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Spatial and seasonal dynamics of surface soil carbon in the Luquillo Experimental Forest, Puerto Rico

Hongqing Wang *, Joseph D. Cornell, Charles A.S. Hall, David P. Marley

Systems Ecology Laboratory, 301 Illick Hall, College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA

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Abstract

We developed a spatially-explicit version of the CENTURY soil model to characterize the storage and flux of soil organic carbon (SOC, 0–30 cm depth) in the Luquillo Experimental Forest (LEF), Puerto Rico as a function of climate, vegetation, and soils. The model was driven by monthly estimates of average air temperature, precipitation, and potential evapotranspiration (PET), which in turn were simulated as a function of elevation, slope, and aspect using a spatially-explicit and validated model (TOPOCLIM) of solar insolation/microclimate in mountainous areas. We simulated forest gross primary productivity (GPP) and distribution of above- and below-ground biomass production using a forest productivity model (TOPOPROD). Output from TOPOCLIM and TOPOPROD models was used to run the CENTURY soil model for 1200 months under current climate conditions and in response to potential global warming. We validated our version of CENTURY soil model using 69 soil samples taken throughout the LEF. Simulated SOC storage agrees reasonably well with the observed storage ($R^2 = 0.71$). The simulated SOC storage in the top 30 cm within the LEF is highly variable, ranging from approximately 20–230 Mg/ha. The rates of decomposition were especially sensitive to changes in elevation. Carbon release rates due to decomposition were close to carbon assimilation rates and ranged from 0.6–0.96 Mg/ha per year at high elevations to 1.2–1.68 Mg/ha per year at lower elevations. Our simulations indicated that differences in elevation affect decomposition and SOC content primarily by changing microclimate. Finally, we found that a projected warming of 2.0 °C is likely to result in losses of SOC in the lower and higher elevation, but increased storage in the middle elevations in the LEF.

Keywords: CENTURY soil model; Soil organic carbon; Tropical forests; Luquillo Experimental Forest; Climate change

1. Introduction

Spatial heterogeneity of soil organic carbon (SOC) storage and flux is a general characteristic of terrestrial ecosystems over large areas (horizontal variation) and within complex landscapes (vertical variation) (Burke et al., 1991; Raghubanshi,

* Corresponding author. Tel.: +1-315-470-6812; fax: +1-315-470-6934.

E-mail address: hqwang@mailbox.syr.edu (H. Wang).

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1992; Schimel and Burke, 1993; Schimel et al., 1996; Kern et al., 1997). Maps of tropical soils, however, often fail to represent this variation, due, at least in part, to the limited availability of spatial data at fine spatial resolutions (Band et al., 1991; Mudrick et al., 1994; Silver et al., 1994; Kern et al., 1997). Nevertheless, estimates of the spatial variability of SOC storage and flux are critical for understanding the role of soil in regional and global carbon cycles and for assessing responses of soil and vegetation to natural and anthropogenic disturbances such as hurricanes, landuse change and climate change (Raich, 1983; Detwiler, 1986; Detwiler and Hall, 1988; Brown and Lugo, 1990; Sanford et al., 1991; Zou et al., 1995; Everham, 1996).

A few previous studies of the spatial distribution of SOC pools and fluxes have been accomplished with relatively coarse spatial resolution, using grid cells greater than 4-km for region-specific patterns and greater than 50-km for global patterns (Parton et al., 1987, 1988; Kern et al., 1997). At these resolutions, however, they failed to describe any of the variations of SOC pools and flux as a function of differences in vegetation, soil characteristics, topography, and microclimate within the landscape of, for example, a mountain area. This level of detail, however, is particularly important since the 'altitudinal variation' within a given mountain area can be even greater than the 'horizontal variation' between areas broadly defined in terms of climate. In addition, because of the difficulty in acquiring extensive and systematic soil samples throughout large regions of the tropics, we need to use some sort of spatial modeling approach to characterize the distribution of SOC. Furthermore, due to small-scale variations in vegetation, topography, microclimate, and physical factors we require a dynamic model that simulates the storage and flux of SOC as a function of these factors. We applied such a modeling approach in this study to examine the spatial and temporal variability of SOC storage and fluxes along elevational and topographic gradients in humid montane tropical forests on the island of Puerto Rico. Our objectives were to determine: (1) how do SOC pools and fluxes vary spatially and temporally in these tropical forests under relatively steady state conditions; (2) how the distribution of SOC pools are related to the distribution of physical and topographic features; and (3) how patterns of SOC storage and flux may be altered by potential climate change.

2. Study site

The Luquillo Experimental Forest (LEF, 18°18' N; 65°50' W), located within the Caribbean National Forest (CNF), Puerto Rico, is a tropical montane forest and is one of the Long Term Ecological Research (LTER) sites administered by the National Science Foundation (NSF). The Luquillo Mountain area ranges in elevation from about 100 m.a.s.l to 1075 m.a.s.l over a distance of 10 km (Scatena and Lugo, 1995). The mean annual rainfall increases with elevation from approximately 2450 mm per year at lower elevations to over 4000 mm per year at higher elevations. The mean annual temperature declines from 23 to 19 °C along the elevation gradient (Weaver and Murphy, 1990; Silver et al., 1999). Within the Luquillo Mountains, there are four forest types along the elevation gradient: lower montane rain forest below 600 m.a.s.l (Tabonuco forest), montane rain forest between 600 and 900 m.a.s.l (Colorado forest), and Elfin/dwarf forest on the exposed slopes or ridges above 900 m.a.s.l, and Palm forest scattered on steep slopes and near riparian areas especially above 500 m.a.s.l (Weaver and Murphy, 1990). Each forest type differs greatly in species composition, richness, structure, productivity, litterfall and environmental factors (Weaver and Murphy, 1990; Silver et al., 1999). Mountains in the LEF are characterized by steep, highly dissected topography with slopes varying between 2 and 75° (22° on average) and they contain geomorphologically complex combinations of ridge, slope, upland valley and riparian valley (Garcia-Montiel and Scatena, 1994; Scatena and Lugo, 1995). Soils within the LEF are derived from the volcanoclastic sediments and are taxonomically diverse (Brown et al., 1983; Silver et al., 1999).

3. Methods

3.1. Model description

We developed a spatially-explicit version of the CENTURY soil model (Parton et al., 1987, 1988, 1989), which uses a GIS database of digital maps of topography, soil, and vegetation data to characterize the storage and flux of SOC to a depth of 30-cm throughout the entire LEF (Fig. 1). Originally, the CENTURY soil model used a soil depth of 20 cm. We allowed the simulated soil depth to 30 cm in our simulation in order to meet the 15 cm depth intervals in water submodel of the CENTURY model, as well as the fact that soil organic matter decreases greatly with depth and a large amount of SOC is stored at surface layer in the LEF (Lugo et al., 1986, 1995; Odum and Pigeon, 1970; Silver et al., 1994; Weaver and Murphy, 1990).

CENTURY is a model of soil nutrient dynamics that emphasizes the decomposition of soil organic matter (SOM) and the flux of carbon and nitrogen within and between different soil components. The CENTURY model has been applied to many ecosystems, including grassland ecosystems (Parton et al., 1987, 1988), agroecosystems (Metherell et al., 1995; Voroney and Angers, 1995), and forest ecosystems (Sanford et al., 1991; Motavalli et al., 1994). These studies have shown that the CENTURY model is a robust model of decomposition that can be adapted to a variety of ecological regions.

In the CENTURY model, the soil organic carbon (SOC) is subdivided into three pools that are defined kinetically as active, slow, and passive, with turnover times of 1.5, 25 and 1000 years, respectively (Parton et al., 1987, 1988). The active C pool is composed of microbes, microbial products, and labile organic substrates (Parton et al., 1987). The slow pool includes resistant plant material derived from the passive pool and soil-stabilized microbial products derived from the active pool. The passive pool is the largest pool and is composed of chemically and physically stabilized organic matter. Major driving variables for the model include monthly values of precipitation, minimum and maximum temperature, potential evapotranspiration (PET), as well as soil texture, and the quality and quantity of litter (Melillo et al., 1982; Parton et al., 1987, 1988; Scott et al., 1996). Precipitation, PET, temperature and litter quality determine soil respiration rates. Soil texture affects the decay rate of the active SOC pool, with increasing clay and silt contents resulting in increasing the stabilization from active SOC to passive SOC pool. Plant residue, which is characterized by its lignin-to-nitrogen (L/N) ratio, is divided into: (1) Structural C with a 2–5 year turnover time; and (2) Metabolic C with a 0.1–1 year turnover time. For a detailed description of the structure and main parameters of the carbon flow refer to Parton et al. (1987, 1988).

Estimates of above- and below-ground biomass were generated for each month using the TOPOPROD simulation model (Marley, 1998). TOPOPROD is a model of ecosystem productivity in mountainous areas based on the FOREST-BGC model (Running and Coughlan, 1988). In the TOPOPROD model, monthly gross primary productivity (GPP) is calculated as the summation of daily canopy photosynthesis, which is computed as a function of the CO_2 diffusion gradient, a radiation- and temperature-controlled mesophyll CO_2 conductance, canopy water vapor conductance, LAI and the day-length. Plant respiration rate for each grid cell is calculated using a linear regression equation derived from respiration rates for each forest type and elevation. The respiration rate for each forest type is estimated by subtracting the observed net primary productivity (NPP) (Weaver and Murphy, 1990) from the simulated gross primary productivity (GPP) (Table 1). Then, net primary productivity (NPP) for each grid cell is obtained by subtracting respiration rate from GPP. We allocated NPP to above- and below-ground biomass for each grid cell based on the root/shoot ratio (0.4, Everham et al., 1993). Fifty to eighty-nine percent of the above-ground biomass (based on different vegetation types) was apportioned eventually into surface litter (Weaver and Murphy, 1990). Six percent of the below-ground biomass died monthly and turned into root litter (Weaver and Murphy, 1990).

The soil water submodel in the CENTURY was used to calculate available soil water based on the

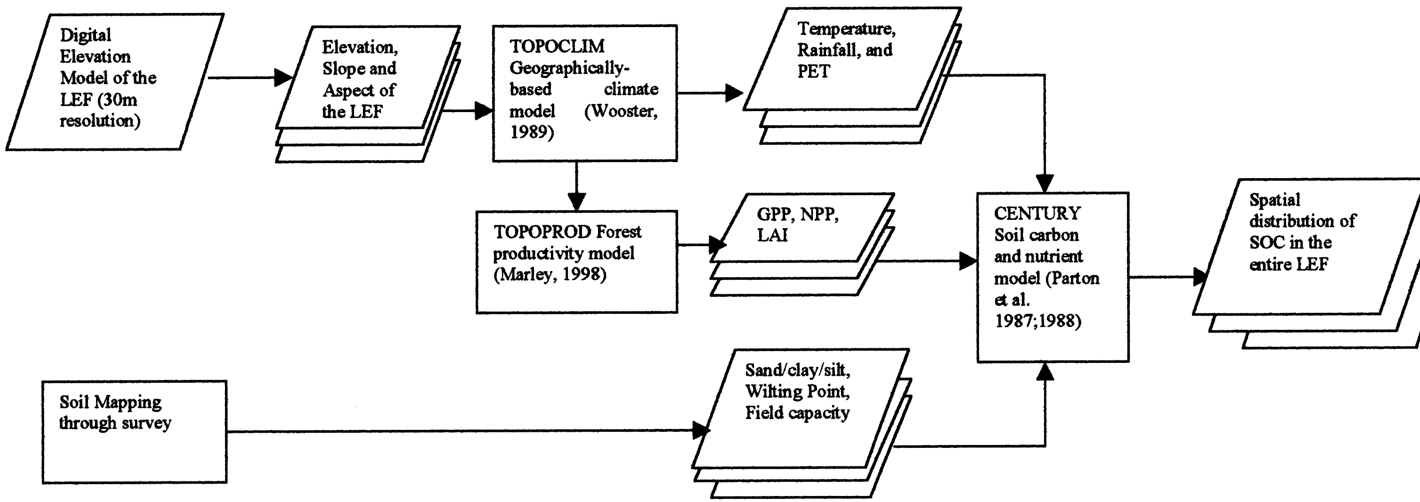

Fig. 1. Flowchart of spatial modeling of soil organic carbon (SOC) in the Luquillo Experimental Forest (LEF), Puerto Rico. This diagram illustrates the incor of a topography-related climate model, TOPOCLIM, a forest Gross Primary Production model, TOPOPROD, and a soil carbon model, CENTURY (core this simulation), connecting with a GIS (IDRISI) to simulate the distribution of SOC storage and fluxes along elevation and topographic gradients over the en

water balance among rainfall, evaporation, transpiration and saturated water flow between soil layers. A soil moisture index, which is defined as the ratio of rainfall plus soil available water to potential evapotranspiration (PET), was calculated for each grid cell as a factor limiting maximum decomposition rate.

We simulated the distribution of climatic variables (monthly average temperature, precipitation, and PET) using the TOPOCLIM model, which is a spatially-explicit solar insolation/microclimate model developed using data for the LEF (Wooster, 1989; Marley, 1998; for details refer to http: / / www.esf.edu / course / sysecol / topoclim/TOPOCLIM.HTM).

Because the CENTURY model has been applied successfully to a variety of ecosystem types we did not adjust the non-site-specific parameters in the model. These parameters include the constants that partition the flows of decomposition products, and the parameters that control the effects of soil texture, L/N ratios, temperature, and moisture on decomposition rates and decomposition product partitioning. Nevertheless, the settings of the maximum specific decomposition rates for each soil carbon pool tended to over-estimate decomposition of soil organic matter (Voroney and Angers, 1995). Therefore, we adjusted these rates to meet soil conditions at the LEF. In the LEF, necromass turnover time was available only for the Tabonuco forest (9350 days). We assigned this turnover rate to the slow carbon pool, and assigned turnover rates to the active and passive pools by multiplying this rate by the relative proportion of the base settings of the CENTURY model (Brown et al., 1983, and Table 2). We used the fixed turnover rates for each soil carbon pool for the entire LEF.

Table 1
Simulation parameters of different vegetation types in the LEF

Forest type	Average elevation (m)	GPP[a] (Mg C/ha per month)	NPP[b] (Mg C/ha per month)	Respiration[c] (Mg C/ha per month)
Tabonuco forest	402	4.41	1.23	3.18
Colorado forest	720	2.79	0.89	1.90
Palm forest	711	2.86	2.28	0.58
Elfin forest	897	2.00	0.43	1.57

[a] Marley (1998).
[b] Weaver and Murphy (1990).
[c] Derived by the difference between GPP and NPP.

Table 2
Some model parameters for SOC constituents for simulation using spatially explicit version of the CENTURY model

Carbon pool	Distribution of soil C (% of total SOC)		Specific decay rate (per month)	
	Parton et al., 1987	This study[a]	Parton et al., 1987	This study[b]
Surface microbial		0.53	0.50	0.1261
Active C	7	1.39	0.56	0.1412
Slow C	50	37.72	0.0152	0.00326
Passive C	43	60.36	0.0005	0.00008

[a] Derived from Pulliam (unpublished data).
[b] Derived from Odum and Pigeon (1970), Brown et al. (1983).

3.2. Data inputs

A spatially-explicit version of the CENTURY model requires that the data used as inputs and all model outputs be represented as maps in a GIS. We used IDRISI (Clark University) to create a GIS database of input and output images of the LEF at a grid cell resolution of 30 m (384 by 671 gridcells) that is currently the only available resolution for the elevation data. This resolution is appropriate to reflect the landscape variations in climate, vegetation, soils and topography in the Luquillo Mountains within the resolution of the available data. A digital elevation model (DEM) of the LEF at a 30-m resolution (digitized from 1:24,000 USGS Forest Service map by the University of Puerto Rico) was used as the topographic input.

We obtained maps of soil types (digitized from the 1:24,000 USDA soil survey of 1991) and vegetation types (digitized from the USGS 1:24,000 Forest Service map of 1989) of the LEF at a 30-m resolution. We used the soil type map to generate maps of percent clay content, percent sand content, wilting point, and field capacity based upon values given with the soil map itself and in Brady (1990). We derived a map of leaf area index (LAI) from the vegetation map based on average LAI values for the four major types of vegetation in the LEF (Weaver and Murphy, 1990).

We initialed SOC values for each vegetation type from a set of multiple regressions between SOC and elevation and topographic features (ridge, slope and valley) for each vegetation type based on 50 soil samples, which we took within the LEF. Then we apportioned the percentage of SOC in each soil carbon pool for each grid cell, using data from the Tabonuco forest (William M. Pulliam, unpublished, Table 2). We derived maps of initial above-ground biomass and litter biomass by applying Weaver's (1990) biomass values for different forest types to the corresponding map of vegetation.

We used the IDRISI-based database and initial conditions for the LEF as inputs to our version of CENTURY and ran the model using a monthly time step for 100 years, at which time the total SOC pools approximately reached steady state. We saved the output images of SOC storage, monthly decomposition fluxes, and CO_2–C releases for each location in the LEF for the last 12 months for each model scenario as a new series of IDRISI images.

3.3. Sensitivity analysis and effects of possible warming on soil carbon

A formal sensitivity analysis of the model (sensu Hall and Day, 1990) was conducted to see how changes in the forcing functions (i.e. average monthly air temperature, average monthly rainfall, LAI, percentages of sand and clay, L/N ratios in above-and below-ground biomass) and in the most important structural parameters (i.e. specific decay rates in surface microbial, active, slow and passive pools) would affect the simulated distributions of SOC storage and fluxes.

We also investigated the potential effects of predicted climate change on the distribution of SOC assuming an average increase of 2.0 °C in surface temperature and an average decrease of rainfall of 22% over the 21st century (a change of 0.002688 °C per month for temperature and 1.2 mm per month for rainfall, evenly distributed) based on calculations by Scatena and Lugo (1998). We ran the model for 100 years under these new conditions and compared the results with the spatial and temporal patterns of SOC under steady state in the LEF. We used the SAMPLE command in IDRISI to select 100 spatial points in the LEF both randomly and systematically, and then used them as the samples to conduct multiple regression analyzes using STATISTICA version 5.1 (Statsoft, 1997).

3.4. Field sampling and laboratory analysis

Soil samples were taken over the entire LEF during the period of June to July in both 1998 and 1999 using a combination of random and systematic sampling protocols, in other words, samples were systematically taken in all four vegetation types and randomly taken in each type. We were not able to sample systematically along the entire elevation gradient in the forest due to the difficulty in accessing some areas (e.g. inaccessible valleys, the Puerto Rican Parrots protection area). Thus, we collected a total of 119 soil samples (100 in 1998 and 19 in 1999) relatively close to forest trails, which were distributed throughout the LEF. Generally speaking, these samples covered well the four major vegetation types and the topographic gradient, and somewhat less well the entire elevation gradient in the LEF (for details refer to http://www.ites.upr.edu/sunceer/DATA/lterdb110/metadata/lterdb110.htm # top). At each sampling site, within a radius of approximate 15 m, we removed the leaf litter from the forest floor and took five subsamples to a depth of 30 cm of mineral soil with a 1.85-cm diameter soil corer. Then the subsamples were mixed in plastic bags as the representative soil sample for that site. Meanwhile, we used a global positioning system (GPS Pathfinder Basic Receivers, Timble Navigation Ltd.) to determine the geographic location of each site. Soil samples were air-dried, ground and sieved (<2 mm) for soil organic carbon by the Walkley–Black method.

3.5. Validation

We divided our 1998 field data into two sets based on random numbers: one (50 samples) for initial SOC values and another set (50 samples) for validation. We included 19 samples taken in 1999 to add to the validation set based on the assumption that there is no significant change in SOC storage between 1998 and 1999. We validated our model by comparing simulation with field data (69 samples). The degree of agreement between simulated and observed SOC values is determined by the R^2 of regression model between the two data sets.

4. Results

4.1. Pattern and dynamics of soil organic carbon

The simulated total soil organic carbon pool (0–30 cm) over the entire LEF ranged from approximately 20 Mg/ha at lower elevations to 230 Mg/ha at higher elevations (Fig. 2). The largest SOC pools in this forest are found near the peaks (i.e. 170–230 Mg/ha near El Yunque, El Toro and Pico del Este). A regression analysis of our model results showed that the simulated distribution of SOC was correlated positively with elevation ($P < 0.0001$), negatively with slope ($P < 0.0779$), and not related significantly to aspect (Table 3). The regression analysis also showed that simulated patterns of SOC storage in the LEF were different within the Tabonuco, Colorado, Palm and Elfin forests (Table 4). In general, SOC storage increases from the Tabonuco forest at lower elevations, to Palm and Colorado forests at middle elevations, to the highest storage of SOC in the Elfin/Dwarf forest near the peaks in the LEF (Table 4).

Decomposition throughout the LEF showed a strong seasonal pattern with the highest rates occurring during the wetter and warmer months of June to September. The decomposition of soil organic matter (SOM) and the release rates of CO_2–C due to decomposition of SOM also exhibited strong spatial patterns with both being correlated significantly with elevation (Tables 3 and 4). In general, locations at higher elevations tend to decompose less and release less CO_2 over the course of a year than those at lower elevations (Fig. 3). However, these patterns do not always hold true. For example, palm forests have the lowest decomposition fluxes although they are located along much of the elevational gradient, presumably due to the distribution of palm trees along the steeper and wetter locations. On the other hand, the month-to-month variability in the decomposition flux for each forest type was generally smaller than the differences from one forest type to another except for the low elevation Tabonuco forest in March (Fig. 3). Tabonuco and Colorado forests have a higher CO_2–C release per hectare than Palm and Elfin/Dwarf forests, and the variation within-forest-type is smaller than the variation between-forest-type (Fig. 3).

4.2. Sensitivity analysis

Our sensitivity analysis indicated that LAI, average monthly air temperature and average monthly rainfall are the forcing functions that produce the largest response in simulated SOC

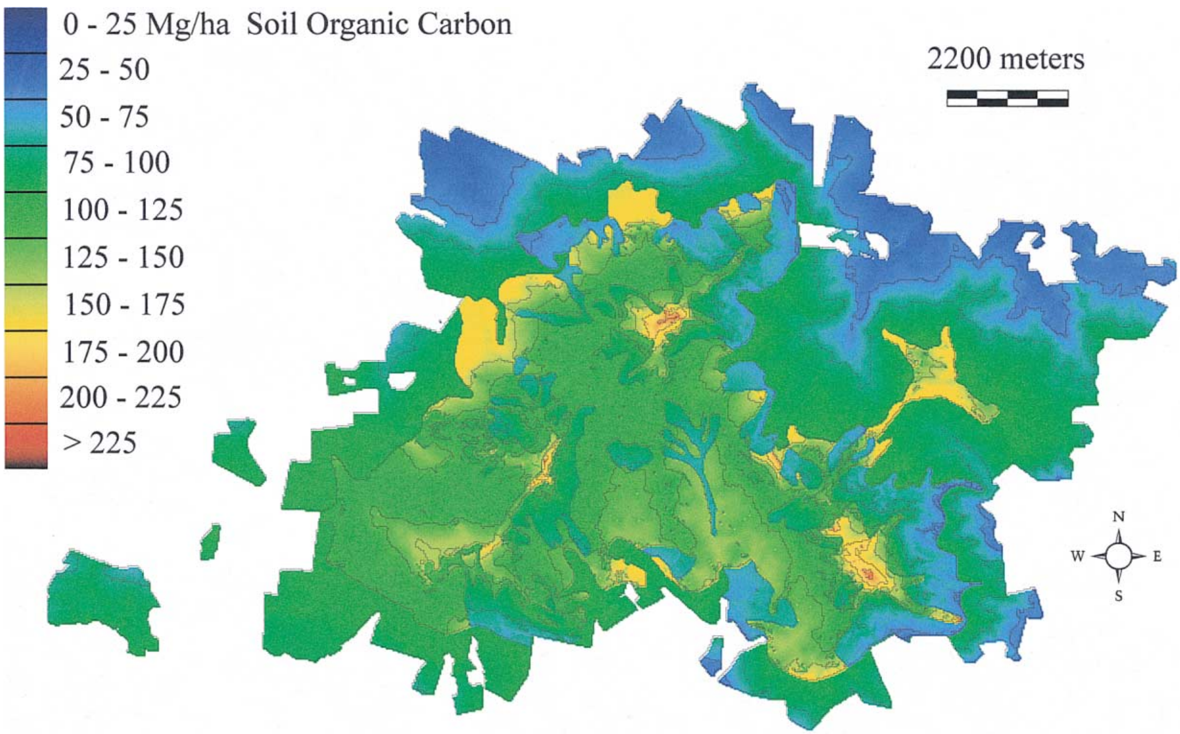

Fig. 2. Simulated distribution of soil organic carbon (SOC) storage (0–30 cm depth, (unit: Mg/ha) in the Luquillo Experimental Forest (LEF), Puerto Rico. This image was created by IDRISI-GIS after running the spatially-explicit version of the CENTURY model (timestep = monthly) for 100 years (1200 months) under current climate conditions.

storage and decomposition rates (Fig. 4; Table 5). The model is most sensitive to LAI, e.g. SOC increases from 43.4 to 78.5 Mg/ha as LAI increases from 3 to 5.5 and then decreases to 45 Mg/ha when LAI is larger than 5.5. This is because LAI plays an important role in determining forest production in the TOPOPROD model and the net forest production determines the rate of plant biomass inputs to the soil subsystem (Marley, 1998). There is no linear relationship between net forest production and LAI at high LAI values. Trees need to invest more energy in support organs at larger LAI, thereby increasing maintenance respiration cost (Medina, 1995). Therefore, maximum SOC storage at middle LAI (5.5) is the result of highest net forest production input to soils. In terms of the effects of climatic factors on soil decomposition, the SOC storage and decomposition rates in the model are more sensitive to average monthly air temperature than to average monthly rainfall. For instance, the SOC decomposition would increase from 0.094 to 0.174 Mg/ha per year (about 86% increase) if average monthly temperature increases from 15 to 30 °C, whereas it would increase from 0.116 to 0.149 Mg/ha per year (about 28% change) if average monthly rainfall increases from 10 to 50 cm (Table 5). Actually, SOC storage and fluxes increase as rainfall increases up to only 15 cm per month over the possible range of 10–50 cm/month (Fig. 4). Changes in the percentages of sand and clay, as well as changes in the L/N ratios in above- and below-ground biomass produced little response in simulated SOC storage and decomposition (Table 5). The simulated SOC storage and fluxes are more sensitive to the decay rates of slow pool and active pool than the decay rate of passive pool (Fig. 4; Table 5). Therefore, selection of sets of decay rates for each soil carbon pools is important for model performance.

4.3. Effects of climate change on soil carbon

Simulation of the potential effects of the climate change showed that the most likely climate change scenario (e.g. Scatena and Lugo, 1998) is likely to result in losses of SOC up to 4.5 Mg/ha at lower and higher elevations of the LEF. This is approximately 15% of the total SOC at lower

Table 3
Multiple regressions of simulated SOC storage and fluxes of decomposition of SOC and CO_2–C release from the CENTURY model against elevation, slope, aspect and vegetation type in the LEF

Variable	Coefficient	Standard error	T value	P-level	R^2
SOC					0.4976
Intercept	88.41	11.92	7.41	0.0000	
Elevation	0.16	0.02	8.16	0.0000	
Slope	−0.64	0.36	−1.78	0.0779	
Aspect	0.03	0.03	0.11	0.9159	
Vegetation type	−18.78	4.78	−3.93	0.0002	
Decomposition					0.2105
Intercept	7.08	0.72	9.80	0.0000	
Elevation	0.01	0.00	3.34	0.0012	
Slope	−0.02	0.02	−1.09	0.2795	
Aspect	0.00	0.00	0.77	0.4455	
Vegetation type	−1.29	0.29	−4.47	0.0000	
CO_2-release					0.3092
Intercept	11.62	1.14	10.23	0.0000	
Elevation	0.01	0.00	3.03	0.0032	
Slope	−0.04	0.03	−1.06	0.2899	
Aspect	0.00	0.00	0.56	0.5765	
Vegetation type	−2.65	0.46	−5.82	0.0000	

Significant level was set at $\alpha = 0.10$

Table 4
Descriptive statistics for simulated SOC storage, fluxes of decomposition of SOC and CO_2–C release among different vegetation types in the LEF

Variable	Sample size	Mean	Minimum	Maximum	Standard deviation	C.V. (%)
SOC (Mg/ha)						
Tabonuco forest	50	123.54	68.61	154.32	27.98	22.65
Colorado forest	30	176.20	150.24	228.21	23.16	13.14
Palm forest	15	101.19	75.93	134.92	13.03	12.88
Elfin forest	5	186.25	172.15	202.49	15.28	8.20
Decomposition (g C/m^2 per month)						
Tabonuco forest	50	7.17	3.76	8.88	1.68	23.43
Colorado forest	30	7.75	5.20	11.18	1.79	23.10
Palm forest	15	5.11	3.76	7.66	1.14	22.31
Elfin forest	5	5.43	5.36	5.47	0.06	1.10
CO_2–C release						
Tabonuco forest	50	10.86	5.96	13.99	2.74	25.23
Colorado forest	30	10.83	6.07	15.56	2.77	25.58
Palm forest	15	6.38	3.21	8.63	1.57	24.61
Elfin forest	5	5.55	5.24	5.88	0.32	5.77

Table 5
Results of sensitivity analysis of forcing functions and specific decay rates in the simulation of SOC storage and decomposition in a Tabonuco site in the L
the spatially explicit version of CENTURY model

Variables	Variable range			SOC		% Change	SOC decomposition (Mg/ha per year)		% Change	Reference for possible variable r
	Low	Best estimate	High	Low	High		Low	High		
Forcing functions:										
LAI (m^2/m^2)	3	3.5	7.5	43.4	78.5	80.8	0.145	0.553	+281	Brown et al., 1983
Average Monthly temperature (°C)	15	15	30	41.5	47.9	15.3	0.094	0.174	+85.9	Brown et al., 1983
Average Monthly rainfall (cm)	10	15	50	40.5	43.8	8.1	0.116	0.149	+28.4	Weaver & Murphy 1990
Sand (%)	5	5	65	41.4	43.6	5.4	0.124	0.148	+18.6	Forest Service Southern Forest Experiment Station, 1991
Clay (%)	10	60	60	43.3	43.4	0.1	0.144	0.146	+1.0	USDA 1991
Specific decay rate in:										
Active pool	0	0	0.56	43.2	46.2	6.9	0.071	0.145	+104.1	Parton et al., 1987, 1988
Slow pool	0	0.0002	0.016	33.4	52.4	56.9	0.073	0.166	+126.2	Parton et al., 1987, 1988
Passive pool	0	0	0.0005	41.7	43.8	4.8	0.131	0.214	+63	Parton et al., 1987, 1988

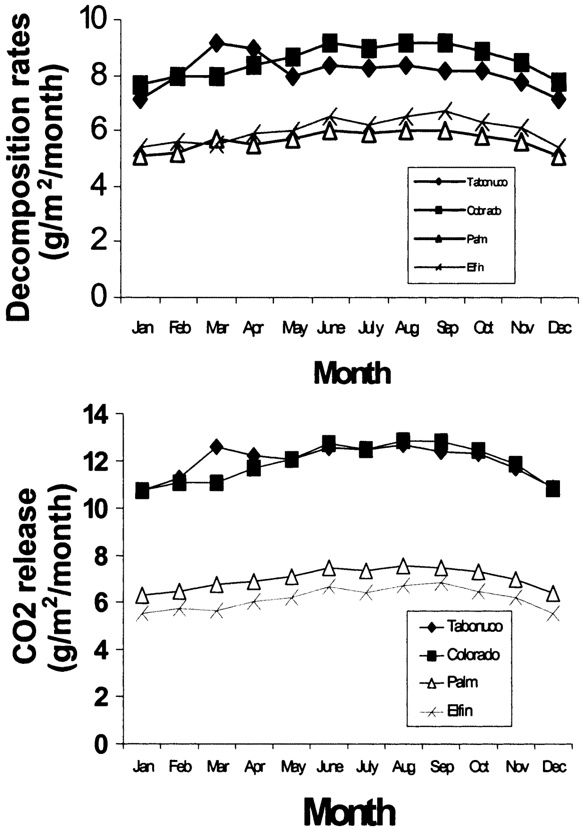

Fig. 3. Simulated decomposition rates of soil organic carbon (SOC) (above) and CO_2–C release (below) for Tabonuco, Colorado, Palm and Elfin forests in the Luquillo Experimental Forest (LEF), Puerto Rico. The two graphs indicate, in general, that higher elevations tend to have slower decomposition of SOC and hence release smaller amount of CO_2 than their lower counterparts. Meanwhile, there are larger variations in SOC decomposition and CO_2–C release between forest types than within-forest variations.

locations and 3% in the peaks. But there would be increases in SOC storage up to 2.3 Mg/ha at middle elevations (Fig. 5). The reason for this pattern is that climate change would affect both soil temperature and moisture, with the greatest change of the combined factors occurring at higher and lower elevations and with a potentially smaller net effect at middle elevations. Thus the effects of projected climate change on the storage and flux of SOC in different parts of the LEF would not be uniform because of the great diversity of microclimates and their impacts in this complex forest ecosystem.

4.4. Model validation

The simulated spatial variations of SOC storage (0–30 cm) in the Luquillo Mountains agree reasonably well with the spatial variations observed from 69 soil samples over the entire LEF ($R^2 = 0.71$) (Fig. 6). The agreement between simulated and observed results decreases in the order of Elfin → Colorado → Palm → Tabonuco forests. For example, the simulation error, or average percent difference increases from 18% for Elfin forest to 27% for Colorado forest, 28% for Palm forest and 33% for the Tabonuco forest (Table 6).

5. Discussion

5.1. Factors affecting soil carbon distribution

Only a few studies have been done on the spatial variability of soil nutrient availability or other soil characteristics at the scale of discrete watersheds or larger within the LEF (Silver et al., 1994). Weaver et al. (1987) and Weaver (1990) found in agreement with our study that soil organic matter content increased with elevation within the Colorado and Elfin/cloud forests. Silver et al. (1994) showed that soil organic matter decreased from ridge tops to riparian valleys within the montane wet tropical forest. Our model generated similar patterns, indicating that both the distribution of SOC pools and decomposition fluxes vary significantly along both elevational and topographic gradients across the landscape of the LEF. SOC pools increase with elevation and decrease with slope (Table 3). Our results demonstrate that abiotic factors, in particular microclimate, control the spatial pattern of SOC storage in the LEF through their influence on biological activities. For example, Silver et al. (1999) found that soil available oxygen decreased as elevation increases. Lower soil temperature, higher soil moisture and lower soil available oxygen at higher elevations result in lower rates of anaerobic decomposition and a buildup of SOC.

Our modeling also showed that actual evapor-transpiration (AET) and soil available water vary greatly across the landscape of the LEF. AET appears to be greater at lower elevations than at higher elevations due to higher air and soil temperatures and lower relative humidity in the lowlands. Our simulated soil moisture index (SMI) increases with elevation due to more rainfall and less potential evaportranspiration (PET) (Fig. 7). AET decreases with decreasing slope while SMI increases. As a result, although NPP tends to decrease with elevation in both our simulation and the relative few measurements (Weaver and Murphy, 1990), SOC storage tends to increase because lower rates of decomposition at higher elevations more than offset decreases in aboveground organic inputs. Sensitivity analysis and response to climate change of SOC storage in the model is affected strongly by seasonality, such that small proportional changes in soil temperature have an even greater effect on SOC storage than larger changes in soil moisture. This has important implications for the storage of SOC in tropical forests. Many studies have reported that forest ecosystems are sources of CO_2 release as a result of disturbance including global warming, cultivation and deforestation (Post et al., 1982; Detwiler, 1986; Lugo et al., 1986; Pastor and Post, 1986; Detwiler and Hall, 1988; Hall et al., 1992; Dale, 1994; Trumbore et al., 1996). Our simulations indicate that any global warming probably would result in increased losses of SOC as well as changes in the patterns of SOC storage and flux. More importantly, even small changes in SOC storage alter the assumption of steady state dynamics of SOC in tropical forests, and thus might change the role of tropical forests as a source or sink of atmospheric carbon.

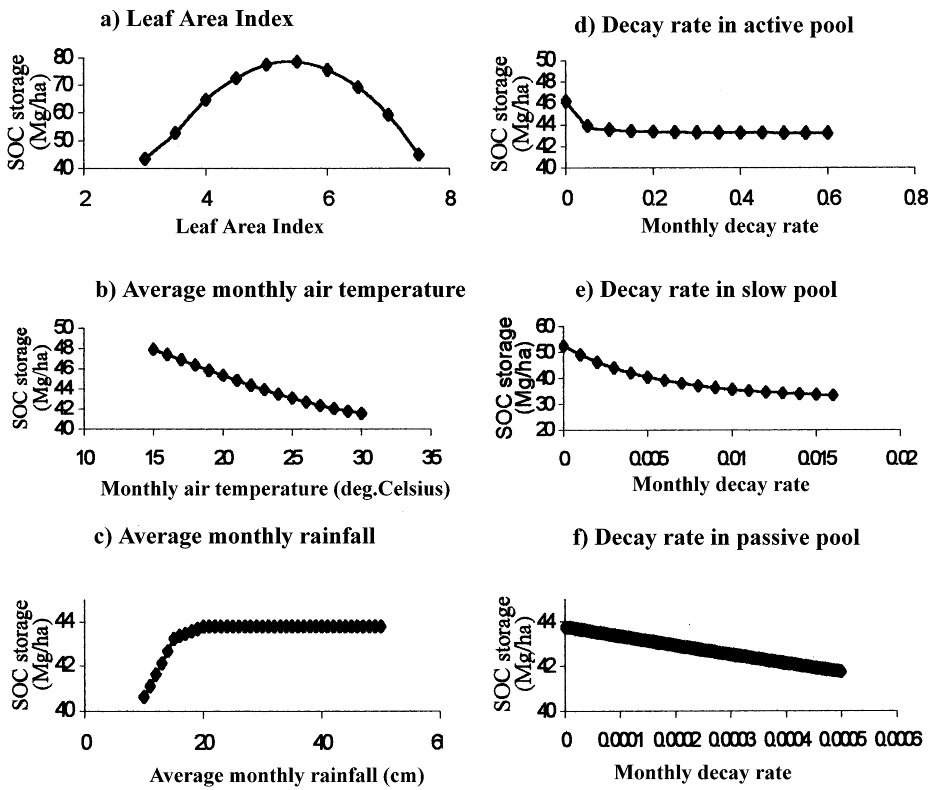

Fig. 4. Sensitivity analysis of major forcing functions (a–c) and decay rates in different soil carbon pools (d–f) in the simulation of SOC distribution in the LEF.

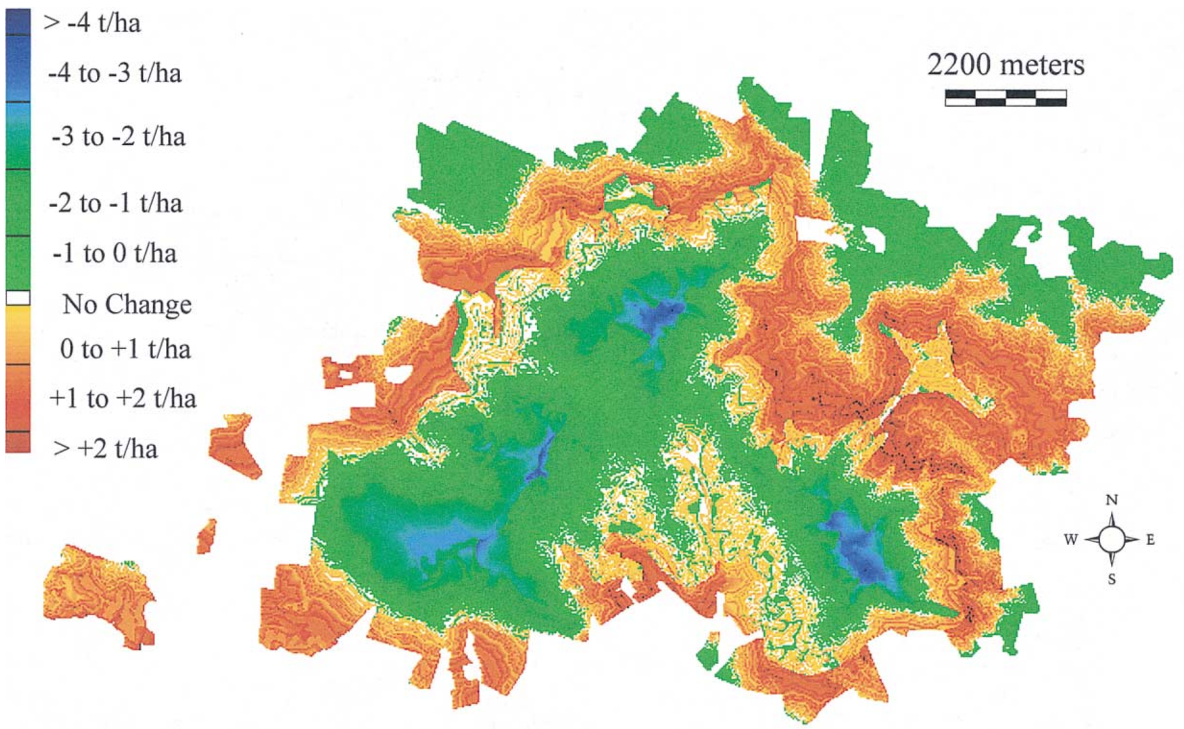

Fig. 5. Image of the changes of soil organic carbon (SOC) under climate warming (an average increase of 2.0 °C in surface temperature and decrease of rainfall of 22% over the next century (Scatena and Lugo, 1998) compared with the distribution of SOC under current climate conditions in the Luquillo Experimental Forest (LEF), Puerto Rico.

5.2. Model validation

The accuracy of our simulations depends on the CENTURY model performance, the accuracy of inputs of spatial data (e.g. DEM, vegetation, and soil maps), and measurements of our field data (i.e. geographic locations and attributes of field SOC data). In this research, we assumed that the inputs of spatial data and the measurements of field data have acceptable accuracy for our modeling purposes due to the scarcity of spatial information on vegetation and soil that might allow us to conduct accuracy assessments. Therefore, we will focus on the performance of our model in order to assess our modeling efforts.

The accuracy of our SOC simulation depends greatly upon the CENTURY model parameters and the initial values used to set up the model (Parton et al., 1987, 1988). In particular, the allocation of total SOC to different pools affects the pattern of SOC storage greatly due to the different turnover rate of each pool. The initial values and distribution of the SOC play an important role in determining the accuracy of the model. We attempt to use as much of the available spatial information about microclimate, vegetation, soils, and topography in our simulation. However, we were unable to obtain spatial data for many parameters. For example, ideally, we would have information for different soil types on the allocation of total SOC to different pools (microbial, active, slow and passive) and also initial SOC values. But, we had this data only for the Tabonuco forest. We did have and use multiple regression equations for initial SOC with elevation from our first set of field data. These samples were well distributed overall except for those elevations between 500 and 650 meters where large areas are off limits for protecting the endangered Puerto Rico parrots. This limited the

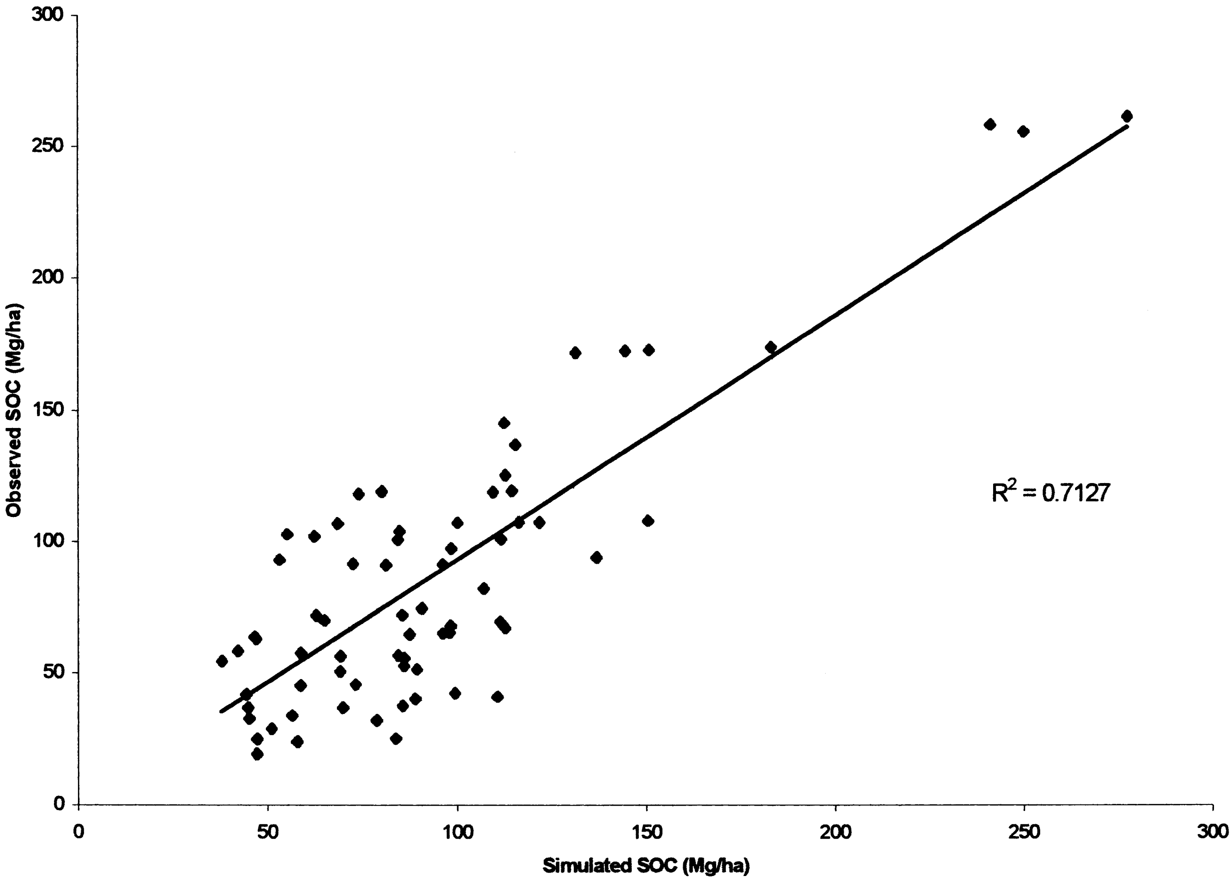

Fig. 6. Comparison between simulated storage of soil organic carbon (SOC, top 30 cm) in Mg/ha and observed SOC ($n = 69$) across the entire Luquillo Experimental Forest (LEF), Puerto Rico.

accuracy of our initial SOC image. As a result, we could not obtain a high-level modeling accuracy. Nevertheless, the moderate correlation between simulated and observed SOC ($R^2 = 0.71$) indicated that our spatial version of the CENTURY model was capable of capturing the essential geographic and topographic variability in SOC storage and fluxes within the LEF. The lower simulation accuracy for the Tabonuco forest compared to the Colorado, Palm and Elfin forests is probably the results of more heterogeneous pattern of soil physical and chemical properties resulting from past human disturbances (deforestation, agriculture and other activities) that were much more prevalent at low elevations than at higher elevations (Brown et al. 1983;

Table 6
Comparison between simulated SOC and observed SOC for different vegetation types in the LEF

Vegetation type	Sample number	R^2	Simulation error (%) [a]
Tabonuco forest	27	0.2397	33.2
Colorado forest	14	0.4559	27.0
Palm forest	18	0.7710	28.8
Elfin forest	10	0.9025	18.0
Overall	69	0.7151	28.6

[a] Simulation error (%) = [{Σ(((simulated SOC − observed SOC)/observed SOC) × 100)}/sample number.

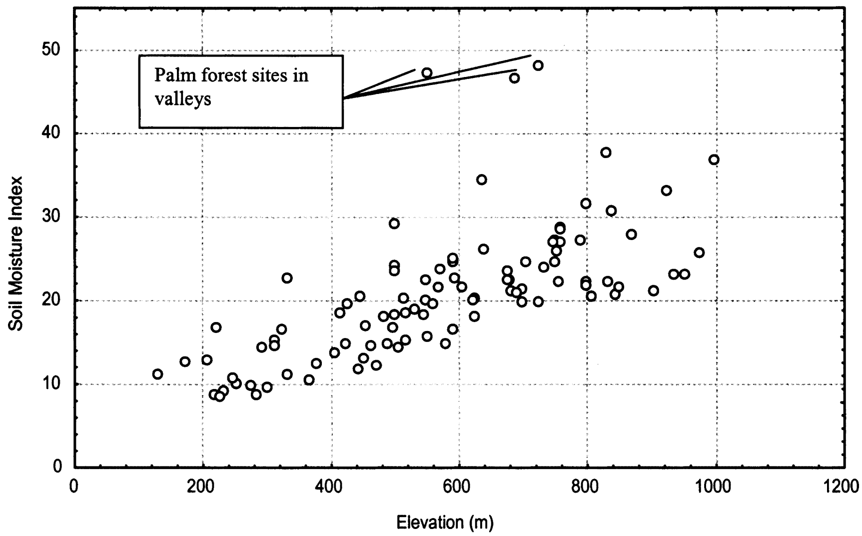

Fig. 7. Relationship between elevation and simulated soil moisture index, defined here as the ratio of rainfall plus soil available water to potential evapotranspiration (PET) in December in the Luquillo Experimental Forest (LEF), Puerto Rico. At a given elevation, variation in SMI is due to variation in topographic features: valleys tend to have higher SMI values than ridges especially for palm forest between 500 and 800 m.

Scatena and Lugo, 1995). Thus, if we were to include the spatial pattern of the influences of disturbances (e.g. hurricanes, landslides, etc) and landuse history, we presumably could improve the performance of our modeling due to the contribution of disturbances to the spatial and temporal variability of soil physical, chemical and biogeochemical features in this forest (Sanford et al., 1991; Zimmerman et al., 1996). In addition, we used the repeated mean monthly temperature, rainfall and potential evapotranspiration for different years in our simulation. In other words, we did not simulate SOC with changing monthly climatic factors over the simulation years, which might also cause discrepancy between simulated and observed SOC values.

6. Conclusion

Simulated soil organic carbon (SOC, 0–30 cm) storage in the Luquillo Experimental Forest (LEF) is highly variable, ranging from approximately 20–230 Mg/ha with elevation. Carbon release rates due to decomposition were close to carbon assimilation rates and ranged from 0.6 to 0.96 Mg/ha per year at higher elevations to 1.2–1.68 Mg/ha per year at lower elevations. The variability is the reflection of the heterogeneity in vegetation, soil and climate, which results from the complex topography in the Luquillo Mountains. For example, rainfall, relative humidity, soil moisture and wind velocity increase with elevation, while air temperature, evapotranspiration, insolation decrease with elevation. The interaction of these climatic factors with vegetation (Tabonuco, Colorado, Palm and Elfin/dwarf forests) and soils determines the gradient distribution of SOC across the Luquillo landscape. Sensitivity analyzes indicate our spatial modeling of the CENTURY soil model is more sensitive to leaf area index (LAI), monthly air temperature and monthly rainfall, as well as sensitive to the decay rates of slow and active carbon pool. Our simulation indicates that potential warming plus decreases of rainfall in the Luquillo Mountains is likely to result in losses of SOC at lower and higher elevations but increases of SOC at middle elevations due to the effects of combined effects of temperature and soil moisture on decomposition processes.

Comparison between simulated SOC values and observed SOC values indicated that our geographical modeling approach works reasonably well to describe the spatial and seasonal variation in SOC storage and fluxes in the LEF. Our simulation accuracy is a function of spatial data inputs (e.g. vegetation and soil types, DEM), initial SOC values, maximum decay rates of each soil carbon pool and the number and representativeness of field samples. Past disturbances such as landuse change, hurricanes, landslides, treefall and others) contribute greatly to the variability in SOC in the Luquillo landscape, therefore, we need to consider the effects of disturbances on spatial and temporal dynamics of SOC as well as the responses of ecosystem processes (e.g. photosynthesis, decomposition, mineralization, etc.) to disturbances in our future modeling efforts. In addition, we call for more field studies on soil carbon partitioning, monitoring of decomposition and mineralization especially for Colorado, Palm and Elfin/dwarf forests in the LEF. Meanwhile, we also call for applications of advanced techniques such as remote sensing, global positioning system in obtaining more and accurate spatial information for ecosystem modeling (e.g. using latest LANDSAT TM data for deriving accurate LAI images) in the LTER_LUQ project.

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