & moisture. Multiple paired-t tests were used to test the effects of initial SOC and SOM contents on Rs rate. Repeated measurement analysis of variance (RMANOVA) and two-way ANOVA were used to evaluate the impacts of the treatments (the soil source and destination plot) on Rs rates. For all analyses, the significance level was set at  $P\text{-value} \leq 0.05$ . The units for soil respiration rate and daily respiration fluxes were  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $\text{g-CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ , respectively. Statistical analyses were run in R software (2.15.1, R Development Core Team 2010). To account for the daily variation, Rs rates were standardized by  $Q_{10}$  values using the formula of  $R_{S_t}/R_{S_{t_{\text{ave}}}} = Q_{10}^{((t-t_{\text{ave}})/10)}$  at the daily average temperature (Van't Hoff 1898). The  $Q_{10}$  values for the three soil translocation plots were estimated by regression of Rs on temperature. Daily soil respiration fluxes were estimated by the  $Q_{10}$  values. By comparing the adjusted Rs rates, we analyzed the impacts of microclimate conditions and initial SOC and SOM on soil carbon processes in the LEF.

## **Results**

### *Patterns of soil temperature and moisture*

The monthly average temperature decreased with elevation from 350 m to 1000 m (Figure 3.1). Through the experiment period from July 2011 to March 2012, the monthly average temperature in each of the three soil translocation plots also decreased over time (Figure 3.1). However, in January 2012, the monthly average temperature in plot 600 m was slightly higher than that of plot at 350 m (less than  $0.5^\circ\text{C}$ ). The patterns of the monthly average soil moisture were relatively complex. At 600 m, the surface moisture was the

lowest, while the moisture at the depth of 15 was the highest, among the three plots (Figure 3.1), which may be related to the vegetation dominated by palms. With the floating roots of palms, the surface runoff was increased while the subsoil water was prevented to leach away by the thick fibrous roots of palms. However, through the experiment period from July 2011 to March 2012, the average soil moisture (0-15 cm) still showed increased trend with increased elevation (Figure 3.1). For the three soil translocation plots, the moisture increased with elevation, from  $0.27 \text{ m}^3/\text{m}^3$  at 350 m, to  $0.32 \text{ m}^3/\text{m}^3$  at 600 m, and to  $0.4 \text{ m}^3/\text{m}^3$  at 1000 m (Figure 3.2), while the average temperature decreased with elevation, from  $22.2^\circ\text{C}$  at 350 m, to  $21.2^\circ\text{C}$  at 600 m, and to  $20.2^\circ\text{C}$  at 1000 m (For the plot at 1000 m, the temperature data at both 0 cm and 15 cm in November 2011 were missing, since too few days were recorded to estimate monthly average. From December 2011 to February 2012, the temperature data at 15 cm were missing.) (Figure 3.2).

#### *Variation in SOC and SOM after translocation*

Prior to the soil translocation experiment, both SOC and SOM (measured as loss-on-ignition percentage, LOI) in the three soil translocation plots increased significantly with elevation from low to top. SOC increased from 5.36% at 350 m to 6.76% at 600 m, and to 20.54% at 1000 m, and SOM increased from 22.55% to 26.37% to 48.25%, respectively (Figure 3.3). When measured 11 months after translocation, both SOC and SOM contents still increased with elevation from low to top (Figure 3.3). However, compared to the contents before translocation, SOC increased to 6.35% of the soils with the source plot at 350 m, 7.48% for the soils with the source plot at 600 m, and 21.35% for the soils with the source plot at 1000m (Table 3.1). C to N ratio increased along the elevation gradient from low to top both before and after the soil translocation experiment (Figure 3.3).



### *Variation in of soil respiration rates*

The results ( $P$ -values) of Pearson product-moment correlation coefficients showed that the natural logarithms of daily  $R_s$  fluxes were positively related with temperature, and the correlation between temperature and the natural logarithms of  $R_s$  rates of the soils originating from the plot at 1000 m was significant ( $P \leq 0.05$ ) (Table 3.2). The correlations between moisture and the natural logarithms of  $R_s$  rates were not significant ( $P > 0.05$ ) (Table 3.2).

Multiple paired- $t$  tests, RMANOVA, and two-way ANOVA were used to test the impacts of the treatments (the soil source and destination plot) on the  $R_s$  rates. The multiple paired- $t$  tests showed that the mean  $R_s$  rates between the soils originating from 350 m and those from 1000 m, between the soils originating from 600 m and those from 1000 m, were significantly different ( $P < 0.05$ ) (Table 3.3). The mean  $R_s$  rates between the soils with the destination plots at 600 m and those with destination at 1000 m, between the soils with the destination plots at 600 m and those with destination at 350 m, were also significantly different ( $P < 0.05$ ) (Table 3.3). The results of RMANOVA were not significant ( $P > 0.05$ ). The results of two-way ANOVA indicated that the treatments (both the soil source and destination plot) had significant impacts on  $R_s$  rates in the LEF ( $P < 0.001$ ).

To account for the impacts of the daily variation in temperature on  $R_s$  rates, all the measured  $R_s$  rates were standardized by a  $Q_{10}$  at the daily average temperature (Table 3.4). The  $Q_{10}$  values, estimated by regression of  $R_s$  on temperature, increased with elevation from 3.1 ( $P = 0.04$ ) at 350 m, to 6.9 ( $P = 0.2$ ) at 600 m, and to 8.7 ( $P = 0.12$ ) at 1000 m. Daily  $R_s$  fluxes were estimated by the  $Q_{10}$  values (Table 3.4).

In the plot at 350 m, the differences between daily  $R_s$  fluxes of the soils originating from 350 m and those of 1000 m, between daily  $R_s$  fluxes of the soils origination from 600 m

and those of 1000 m, were significant ( $P<0.05$ ) (Figure 3.4). Daily Rs fluxes of the soils originating from 1000 m were higher than those of the soils originating from 350 m, and 600 m (Figure 3.4). Through the experiment period, the daily Rs fluxes of the soils with the destination plot at 350 m were significantly higher than those of the soils with the destination plot at 600 m ( $P<0.05$ ) (Figure 3.4). The daily Rs fluxes of the soils with the destination plot at 1000 m were also higher than those of the soils with the destination plot at 600 m ( $P<0.05$ ) (Figure 3.4).

Daily Rs fluxes of the soils originating from high elevation, but translocated to low elevation, significantly increased ( $P<0.05$ ) (Figure 3.5). For example, the soils originating from 600 m, and 1000 m, respectively, had higher daily Rs fluxes at 350 m than those at 600 m (Figure 3.5). Daily Rs fluxes of the soils originating from 1000 m, but translocated to 350 m were also higher than those of the soils originating from 1000 m, but translocated to 1000 m (Figures 3.5). However, daily Rs fluxes of some soils originating from low elevation, but translocated to high elevation also increased ( $P<0.05$ ) (Figures 3.5). For example, the soils originating from 350 m, but translocated to 600 m had higher daily Rs fluxes than those of the soils originating from 350 m, but translocated to 350 m (Figures 3.5). Daily Rs fluxes of the soils originating from 600 m, but translocated to 1000 m were also higher than those of the soil originating from 600 m, but translocated to 600 m (Figures 3.5).

## **Discussion**

Temperature usually decreases about 0.5-0.6°C per 100 m with increased elevation. From July 2011 to March 2012, the difference between the monthly average temperature at 350 m and that at 1000 m was less than 2°C (22.2°C at 350 m, and 20.1°C at 1000 m) (Figure 3.2). The monthly average temperature at 600 m was close to that at 350 m in January 2011.

One possible reason was that the plot at 350 m had more rainfall in January than that at 600 m, which eventually lowered temperature at 350 m. Compared to the content before translocation, SOC increased slightly, which might be caused by the degradation of dead roots and litters involved in the soil cores.

Soil  $Q_{10}$  is an exponential coefficient to estimate the variation in soil C fluxes with every 10°C increases in temperature (Van't Hoff 1989). Although there is no consensus about the functions of the relationship between temperature and soil respiration (Xu & Qi 2012),  $Q_{10}$  is still a widely used parameter to describe the temperature sensitivity of soil C (Fang & Moncrieff 2001). Our estimated  $Q_{10}$  values increased along the elevation from low to top in the LEF. This result was consistent with the existing studies that  $Q_{10}$  values increases with increased elevation, whereas decreased temperature (Sjögersten & Wookey 2002, Chen & Tian 2005, Zimmermann *et al.* 2009).

As one important factor influencing carbon processes, temperature is considered to have positive effects on SOM decomposition and soil respiration rate (Kirschbaum 2006, Li *et al.* 2006, Sayer *et al.* 2011). In our experiment, daily  $R_s$  fluxes of the soils translocated from high elevation (600 m, and 1000 m) to low elevation (350 m) increased (Figures 3.4 and 3.5). Daily  $R_s$  fluxes of the soils at 350 were higher than those at 600 m (Figure 3.4). These increases in daily  $R_s$  fluxes indicated that temperature had a positive effect on soil respiration. However, the results of Pearson product-moment correlation (Table 3.2), and two-way ANOVA analysis showed that other conditions such as the soil source, and moisture could impact soil respiration. The increases in the  $R_s$  rates of the soils translocated to high elevation (Figures 3.5) also indicated that temperature alone could not predict the pattern of

soil respiration rates in the LEF. Soil moisture had a positive effect on soil respiration (Table 3.2).

The Rs rates varied among soil cores in the plot at 350 m ( $P < 0.05$ ), particularly, the soils originating from 1000 m had higher Rs rate than those from 350 m and 600 m (Figure 3.4). These soils were translocated from different source plots, thus with different SOC and SOM, to the same destination plot with the same climate and other environmental conditions. The variation in the Rs rates of these soils revealed that the quality and quantity of initial SOC and SOM had significant impacts on decomposition rates.

The environmental controls on soil carbon processes are complex. As our results showed, the soils with the destination plots at low elevation with high temperature were not certain to have higher Rs rates than those of the soils with the destination plots at high elevation with low temperature (Figure 3.4). For example, the Rs rates of the soils at 1000 m were higher than those of the soils at 600 m (Figure 3.4). These changes in Rs rates might be explained by the interaction among temperature, soil moisture, soil fauna and soil microbial biomass. Soil moisture increased with increased elevation and reached the highest at 1000 m (Figure 3.2), which stimulated the decomposition rate. Many experimental studies showed that soil fauna and microbes vary with microclimate conditions, soil properties (e.g., clay), and vegetation (which mainly affects litter fall input, and substrate supply) (Wang *et al.* 2003, Müller & Höper 2004, Ruan *et al.* 2004, Wang *et al.* 2009). The soil fauna and microbes from high elevation (e.g., 1000 m) might prefer the SOC and SOM with lower C to N ratio originating from lower elevation (e.g., 600 m) (Sjögersten & Wookey 2002). Particularly, soil microbial mass positively relate to SOM (Wang *et al.* 2003, Müller & Höper 2004). In our case, since SOM increases with increased elevation (Figure 3.4), soil microbial mass

might increase along the elevation from low to top in the LEF. Therefore, the increased  $R_s$  rates of the soils translocated from low elevation to high elevation might indicate that the impacts of soil moisture, microbes, and microbial mass outweighed the limitation of decreased temperature.

Our results were consistent with the conclusions of other studies. Kane *et al.* (2003) measured soil respiration rates along a gradient in the Olympic National Park, Washington, U.S.A, and their results showed that soil temperature at higher elevation site were 4.5°C lower than that at low elevation. However, “there were no significant relations between soil respiration rates and temperature” (Kane *et al.* 2003). Similarly, in a study on climate dependence of heterotrophic soil respiration along a 3000 m elevation gradient in a tropical forest in Peru, Zimmermann *et al.* (2009) also concluded that soil respiration rate did not vary significantly along the elevation gradient with temperature decreasing from low to high elevation, although SOC stocks increased markedly and linearly with increased elevation.

Under current global warming, the balance of carbon cycle primarily depends on the differences between the responses of productivity and respiration to climate change (Malhi *et al.* 2000, Clark 2004, Sayer *et al.* 2011). Soil respiration is controlled by multi-factors, including temperature, moisture, soil microbial, and vegetation type (Cramer *et al.* 2001, Conant *et al.* 2004, Li *et al.* 2005, Zimmermann *et al.* 2009). Existing studies found that the resource quality could significantly affect the temperature sensitivity of SOM decomposition (Sjögersten & Wookey 2002, Plante *et al.* 2010). The labile SOM is sensitive to climate change and generally decomposed rapidly, which can largely contribute to soil CO<sub>2</sub> fluxes increases (Conant *et al.* 2008, Von Lützwow & Kögel-Knabner 2009). Therefore, understanding the environment controls on temperature sensitivity of soil respiration is

critical to predict the responses of carbon processes to climate change (Davidson & Janssens 2006, Kirschbaum 2006, Contant *et al.* 2008 & 2011, Balsler & Wixon 2009). In this study, soil temperature, moisture, litter quality and quantity, and other environmental conditions have been revealed to have a significant impact on soil respiration rate, although the magnitude of the impacts of different influencing factors could not be specifically measured. With the predicted warming climate in the Caribbean regions, tropical soils are at severe risk to release large amounts of CO<sub>2</sub> to the atmosphere.

Our soil translocation experiment improved the understanding of the impacts of environmental conditions on soil carbon processes. Further studies may consider large-scale experiment on soil translocation. The small sample size in this study might limit the extrapolation of the conclusions. Also, the effects of soil microbes and litter input need to be incorporated in future study. Understanding the responses of soil in the LEF to climate change provide a good example to evaluate the impacts of global warming on other tropical forests. Further long-term and multi-factor soil translocation experiment at the ecosystem level should be developed to study the impacts of climate change on tropical soil carbon balance, as well as the feedbacks of the carbon cycle to the future climate.

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## TABLES

Table 3.1 Variation in soil organic carbon (SOC, %) and soil organic matter (SOM, %) of the soils originating from the plots at 350 m, 600 m, and 1000 m, respectively, at the end of the soil translocation experiment. The experiment period was from July 2011 to May 2012. SP stands for the soil source plots. Ave stands for the average contents of SOC or SOM of the soils from the same source, Prior stands for the contents of SOC or SOM measured before the soil translocation experiment. Standard deviations are in parentheses.

	SP_350 m		SP_600 m		SP_1000 m	
Plot	SOC	SOM	SOC	SOM	SOC	SOM
<b>350 m</b>	6.40	22.58	6.99	25.85	20.56	47.71
<b>600 m</b>	6.31	22.83	7.20	26.50	20.25	47.05
<b>1000 m</b>	6.35	22.70	8.27	27.98	23.23	49.67
	6.35	22.70	7.48	26.77	21.35	48.14
<b>Ave</b>	(0.04)	(0.10)	(0.56)	(0.89)	(1.33)	(1.11)
	5.36	22.55	6.76	26.37	20.54	48.25
<b>Prior</b>	(1.64)	(2.03)	(1.14)	(1.72)	(2.35)	(2.72)

Table 3.2 Pearson product-moment correlations between the natural logarithm of daily soil respiration fluxes ( $R_s$ ,  $\text{g-CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) and temperature ( $T$ ,  $^\circ\text{C}$ ) & moisture ( $M$ ,  $\text{m}^3/\text{m}^3$ ) along the elevation gradient in the Luquillo Experimental Forest, Puerto Rico. SP and DP stand for the soil source and destination plots, respectively.

<b>ln(Daily <math>R_s</math>)</b>	<b>T</b>			<b>M</b>		
	df	<i>P</i> -value	r	df	<i>P</i> -value	r
<b>SP_350 m</b>	23	0.80	0.00	19	0.66	0.10
<b>SP_600 m</b>	21	0.52	0.14	18	0.28	0.25
<b>SP_1000 m</b>	23	0.03 *	0.44 *	19	0.74	-0.08
<b>DP_350 m</b>	23	0.79	0.06	17	0.21	-0.30
<b>DP_600 m</b>	22	0.24	0.25	19	0.94	0.02
<b>DP_1000 m</b>	21	0.31	0.22	19	0.10	-0.37

\*Significant level was set at  $\alpha=0.05$ . “r” stands for the correlation coefficient.

Table 3.3 Results (*P*-values) of multiple Paired-t tests assessing the impacts of the treatments (the soil source and destination plot) on daily soil respiration fluxes ( $R_s$ ,  $\text{g-CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) along the elevation gradient in the Luquillo Experimental Forest, Puerto Rico. SP and DP stand for the soil source and destination plots, respectively.

	<b>SP_350 m</b>	<b>SP_1000 m</b>
<b>SP_350 m</b>		0.02*
<b>SP_600 m</b>	0.89	0.02*
	<b>DP_350 m</b>	<b>DP_1000 m</b>
<b>DP_350 m</b>		0.10
<b>DP_600 m</b>	0.01*	0.01*

\*Significant level was set at  $P < 0.05$ .

Table 3.4 Soil respiration rates ( $R_s$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) along the elevation gradient in the Luquillo Experimental Forest, Puerto Rico. The 11 measurements were approximately monthly from July 2011 to May 2012. All the  $R_s$  rates were standardized by a  $Q_{10}$  value at the daily average temperature (Daily T, °C). The estimated  $Q_{10}$  values were 3.1 at 350 m, 6.9 at 600 m, and 8.7 at 1000 m, respectively. SP and DP stand for the soil source and destination plots, respectively. Ave. stands for the average  $R_s$  rate through the experiment period.

DP(m)	SP(m)	1	2	3	4	5	6	7	8	9	10	11	Ave.
<b>350</b>	350	1.03		0.60		1.65	0.61	0.56	0.56	1.35	1.12	1.26	0.97
	600	1.29		0.81		0.69	1.02	1.15	0.72	0.83	1.57	1.32	1.04
	1000	2.73		1.66		2.29	1.61		1.66	2.62	4.54	3.82	2.34
	<b>Daily T</b>	23.9		23.1		22.5	21.0	21.0	20.2	20.9	20.0	23.5	
<b>600</b>	350	1.16			0.60	1.30	0.74	1.02	0.72	1.25		1.76	1.07
	600	1.64			0.61	0.58	0.99	1.07	0.53	0.55		0.81	0.85
	1000	1.60			0.84	0.74	1.21	0.44	0.71	1.21		1.01	0.97
	<b>Daily T</b>	22.3			22.1	21.6	20.8	20.0	19.2	19.2		21.5	
<b>1000</b>	350		1.40	1.55		0.88	1.29	0.93	1.51	2.35	1.23	1.34	1.39
	600		1.52	1.40				1.42	0.94	1.21	1.48		1.33
	1000		1.40	1.11		1.32	1.05	0.81	0.38	1.20	1.39	2.02	1.19
	<b>Daily T</b>		21.2	21.6		20.3	18.1	19.0	18.3	18.4	18.2	20.4	



Table 3.5 Daily soil respiration fluxes in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) along the elevation gradient in the Luquillo Experimental Forest, Puerto Rico. The 11 measurements were approximately monthly from July 2011 to May 2012. Daily T stands for the daily average temperature (°C). SP and DP stand for the soil source and destination plots, respectively. The unit for daily soil respiration is g-CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>.

DP(m)	SP(m)	1	2	3	4	5	6	7	8	9	10	11
<b>350</b>	350	4.75		2.34		6.19	2.40	2.18	2.31	5.01	4.26	4.78
	600	6.60		3.41		2.67	4.76	4.61	3.12	3.02	5.96	4.99
	1000	14.24		6.77		8.62	7.65		7.20	9.53	16.76	13.16
	<b>Daily T</b>	23.9		23.1		22.5	21.0	21.0	20.2	20.9	20.0	23.5
<b>600</b>	350	4.40			2.31	4.69	2.68	4.03	2.78	4.59		6.37
	600	6.25			2.25	2.05	3.50	4.38	2.07	2.24		3.07
	1000	6.17			3.10	2.62	4.26	1.82	2.79	4.46		3.56
	<b>Daily T</b>	22.3			22.1	21.6	20.8	20.0	19.2	19.2		21.5
<b>1000</b>	350		5.04	5.73		2.69	5.64	3.52	5.77		4.69	5.07
	600		5.73	5.03				5.71	3.64	3.68	4.71	
	1000		5.48	3.98		4.05	5.59	3.22	1.50	4.56	5.48	7.64
	<b>Daily T</b>		21.2	21.6		20.3	18.1	19.0	18.3	18.4	18.2	20.4

## FIGURE CAPTIONS

Figure 3.1 Monthly average soil moisture and temperature in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) in the Luquillo Experimental Forest, Puerto Rico. For the plot at 1000 m, the temperature data at both 0 cm and 15 cm in November 2011 were missing, and the temperature data at 15 cm were missing from December 2011 to February 2012. Bars stand for standard errors. a). Monthly average soil moisture ( $\text{m}^3/\text{m}^3$ ) at 0 cm and 15 cm. b). Monthly soil moisture ( $\text{m}^3/\text{m}^3$ ) averaged from 0-15 cm. c). Monthly average soil temperature ( $^{\circ}\text{C}$ ) at 0 cm and 15 cm.

Figure 3.2 Average soil temperature and moisture at 0-15 cm through the experiment period in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) in the Luquillo Experimental Forest, Puerto Rico. For the plot at 1000 m, the temperature data at both 0 cm and 15 cm in November 2011 were missing, and the temperature data at 15 cm were missing from December 2011 to February 2012. Bars stand for standard errors.

Figure 3.3 Variation in SOC, C to N ratio and SOM of the soils at 0-15 cm in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) measured before and after the soil translocation experiment in the Luquillo Experimental Forest, Puerto Rico. The SOM content was estimated by LOI percentage. Bars stand for standard errors. a). Variation in SOC (%) and C to N ratio. b). Variation in SOM (%).

Figure 3.4 Variation in soil respiration fluxes of the soils with the same destination in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) in the Luquillo Experimental Forest, Puerto Rico. SP stands for the soil source plots. The unit for daily Rs fluxes is  $\text{g-CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ . a). Daily Rs fluxes of the soils at 350 m. b). Daily Rs fluxes of the soils at 600 m. c). Daily Rs fluxes of the soils at 1000 m. d). Daily Rs rates averaged from the soils originating from different source plots in each of the three soil translocation plots. The letters above the bars indicate significant differences at  $P < 0.05$ .

Figure 3.5 Variation in daily soil respiration fluxes of the soils originating from the same source plots in the three soil translocation plots (with elevation at 350 m, 600 m, and 1000 m, respectively) in the Luquillo Experimental Forest, Puerto Rico. DP stands for the soil destination plots. The unit for daily Rs fluxes is  $\text{g-CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ . a). Daily Rs fluxes of the soils originating from 350 m. b). Daily Rs fluxes of the soils originating from 600 m. c). Daily Rs fluxes of the soils originating from 1000 m. The letters above the bars indicate significant differences at  $P < 0.05$ .

Figure 3.1

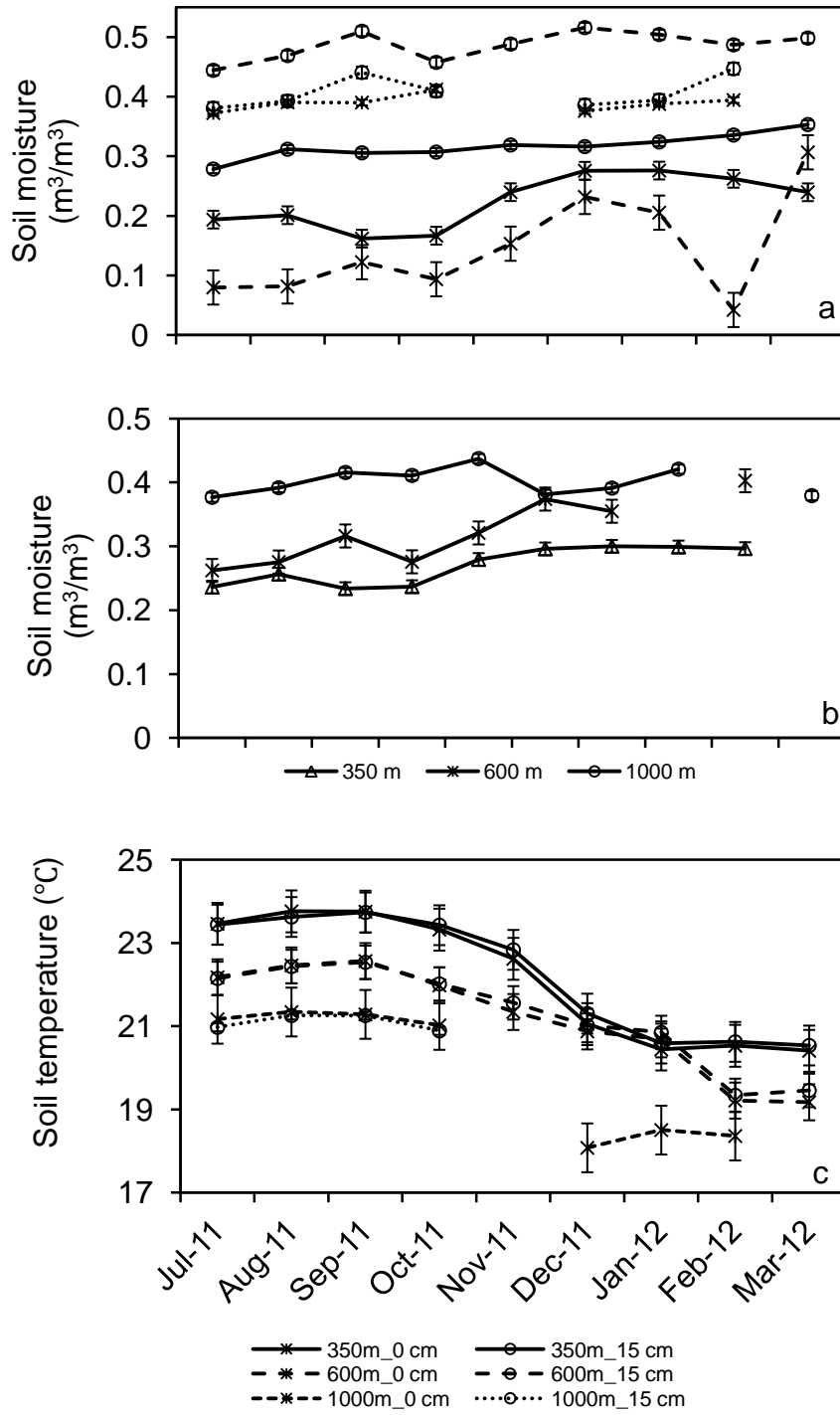


Figure 3.2

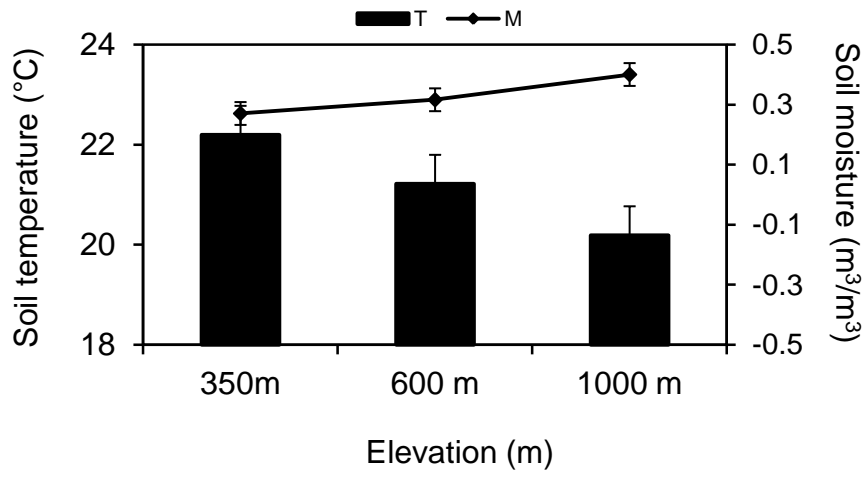


Figure 3.3

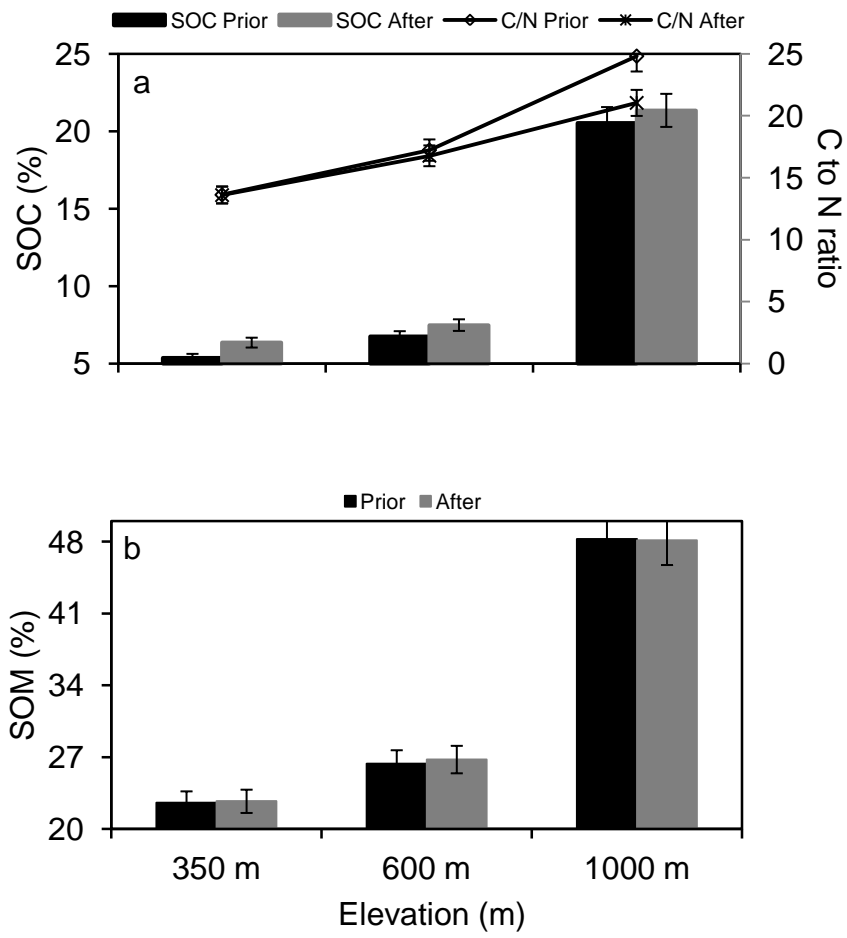


Figure 3.4

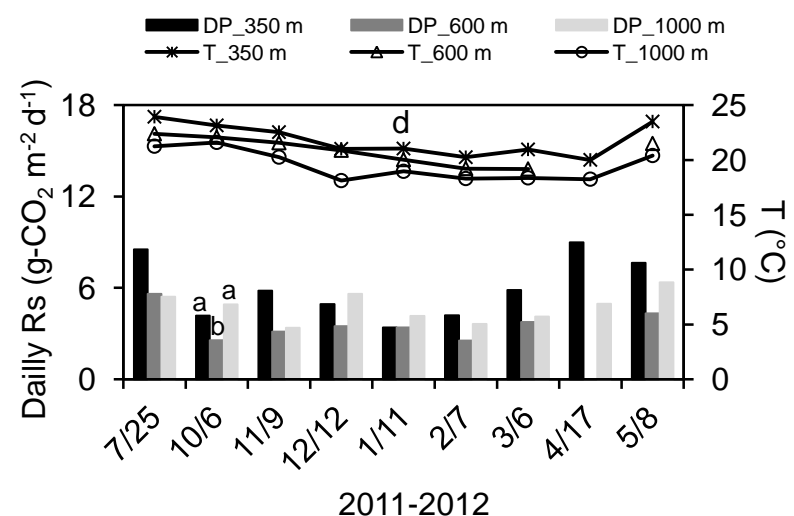
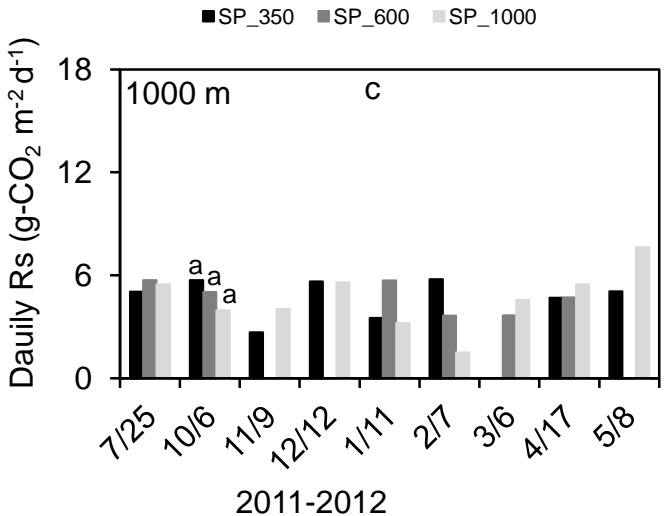
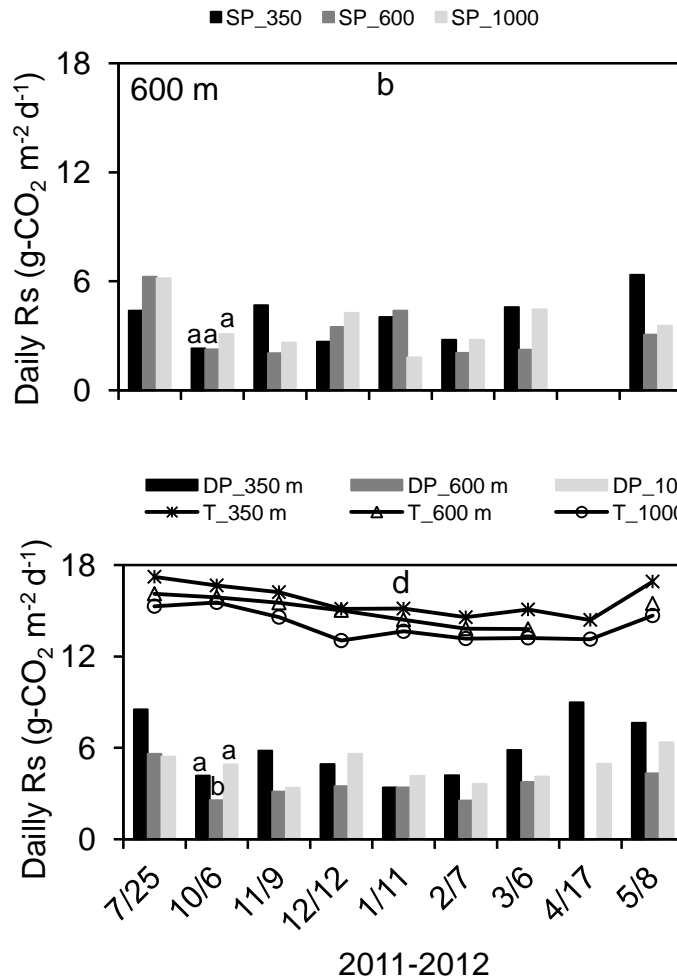
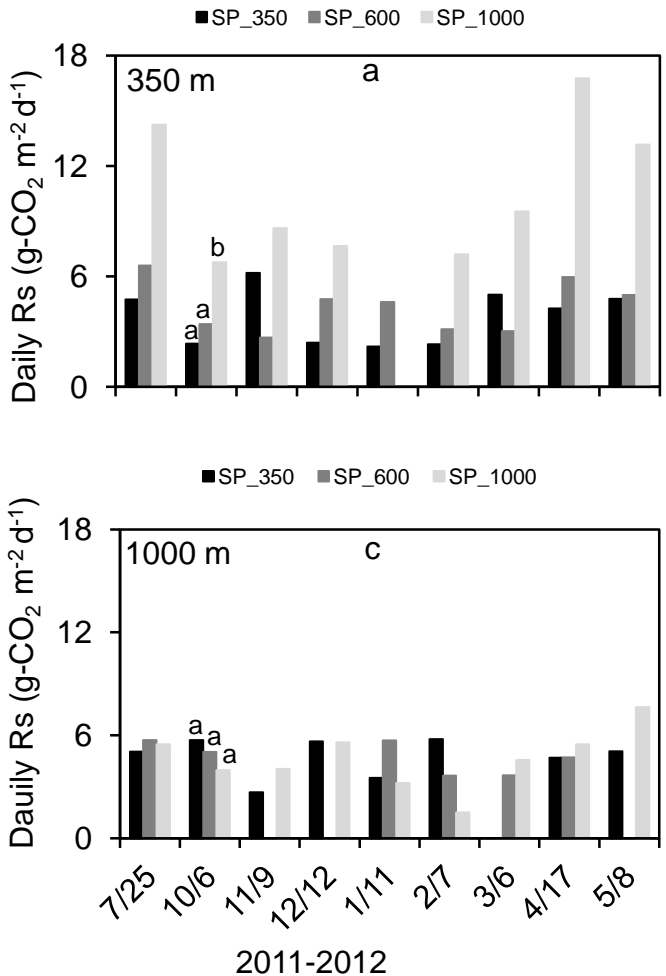
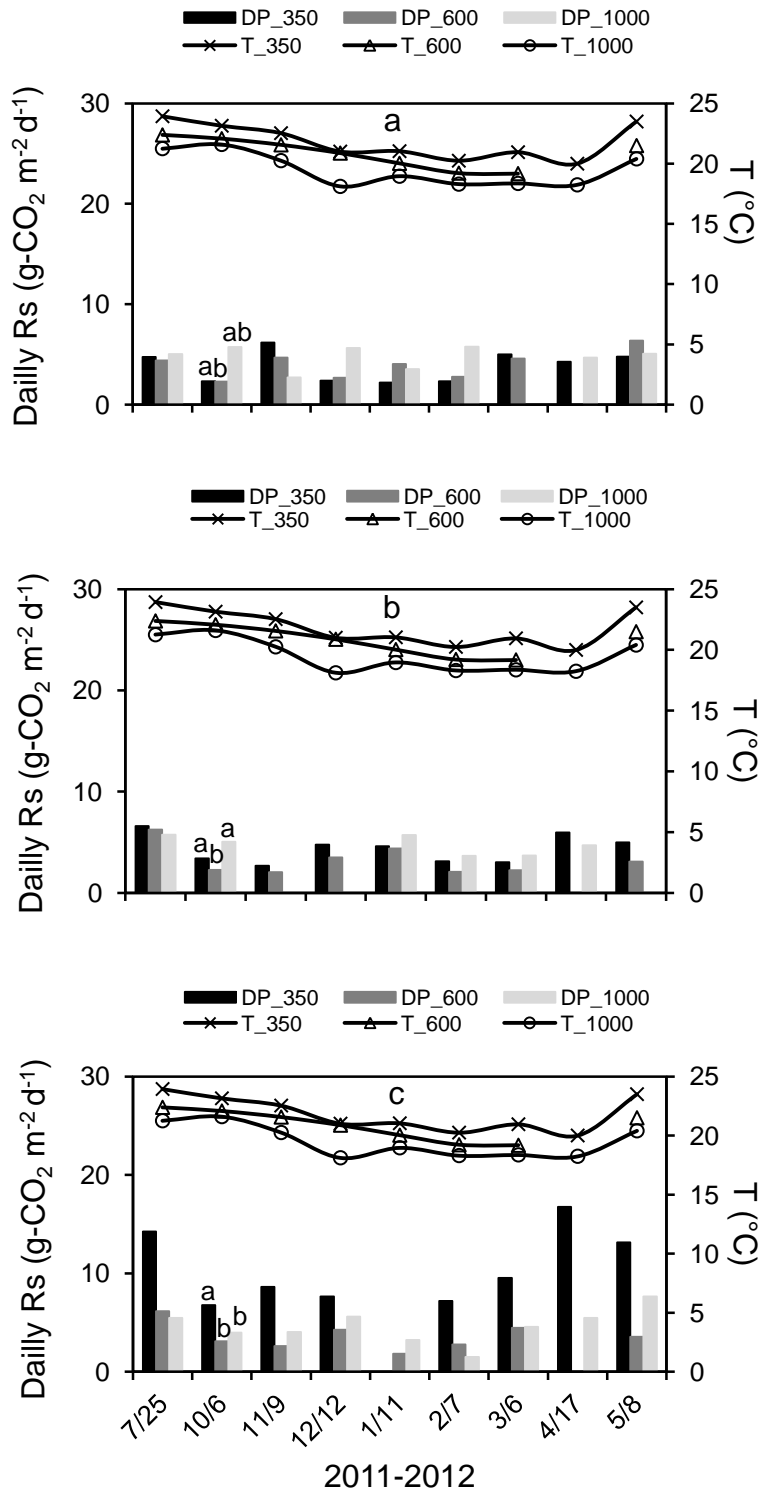


Figure 3.5





Appendix 3.1 Soil respiration rates ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measured in the field in the three soil translocation plots (with elevations at 350 m, 600 m, and 1000 m, respectively) in the Luquillo Experimental Forest, Puerto Rico. The measurements were approximately monthly, and the experiment period was from July 2011 to May 2012. SP stands for the soil source plot. T ( $^{\circ}\text{C}$ ), and M ( $\text{m}^3/\text{m}^3$ ) stand for the real-time soil surface temperature and moisture in the field, respectively.

<b>Plot</b>	<b>SP (m)</b>	<b>Jul</b>	<b>Aug</b>	<b>Oct</b>	<b>Oct</b>	<b>Nov</b>	<b>Dec</b>	<b>Jan</b>	<b>Feb</b>	<b>Mar</b>	<b>Apr</b>	<b>May</b>
<b>350 m</b>	<b>350</b>	1.18		0.65		1.73	0.72	0.59	0.62	1.35	1.12	1.26
	<b>600</b>	1.63		0.92		0.75	1.36	1.26	0.83	0.83	1.57	1.32
	<b>1000</b>	3.53		1.91		2.51	2.22		1.95	2.64	4.54	3.82
	<b>T</b>	25.1		23.8		22.9	22.5	21.5	21.0	21.0	20.0	23.5
	<b>M</b>	0.14		0.33		0.25	0.24	0.27	0.30	0.20		
<b>600 m</b>	<b>350</b>	1.19			0.60	1.30	0.74	1.08	0.75	1.30		1.76
	<b>600</b>	1.70			0.60	0.58	0.99	1.17	0.56	0.59		0.81
	<b>1000</b>	1.67			0.83	0.74	1.21	0.49	0.75	1.29		1.01
	<b>T</b>	22.5			22.0	21.1	20.5	20.5	19.5	19.5		21.5
	<b>M</b>	0.07			0.14	0.15	0.23	0.21	0.04	0.31		
<b>1000 m</b>	<b>350</b>		1.58	1.48		0.88	1.60	0.99	1.55	2.35	1.26	1.34
	<b>600</b>		1.86	1.28				1.58	0.98	1.21	1.55	
	<b>1000</b>		1.76	1.01		1.33	1.58	0.91	0.40	1.20	1.47	2.02
	<b>T</b>		22.3	21.1		20.2	20.0	19.5	18.5	19.0	18.5	21.5
	<b>M</b>		0.38	0.32		0.45	0.34	0.37	0.38	0.36	0.37	

Appendix 3.2 Variation in rainfall at the El Verde Field Station from July 2011 to May 2012.

The data were cited from the Luquillo LTER Database. Bars stand for standard errors.

