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Atypical soil carbon distribution across a tropical steepland forest catena

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ABSTRACT

Soil organic carbon (SOC) in a humid subtropical forest in Puerto Rico is higher at ridge locations compared to valleys, and therefore opposite to what is commonly observed in other forested hillslope catenas. To better understand the spatial distribution of SOC in this system, plots previously characterized by topographic position, vegetation type and stand age were related to soil depth and SOC. Additional factors were also investigated, including topographically-related differences in litter dynamics and soil chemistry. To investigate the influence of litter dynamics, the Century soil organic model was parameterized to simulate the effect of substituting valley species for ridge species. Soil chemical controls on C concentrations were investigated with multiple linear regression models using iron, aluminum and clay variables. Deeper soils were associated with indicators of higher landscape stability (older tabonuco stands established on ridges and slopes), while shallower soils persisted in more disturbed areas (younger non-tabonuco stands in valleys and on slopes). Soil depth alone accounted for 77% of the observed difference in the mean 0 to 60 cm SOC between ridge soils (deeper) and valley soils (shallower). The remaining differences in SOC were due to additional factors that lowered C concentrations at valley locations in the 0 to 10 cm pool. Model simulations showed a slight decrease in SOC when lower litter C:N was substituted for higher litter C:N, but the effects of different woody inputs on SOC were unclear. Multiple linear regression models with ammonium oxalate extractable iron and aluminum, dithionite–citrate-extractable iron and aluminum, and clay contents explained as much as 74% of the variation in C concentrations, and indicated that organo-mineral complexation may be more limited in poorly developed valley soils. Thus, topography both directly and indirectly affects SOC pools through a variety of inter-related processes that are often not quantified or captured in terrestrial carbon models.

1. Introduction

The spatial distribution of soil organic carbon (SOC) at landscape scales is controlled by interactions of edaphic, topographic, and biological factors through time, and understanding these interactions is essential to quantifying the role of SOC in the global carbon cycle (Amundson, 2001; Janzen, 2004; Post et al., 2001; Smith and Fang, 2010). Soil catena models have been widely applied to relate soil forming processes to the spatial distribution of soil properties (Jimenez and Lal, 2006; Scatena and Lugo, 1995; Silver et al., 1994), which can then be used to map soil properties, including SOC, at larger scales. In many dry, temperate, and humid landscapes, the largest SOC pools tend to occur in topographically low areas (i.e. valleys). This pattern of accumulation has been attributed to various factors, including the chemical stabilization and burial, decreased decomposition because of low redox conditions, and higher litter inputs from vegetation and upslope contributions (Berhe et al., 2007; Gregorich et al., 1998; Jenny, 1941). However, in the tabonuco (*Dacroydes excelsa*) forests that are the focus of this study, SOC pools are smallest in valley positions and largest on ridges (Scatena and Lugo, 1995; Silver et al., 1994; Silver et al., 1999; Soil Survey Staff, 1995).

Previous studies have identified factors that control the spatial patterns in soil development and trees species composition in the tabonuco forest and have suggested that the primary control on soil development (and SOC contents) is landscape stability. The tabonuco tree, which typically grows on ridges, forms root grafting networks that reduce damage from hurricanes and other disturbances (Basnet et al., 1993; Lugo and Scatena, 1995; Scatena and Lugo, 1995). Additionally, "low quality" litter inputs (e.g. higher C:N ratios, higher lignin contents) from trees such as the tabonuco, may decompose more slowly than other species and thus increase SOC (Fonte and Schowalter, 2004; Myster and Schaefer, 2003; Ostertag et al., 2003; Zalamea et al., 2007). Other factors that may influence SOC spatial distribution, and that have not been explicitly explored before, include soil Fe, Al, and texture and litter quantity via changes in tree mortality. It is well known that Fe and Al are not only important components of tropical soils, but are also often correlated with SOC

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and provide a mechanism of protection from microbial decomposition (e.g. Kleber et al., 2005; Powers and Schlesinger, 2002). Additionally, higher tree mortality may cause less C to accumulate in woody pools, and therefore reduce the amount of recalcitrant woody inputs that would otherwise be stabilized in soils over long periods of time (e.g. 300+ years; Johnson et al., 2010).

This study investigates the relative influence of vegetation and topographic factors on SOC accumulations in a humid tropical steepland environment. Although some of these topographic patterns have been previously documented for the tabonuco forest, their relative influence on the distribution of SOC has not been determined. To better understand the controls on SOC spatial distributions, our objectives were to: 1) determine the role of topography and soil physical characteristics with SOC content, and 2) investigate secondary controls, in particular litter quality, litter quantity, and Fe, Al, and soil texture. We used the Century model to address our second objective, and discuss the caveats and advantages to this approach in future analyses.

2. Methods

2.1. Study Area

The focus of this study is the tabonuco forest, one of four major forest types found in the Luquillo Experimental Forest, Puerto Rico, and which typically occurs between 200 and 600 masl. The underlying parent material is mostly volcaniclastic that has weathered to a saprolite as thick as 20 m in some areas (Schellekens et al., 2004). Four general categories describe the typical geomorphic settings (topographic positions) found — ridge, slope, upland valley and riparian valley (Scatena, 1989) (Fig. 1). For the purposes of this study, upland valleys (first order intermittent streams) and riparian valleys (permanent streams) were lumped into one valley category. Ridges and slopes are dominated by tabonuco (*D. excelsa*), *Sloanea berteriana*, *Manilkara bidentata* and other late successional species. In contrast, vegetation at valley locations is comprised of mainly *Prestoa montana*, *Guarea guidonia, Inga sp.* and other early successional species (Basnet, 1992; Heartsill Scalley et al., 2010; Johnston, 1992; Scatena and Lugo, 1995; Wadsworth, 1957).

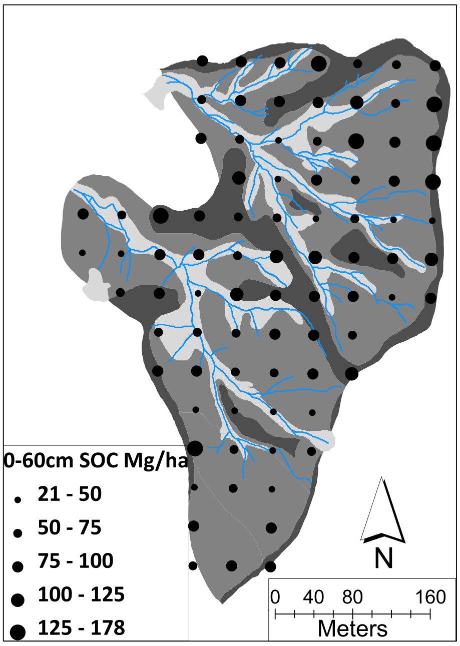

Fig. 1. Map of ridge, slope, and valley topographic positions (darkest gray, medium gray, light gray, respectively) and 0–60 SOC (Mg ha^{-1}) at sampled grid points in the Bisley watersheds.

The soils at ridge and slope positions of the tabonuco forest are moderately well-drained to well-drained Aquic Haplohumults and Typic Kandiudoxes of the Cristal and Zarzal soil series (Johnston, 1992; Soil Survey Staff, 1995; this study). Several characteristics related to drainage distinguish ridge and slope soils from valley soils. Upland soils are high in EDTA-extractable Fe and Al and percent clay, but low in base cations and have oxic and argillic horizons with subangular blocky structure (Silver et al., 1994; Soil Survey Staff, 1995). Upland locations are also highly chemically weathered, as indicated by the presence of hematite and goethite, little or no albite, and subangular blocky soil structure (Johnson, 2008; Soil Survey Staff, 1995). Valley soils are typically structureless, Typic Tropaquepts soils of the Prieto series. In contrast to upland soils, valley soils have higher extractable cations, but lower soil carbon concentrations, EDTA-extractable Fe and Al, and percent clay (Silver et al., 1999; Soil Survey Staff, 1995). Valley soils are also less chemically weathered, have albite throughout all depths, and have less developed horizons (Johnson, 2008; Soil Survey Staff, 1995).

Heavy rains and hurricanes often trigger shallow landslides and tree falls so that the tabonuco forest is steep and deeply dissected in many places (Scatena, 1989). Tabonuco trees are most abundant on ridges and typically have extensive networks of root grafts which decrease uprooting and ultimately stabilize ridge top soils (Basnet et al., 1993; Lugo and Scatena, 1995; Scatena and Lugo, 1995). Slope failures and tree-falls occur much more frequently in valleys than on slopes or ridges such that the average turnover time of biomass from landslides on upper slopes and ridges is 2000 years compared to only 680 years in valleys (Scatena and Lugo, 1995). Moreover, treefall gaps are four to six times more likely to occur and slope failures are two times more likely to occur in valleys than on adjacent upper slopes (Scatena and Lugo, 1995). This instability results from high pore pressures at the bottom of slopes after water drains laterally from upslope positions (Schellekens et al., 2004; Simon et al., 1990).

2.2. Analysis of controls on SOC contents

The roles of landscape topography, soil depth, stand age, litter inputs, and soil chemical characteristics in SOC distribution were addressed using both statistical comparisons and processed based simulations. These analyses were done using data and observations from previous studies of these tabonuco forest soils (Beard et al., 2005; Scatena et al., 1993; Scatena and Lugo, 1995; Silver et al., 1994; Soil Survey Staff, 1995; Vogt et al., 1996).

2.2.1. Characterization of the landscape

For 84 plot locations in the Bisley Research Watersheds, Scatena (1989) and Scatena and Lugo (1995) classified each plot according to topographic position, vegetation type and stand age class. The plots were spaced 40 m apart in a grid pattern and covered two watersheds that had a total areas of 13 ha (Fig. 1). The distribution of plot locations among these landscape classes allowed for a spatially unbiased estimate of the occurrence of specific attribute combinations and their relationship to soil depth and SOC pools. While the whole study area is dominated by tabonuco canopy cover, the vegetation of each plot was characterized as "tabonuco" and "non-tabonuco" on the basis of the presence of tabonuco trees in the plot. Tree age was estimated from species specific annual tree increments and age groups (<60, 60–120, >120 yr) were determined using the estimated age of the oldest tree in the plot (Scatena and Lugo, 1995).

2.2.2. Soil depth and soil carbon distributions

The grid system and Bisley also allowed us to make spatially unbiased comparisons of soil depth and SOC that were measured by Silver et al. (1994). Soil organic carbon content (SOC, Mg ha^{-1}) was calculated by

$$SOC = 100*(thickness*\%C*bulkdensity) \qquad (1)$$

where *thickness* is the thickness of the soil layer (cm),*%C* is the concentration of total carbon measured by the Walkley–Black method (Nelson and Sommers, 1982; Silver et al., 1994), and *bulk_density* refers to the bulk density of the sample (g cm^{-3}). Three soil depths (0–10 cm, 10–35 cm, and 35–60 cm) were sampled in June 1988, prior to Hurricane Hugo. Carbon concentration and bulk density for the 0–10 cm depth were measured from excavating a 10 cm mineral soil block. The 10–35 cm and 35–60 cm depths were sampled for C concentrations with a soil corer. Mean bulk density for the deeper samples was estimated by excavating eight quantitative pits that represented topographic positions in the watershed (Hamburg, 1984; Silver et al., 1994).

Importantly, not all the grid points at Bisley had soil at depths >10 cm because of boulders and other solid regolith (Silver et al., 1994). For plots that did not have soil at depths >10 cm, SOC was assumed to be 0 Mg ha^{-1} for the 10–35 cm SOC, 35–60 cm SOC, and combined 0–60 cm SOC estimates. Using a 0 value, instead of simply omitting the sample, results in a weighted value that accounts for soil depth in the calculation of mean SOC for grouped comparisons. Thus, means comparisons are unbiased both in terms of their representativeness of the landscape and soil depth. Comparisons of SOC between groups were made using the Tukey–Kramer test at $p=0.05$ level. If the assumption of equal variances was not met according to Levene or Bartlett tests, then statistical significance was confirmed by the Welch's test which allows for unequal standard deviations. Further, when populations appeared to not be normally distributed, especially when many 0 values were present, statistical significance was confirmed with the nonparametric Wilcoxon rank sums test. All statistical analyses were carried out with JMP® software (v. 8.0.1, SAS, Cary, N.C.).

2.2.3. Soil Fe, Al, and texture

Relationships of C concentrations with Fe, Al, and soil texture were explored with data from the El Verde soil survey; this site is nearby and in the same forest type, at similar elevation, and has the same soil series and geomorphic setting as Bisley (Soil Survey Staff, 1995). Iron and aluminum chemistry data included two extractable forms. Ammonium oxalate extractable iron and aluminum (Fe_o and Al_o) solutions were measured by inductively coupled plasma spectrometry (method 6C9a; U.S. Department of Agriculture, 1996) and dithionite–citrate-extractable iron and aluminum (Fe_d and Al_d) solutions were measured by atomic absorption spectrometry (method 6C2b; U.S. Department of Agriculture, 1996). Ferrihydrite, a poorly crystalline Fe oxide, can be approximated by Fe_o. More crystalline Fe oxide forms, in addition to poorly crystalline and noncrystalline forms, can be represented by Fe_d. Fe and Al (hydr-) oxides are dominant binding agents for soil aggregation in Oxisols, partly because they adsorb organics or bond electrostatically with organic materials and clays (Lutzow et al., 2006; Six et al., 2004). Therefore, poorly crystalline Fe_o and Al_o ("active (hydr-) oxides"), and Fe_d and Al_d ("free (hydr-) oxides"), may be predictors of soil carbon concentrations (Bruun et al., 2010; Kleber et al., 2005). We included these variables ($\%Fe_o$, Fe_d, $\%Al_o$, %clay) and their derivatives ($\%Fe_o{}^*\%clay$, $\%Fe_o+\%Al_o$, $\%clay+\%silt$, $(\%Fe_o+\%Al_o)$ $(\%clay+\%silt)$) in multiple linear regression models to explain variability C concentration in samples grouped by soil horizon. Models were selected using a forward stepwise process and limited to 4 parameters for simplicity. We did not constrain model intercepts to 0%C because our purpose was to simply explain the variation in C concentration with linear models. All reported model parameters were significant at $p<0.05$.

2.2.4. Litter quality and quantity

We used the Century Soil Organic Model (v. 4.5; Parton et al., 1987, 1993) to determine the potential effects of long-term, topographically driven patterns in litter quality and litter quantity (via tree mortality) on SOC pools. Century has been used to model soil and ecosystem dynamics in Puerto Rico and other tropical forests on highly weathered soils (Cerri et al., 2003; Sanford et al., 1991; Silver et al., 2000; van Santen et al., 2002; Wang et al., 2002; Zimmerman et al., 1995). The model was calibrated to simulate a "typical" stable upland soil environment (i.e. no landslides or tree throws) which was then subjected to two treatments. The first treatment substituted plant C:N, C:P, and lignin values of ridge species with the corresponding values of valley species to simulate the effect of imposing lower litter quality and higher litter decomposition rates. Similarly, the second treatment replaced the large wood and coarse root mortality rates of ridge locations with those of valley locations to simulate the effect of lower long-term, large wood and coarse root inputs associated with less developed stands in areas of higher landscape stability. The model parameters were determined from various data sources, most of which were specific to the Bisley watersheds (see Table 3 of this study; see also Table 3 in Johnson (2008) for more detail).

3. Results

3.1. Topographic and biophysical controls on SOC

3.1.1. Spatial distribution of combinations of landscape attributes

Before relating SOC to landscape attributes, we first quantified which attribute combinations were most common in the tabonuco watersheds. The prevailing pattern was shown by histograms of 0–10 cm samplings (one for each of the 84 plots) among topographic, vegetation, and stand age classes (c.f. Scatena and Lugo, 1995) (Fig. 2). Ridges were dominated by older tabonuco stands, valleys were dominated by younger non-tabonuco species, and slopes had a variety stand ages and species. In addition to the individual combinations of attributes, two major groups were identifiable: 1) "Group A", where 41% of the watersheds were characterized by tabonuco stands located on ridges or slopes, and 2) "Group B", where 49% of the plots were characterized by non-tabonuco stands located on slopes or in valleys. In contrast, combinations of tabonuco and valley classes, and non-tabonuco and ridge classes were uncommon. Additionally, stand ages and vegetation types were unevenly distributed over the topographic positions. For example, all but one of the >120 yr stands were from Group A, and none were from Group B. In contrast, 84% of the <60 yr stands were from Group B, and only one <60 yr stand was from Group A.

3.1.2. Spatial distribution of soil depth

The soils were deeper on tabonuco ridges and shallower on non-tabonuco slopes and in non-tabonuco valleys. More specifically, the proportions of plots from Group A and Group B that lacked deep soil were 20% and 41%, respectively (Fig. 2). The proportions of plots that lacked deep soil (i.e. the 35–60 cm depth) for ridge, slope, and valley positions, regardless of vegetation type or stand age, were 9%, 38%, and 46%, respectively. Determining the difference in soil depths between stand age classes was more difficult because fewer plots were available for comparison, and because stand age class was strongly related to topographic position and vegetation type. Nonetheless, the proportions of plots lacking deep soil for the 60–120 yr and >120 yr age classes within Group A were 15% and 20%, respectively. Similarly, within Group B the same statistics for the <60 yr and 60–120 yr age classes were 41% and 50%, respectively.

3.1.3. Quantification of SOC contents for each depth

We found that SOC in the 0–10 cm, and 35–60 cm depths were greatest on ridges and in older stands (Table 1), supporting previous findings for the total 0–60 cm pool (Scatena and Lugo, 1995; Silver et al., 1994). The 10–35 cm depth also had higher mean SOC on ridges, but was only statistically significantly different than slopes at the $p=0.1$ level. As analyzed above, these SOC patterns can mostly be attributed to the occurrence of deeper soils on ridges where tabonuco is most common. Further, the absolute difference in SOC was greater between ridges and valleys than between ridges and slopes (Table 1).

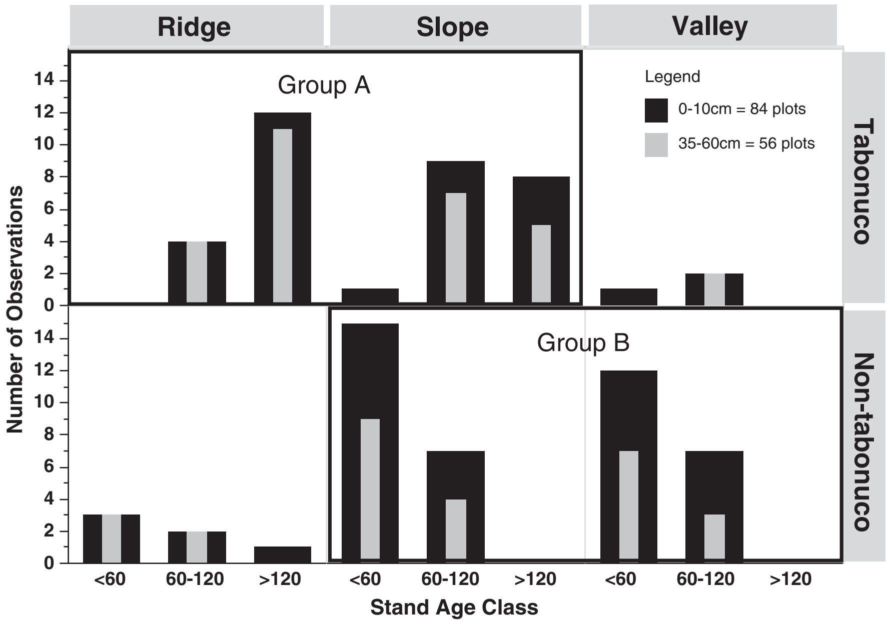

Fig. 2. Histograms of gridded plot locations for different combinations of topographic, vegetation, and stand age attributes for the two Bisley watersheds. N = 84 for the 0–10 cm depth, where all the plots were sampled, indicated by the black bars. N = 56 for 35–50 cm depth that reflects the distribution of plots that had no soil at this depth, indicated by the gray bars embedded within the black bars.

Group A had significantly higher SOC than Group B for the 35–60 cm depth and total 0–60 cm pool ($P<0.05$).

The contribution from each sample depth was not evenly distributed between topographic positions when expressed as a percent of the overall difference in the 0–60 cm SOC pool. When ridges and valleys were compared, 26%, 32%, and 45% of the total difference in the 0–60 cm pool was attributed to the 0–10 cm, 10–35 cm, and 35–60 cm depths, respectively (% of total difference = SOC pool at depth/total SOC pool, from Table 1). When ridges and slopes were compared, 0%, 52% and 48% of the total difference in 0–60 cm SOC was attributed to the 0–10 cm, 10–35 cm, and 35–60 cm SOC depths, respectively.

Carbon concentration (%C), and not bulk density or soil depth, accounted for the difference in 0–10 cm SOC contents between ridge and valley soils. For the 0–10 cm depth, C concentration was significantly higher in ridge soils than in valley soils (Table 2), but there was no significant difference in bulk density (not shown). There was no significant difference in C concentrations between topographic positions for the 10–35 cm or 35–60 cm depths. A similar comparison was not possible for bulk densities at the 10–35 cm and 35–60 cm depths, because these measurements were made differently (see Methods). The C concentration in the 0–10 cm depth was significantly higher in 120 yr stands than <60 yr and 60–120 yr stands, and also significantly higher in Group A compared to Group B ($P<0.05$). The surface soil C concentrations under tabonuco stands were higher than under non-tabonuco stands at the $P<0.1$ level. Taken together, the differences found in %C in the 0–10 cm depth contribute to the analysis of our second objective, which was to explore possible secondary controls on SOC distribution in tabonuco forest soils.

3.2. Additional controls on SOC

3.2.1. Soil Fe, Al, and texture controls

Multiple linear regression models with Fe, Al, and soil texture showed evidence for organo-mineral complexation leading to SOC stabilization in tabonuco forest soils (Table 3). The positive terms in most of the regression models indicated that the highest C concentrations occurred at high levels of Fe_o (1.25 to 2.0%) and clay (50 to 70%). Combinations of Fe, Al, clay, and silt, and their interactions, explained as much as 80% of the variation in C concentrations, depending on the horizon type. For example, 59% of the variation in C concentrations was explained among all soil horizons and soil types with% Fe_o, %clay, and the interaction term. Similarly, 74% of the variation of C concentrations in A horizons was explained by $\%Fe_o + Al_o$ and %clay + %silt and the interaction term. Similar models were found when all B horizons were lumped together, and for the Bo/Bt horizons. In contrast, for lower redox soil environments (i.e. Bg horizons), Fe_d was the strongest predictor and negatively correlated with C concentrations (Table 3), indicating the importance of both crystalline and poorly-crystalline forms of Fe (hydr-) oxides in these wetter soils. In our regressions, Al (hydr-) oxides plus Fe

Table 1
Soil carbon content comparisons by depth and topographic position and the difference in mean SOC contents between ridges and other topographic positions. Standard deviations are in parantheses.

	Soil carbon pools (Mg ha^{-1})			
	0–10 cm	10–35 cm	35–60 cm	0–60 cm
Ridge	28 (15) A	44 (18) A	25 (18) A	96 (36) A
Slope	28 (15) AB	33 (21) A	15 (15) B	75 (32) B
Valley	20 (5) B	34 (18) A	11 (15) B	65 (26) B
Ridge—slope	0	11	10	21
Ridge—valley	8	10	14	31

Capital letters within SOC pools denote significant difference when letters are not the same for the 0.05 level. Unsampled depths were assumed to be 0 Mg ha^{-1}.

Table 2
Soil carbon concentration comparisons by depth and topographic position. Standard deviations are in parantheses.

	Soil carbon concentration (%C)		
	0–10 cm	10–35 cm	35–60 cm
Ridge	4.33 (1.59) A	1.77 (0.73) A	0.96 (0.61) A
Slope	4.12 (2.00) AB	1.56 (0.69) A	0.82 (0.43) A
Valley	3.11 (0.98) B	1.44 (0.67) A	0.70 (0.51) A

Capital letters within SOC pools denote significant difference when letters are not the same for the 0.05 level. Unsampled depths were omitted in the calculation of the means.

Table 3
Multiple linear regression models and their parameters which explain %C in tabonuco forest soils.

Grouping	Model terms	Coefficients (std error)	Parameter p-value	df	Model p-value	adj. R2
All	Intercept	−2.73 (0.61)	<0.0001	70	<0.0001	0.59
	%Feo	2.33 (0.26)	<0.0001			
	%clay	0.06 (0.0096)	<0.0001			
	%Feo *%clay	0.09 (0.020)	<0.0001			
A horizons	Intercept	−10.83 (2.52)	0.0010	12	0.0002	0.74
	%Feo + %Alo	1.47 (0.48)	0.0100			
	%clay + %silt	0.16 (0.028)	0.0001			
	(%Feo + Alo) * (%clay + %silt)	0.36 (0.10)	0.0039			
B horizons	Intercept	−2.08 (0.62)	0.0017	42	<0.0001	0.67
	%Feo	2.13 (0.23)	<0.0001			
	%clay	0.044 (0.0094)	<0.0001			
	%Feo *%clay	0.047 (0.017)	0.0076			
Bo/Bt	Intercept	−7.11 (1.66)	0.0002	31	<0.0001	0.80
	%Feo + %Alo	2.52 (0.22)	<0.0001			
	%clay + %silt	0.077 (0.018)	0.0001			
Bg/Bw	Intercept	11.18 (3.76)	0.0155	9	0.0016	0.71
	%Fed	−2.66 (0.68)	0.0036			
	%clay	0.13 (0.029)	0.0014			
C horizons	Intercept	0.30 (0.010)	0.0122	10	0.0054	0.51
	%Feo	0.36 (0.10)	0.0054			

(hydr-) oxides were important predictors of C concentrations, but were not strong predictors by themselves in any of the horizons.

3.2.2. Influence of litter quality and quantity on 0–10 cm SOC content

The Century model simulated a baseline SOC pool of 104 MgC ha^{-1} which was within the range of the observed 0–35 cm SOC contents at ridge plots (24 to 113 MgC ha^{-1}). However, this baseline was consistently higher than all the mean SOC contents of ridge soils measured (0–10 cm: 28 MgC ha−1, 0–35 cm: 71 MgC ha−1, 0–60 cm: 95 MgC ha−1; for these calculations only plots with deep soils were included). Century model outputs were sensitive to the variations in litter C:N and turnover rates prescribed in our treatments (Table 4). As expected, a higher C:N treatment resulted in lower SOC contents and when plant tissue chemistries of ridge species were substituted with the chemistries of valley species (i.e. a lower C:N treatment), there was a decrease in model simulated SOC of 2.3 MgC ha^{-1}, or 2.2% decrease from the baseline value. If this result were taken literally, then this would account for 15% of the difference in the mean measured 0–35 cm SOC contents between ridges and valleys (15 MgC ha^{-1}). We originally hypothesized that higher live plant mortality rates would cause a decrease in model simulated SOC when other parameters were held constant. However, when the lower mortality rates of ridge species were substituted with those of valley species (Table 4), there was an increase in model simulated SOC of 5.3 Mg ha^{-1}, or 34% of the measured difference.

4. Discussion

Geomorphically stable areas in the tabonuco forest provide the best opportunities for SOC accumulation. The level of stability is related to topographic positions, resulting in an atypical pattern of SOC distribution across soil catenas. Stand age is an important indicator of soil stability and there was a clear association in this study between older tabonuco stands on ridge soils and high SOC. This is due to the resistance of tabonuco uprooting after disturbance and resultant biophysical stabilization provided by tabonuco roots (e.g. Group A) (Scatena and Lugo, 1995). In contrast to slope and ridge locations, valley locations (and some slope locations; Group B) lack the stabilizing factors that are associated with the tabonucos. Instead of growing vertically on relatively flat ridges, riparian trees often grow at angles into the channel to access sunlight and therefore are subject to increased uprooting. Further, riparian soils have infiltration rates that are much lower than ridge and slope soils (Harden and Scruggs, 2003). Most soil water on upland sites infiltrates until it reaches a

Table 4
Litter quality and biomass turnover rates measured in the Bisley forest and the corresponding Century model component.

Parameter	Component	Ridge	Valley	Reference
C:N	Leaf	32	28	Scatena et al. (1993)
	Fine root	50	50	Scatena et al. (1993)
	Fine branch	90	60	Scatena et al. (1993)
	Large wood	235	168	Scatena et al. (1993)
	Coarse root	235	168	Scatena et al. (1993)
C:P	Leaf	674	544	Scatena et al. (1993)
	Fine root	700	700	Scatena et al. (1993)
	Fine branch	1363	1112	Scatena et al. (1993)
	Large wood	4457	3812	Scatena et al. (1993)
	Coarse root	4457	3812	Scatena et al. (1993)
Lignin fraction	Leaf	0.12	0.16	Beard et al. (2005)
	Fine root	0.29	0.27	Beard et al. (2005)
	Fine branch	0.24	0.24	Beard et al. (2005)
	Large wood	0.24	0.24	Beard et al. (2005)
	Coarse root	0.24	0.24	Beard et al. (2005)
Mortality (monthly)	Leaf	0.08	0.08	Vogt et al. (1996); Scatena (Unpublished results)
	Fine root	0.087	0.087	Vogt et al. (1996); Scatena (Unpublished results)
	Fine branch	0.03	0.03	Vogt et al. (1996); Scatena (Unpublished results)
	Large wood	0.00138	0.0049	Scatena and Lugo (1995)
	Coarse root	0.00138	0.0049	Scatena and Lugo (1995)

depth of about 10 cm and then flows laterally to valleys where pore pressure builds up and further contributes to slope instability (Schellekens et al., 2004; Simon et al., 1990). This results in higher frequency of slope failure and tree uprooting that increases soil erosion and limits soil development. Thus, the mass movement of soils persistently draws down soil depths, and therefore SOC, on slopes and in valleys.

Despite the importance of landscape stability and associated soil depth, the spatial differences in the total 0 to 60 cm SOC pool cannot be explained by these factors alone because the 0 to 10 cm SOC pool and 0 to 10 cm C concentrations are also lower in valleys than on ridges. The role of soil chemical and textural differences between ridges and slopes is supported by the relationships among C concentrations, Fe_o and clay found in this study. Similar patterns have been documented elsewhere, especially a strong positive correlation of C concentration and Fe_o (Duiker et al., 2003; Kleber et al., 2005; Lutzow et al., 2006; Paul et al., 2008; Powers and Schlesinger, 2002; Silver et al., 2000). In valley positions, clay and pH are lower than at slope and ridge positions (Silver et al., 1994; Scatena and Lugo, 1995; this study), thus creating conditions that are not optimal for organo-mineral complexation (Gu et al., 1994; Lutzow et al., 2006). Although not part of the analysis of this study, it is possible that complexed organic material in the surface horizons may become disassociated and enter into the DOC pool where it becomes exposed to anaerobic bacteria for decomposition (Kalbitz et al., 2000). Alternatively, DOC may simply adsorb less frequently to mineral surfaces in valleys, which are highly disturbed and wet, and thus results in lower SOC compared to upland locations (Kaiser and Guggenberger, 2000; Neff and Asner, 2001).

Model simulations indicated that litter quality and quantity across topographic positions can affect total SOC pools in the tabonuco forest, but to a lesser degree than landscape related factors. Previous studies have found that the organic inputs from vegetation differ between species in the tabonuco forest and litter quality may be more decomposable in valley species (i.e. lower litter C:N) than in ridge species (Fonte and Schowalter, 2004; Myster and Schaefer, 2003; Ostertag et al., 2003; Zalamea et al., 2007). Our simulations of substituting litter chemistry indicated a slight decrease in SOC when lower litter C:N values were used, which would support that decomposition increases with more available N in the soil matrix. Further, higher concentrations of secondary compounds and tannins found in tabonuco and other late successional species (not included in our analysis), may further arrest litter decomposition (Zalamea et al., 2007). Contrary to our original hypothesis that higher tree mortality would lead to less recalcitrant woody inputs into the soil and subsequently lower SOC pools, SOC pools increased when higher mortality rates were imposed. However, this analysis was hampered by our confidence in Century model outputs. Notably, we parameterized the model to include only non-catastrophic mortality rates (i.e. “background mortality”, c.f. Scatena and Lugo (1995)) in our analysis, but if hurricane disturbance and mortality were added then the increase would probably be even greater.

Our experience using the Century model led us to several important observations. First, our analyses of litter quality and quantity effects on SOC were challenged by model to measurement comparisons. This limitation is unfortunately probably not unique to the Century model, which makes validation of simulation models difficult. According to the Century 4.0 manual, outputs represent 0–20 cm SOC, although it is unclear that this depth is recommended for tropical soils. For example, Wang et al. (2002) compares Century outputs to 0–30 cm measured SOC. Second, it is probably inappropriate to apply the model in highly disturbed areas unless soil disturbance and removal can be accurately parameterized. Third, although soil texture is an important component of the model, there is no explicit modeling of processes related to organo-mineral complexation and its relation to soil drainage in this forest. This limits the model's applicability to tropical soils with high clay contents but also high permeability due to improved soil structure. Lastly, despite these limitations, the Century model may still be useful for applications concerned with studying the relative change in SOC compared to a baseline value. This can be especially useful in situations where it is very difficult to separate processes and achieve control of several simultaneous treatments in field studies. Further, the timescale to observe SOC response to various treatments is often not amenable to field studies.

5. Conclusions

In these watersheds, landscape stability interplays with biotic controls so that most of the carbon is held in stable upland locations where tabonuco trees dominate. Terrestrial carbon modeling of topographically complex areas such as tropical steepland watersheds will have to grapple with SOC distributions that do not follow typical catena models and the processes responsible for these patterns. Predicting future changes in SOC in the tabonuco forest should consider the interactions of topographic position, tabonuco distribution and landscape stability and the possibility of altering the spatial distribution of these factors (Davidson and Janssens, 2006). Additional secondary controls, such as litter quality and organo-mineral complexation, probably also contribute but appear to be less influential. The model simulation approach in this study aided in our interpretations of the relative importance of plant–soil interactions on SOC, but could be more useful if the above mentioned limitations were overcome. One of the greatest advantages in using model simulations in conjunction with direct measurements is that it is possible to explore the effects of different factors that are impractical to duplicate with field experiments. Therefore, opportunities to develop, improve, adapt, and use process-based simulations in SOC studies of tropical soils should be explored. Overall, it can be observed from this study that the steep tabonuco forest is one case in which typical catena models, where maximum soil development and carbon accumulation occur at toeslope positions, do not apply.

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