

THE VERTICAL DISTRIBUTION OF SOIL ORGANIC CARBON AND ITS RELATION TO CLIMATE AND VEGETATION

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Abstract. As the largest pool of terrestrial organic carbon, soils interact strongly with atmospheric composition, climate, and land cover change. Our capacity to predict and ameliorate the consequences of global change depends in part on a better understanding of the distributions and controls of soil organic carbon (SOC) and how vegetation change may affect SOC distributions with depth. The goals of this paper are (1) to examine the association of SOC content with climate and soil texture at different soil depths; (2) to test the hypothesis that vegetation type, through patterns of allocation, is a dominant control on the vertical distribution of SOC; and (3) to estimate global SOC storage to 3 m, including an analysis of the potential effects of vegetation change on soil carbon storage. We based our analysis on >2700 soil profiles in three global databases supplemented with data for climate, vegetation, and land use. The analysis focused on mineral soil layers.

Plant functional types significantly affected the vertical distribution of SOC. The percentage of SOC in the top 20 cm (relative to the first meter) averaged 33%, 42%, and 50% for shrublands, grasslands, and forests, respectively. In shrublands, the amount of SOC in the second and third meters was 77% of that in the first meter; in forests and grasslands, the totals were 56% and 43%, respectively. Globally, the relative distribution of SOC with depth had a slightly stronger association with vegetation than with climate, but the opposite was true for the absolute amount of SOC. Total SOC content increased with precipitation and clay content and decreased with temperature. The importance of these controls switched with depth, climate dominating in shallow layers and clay content dominating in deeper layers, possibly due to increasing percentages of slowly cycling SOC fractions at depth. To control for the effects of climate on vegetation, we grouped soils within climatic ranges and compared distributions for vegetation types within each range. The percentage of SOC in the top 20 cm relative to the first meter varied from 29% in cold arid shrublands to 57% in cold humid forests and, for a given climate, was always deepest in shrublands, intermediate in grasslands, and shallowest in forests ($P < 0.05$ in all cases). The effect of vegetation type was more important than the direct effect of precipitation in this analysis. These data suggest that shoot/root allocations combined with vertical root distributions, affect the distribution of SOC with depth.

Global SOC storage in the top 3 m of soil was 2344 Pg C, or 56% more than the 1502 Pg estimated for the first meter (which is similar to the total SOC estimates of 1500–1600 Pg made by other researchers). Global totals for the second and third meters were 491 and 351 Pg C, and the biomes with the most SOC at 1–3 m depth were tropical evergreen forests (158 Pg C) and tropical grasslands/savannas (146 Pg C).

Our work suggests that plant functional types, through differences in allocation, help to control SOC distributions with depth in the soil. Our analysis also highlights the potential importance of vegetation change and SOC pools for carbon sequestration strategies.

Key words: *belowground processes and global change; carbon content extrapolation; deep soil; depth profiles; ecosystem allocation; plant functional types; root distributions; soil carbon storage; soil gradients; soil–climate–vegetation relationships.*

INTRODUCTION

Soil is the largest pool of terrestrial organic carbon in the biosphere, storing more C than is contained in

plants and the atmosphere combined (Schlesinger 1997). The abundance of organic C in the soil affects and is affected by plant production, and its role as a key control of soil fertility and agricultural production has been recognized for more than a century (Dokuchaev 1883, Hilgard 1906, Jenny 1941, Tiessen et al. 1994). The patterns and controls of soil organic carbon (SOC) storage are critical for our understanding of the

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biosphere, given the importance of SOC for ecosystem processes and the feedback of this pool to atmospheric composition and the rate of climate change (Raich and Potter 1995, Trumbore et al. 1996, Woodwell et al. 1998). Our capacity to predict and ameliorate the consequences of climate and land cover change depends, in part, on a clear description of SOC distributions and the controls of SOC inputs and outputs.

Many important global and regional SOC budgets are available (e.g., Schlesinger 1977, Post et al. 1982, Eswaran et al. 1993, Kern 1994, Batjes 1996), and for some biomes, like temperate grasslands, major environmental controls of SOC have been described (Parton et al. 1987, Burke et al. 1989). One aspect of the organic carbon pool that remains poorly understood is its vertical distribution in the soil and accompanying relationships with climate and vegetation. What are the general vertical patterns of SOC? Do the major determinants of SOC content differ with depth? How much SOC does the biosphere store in deep soil layers and what is the effect of vegetation type on this pool? The aim of this paper is to provide preliminary answers to these and other questions, based on global soil data sets.

SOC storage is controlled by the balance of C inputs from plant production and outputs through decomposition (Jenny 1941, Schlesinger 1977). In humid climates, both production and decomposition increase with temperature, but relative increases in decomposition are greater (Nakane 1975, Schlesinger 1977, Oades 1988). Precipitation constrains plant production and decomposition in arid to subhumid ecosystems (Webb et al. 1978, Sala et al. 1988, Amundson et al. 1989), with a greater response of plant production relative to decomposition (A. T. Austin and P. M. Vitousek, *unpublished manuscript*). In addition to climate, soil texture plays an important role, with increasing clay content decreasing C outputs through its stabilizing effect on SOC (e.g., Paul 1984). As expected from these controls, regional patterns of SOC are positively associated with mean annual precipitation and clay content, and are negatively correlated with mean annual temperature in a diverse array of soils and vegetation types, including those in Australia (Spain et al. 1983, Oades 1988), grasslands in North America (Burke et al. 1989), and grasslands and shrublands in South America (Paruelo et al. 1997, Alvarez and Lavado 1998). Whether the associations among SOC, climate, and soil texture change with depth is unclear; previous regional studies were typically based on the top 20 or 30 cm of soil, where the highest SOC concentrations occur, or in the top (A) horizon (e.g., Spain et al. 1983, Burke et al. 1989).

We hypothesize that vegetation is a major determinant of the vertical distribution of SOC. Although climate and soil texture are the primary regional controls of the total amount of SOC, their influence on the ver-

tical distribution of SOC may be eclipsed by the effects of plant allocation. Plant production and decompositions determine C inputs to the soil profile, and plant allocation above and below ground and between shallow and deep roots may leave distinct imprints on the relative distribution of soil carbon with depth. A recent analysis by Jackson et al. (1996) examined above- and belowground allocation patterns and vertical root distributions for terrestrial biomes and plant functional types, showing differences among grass-, shrub-, and tree-dominated systems. As examples of the expected imprint of plant allocation in the soil, temperate forests with relatively high aboveground allocation may have shallower C profiles than do temperate grasslands, where relative aboveground allocation is lower (Sims and Coupland 1979, Jackson et al. 1996, Cairns et al. 1997). In arid systems, the relatively deep root distributions of shrubs may lead to soil C profiles that are deeper than those in arid grasslands.

Soil C surveys usually consider a fixed soil depth, typically 1 m. Global surveys based on vegetation units (Post et al. 1982) and soil taxonomic units (Eswaran et al. 1993, Batjes 1996) indicate that the soil stores ~1500–1600 Pg of C in this first meter. How much carbon is underestimated in global budgets by fixing a lower boundary at 1 m depends on the vertical distribution of SOC. Based on the FAO soil classification system, Batjes (1996) reported a 60% increase in the global SOC budget when the second meter of soil was included; to our knowledge, this is the only such assessment made to date. The scarcity of SOC data below 1 m constrains estimates for deeper carbon pools. However, the characterization of SOC vertical distribution in shallow soil layers, using mathematical functions that can be extrapolated to deeper layers, should help to improve SOC budgets at depth. Mathematical functions that explain the vertical distribution of SOC in the top 1 m have been made for some soils (Zinke et al. 1978, Arrouays and Pelissier 1994, Carter et al. 1997), but their generality and potential for extrapolation have not been evaluated.

The specific objectives of this study are to (1) examine the association of SOC content with climate and soil texture at different soil depths, (2) evaluate the relationship between the vertical distribution of SOC and dominant vegetation type, and (3) estimate global SOC storage to a depth of 3 m, including an analysis of the potential effects of vegetation change on soil carbon storage. These objectives are approached globally, based on data from >2700 soil profiles. The first two goals are addressed using actual SOC data for the first and, in some cases, the second and third meter of the profiles, complemented with climate and vegetation data. To address the third goal, we compare alternative mathematical characterizations of the vertical distribution of SOC and evaluate their quality in extrapolating SOC content below the first meter. Global SOC

storage in the first, second, and third meter is estimated globally and by biome.

MATERIALS AND METHODS

The databases

The analyses presented here are based on three global databases of soil profiles. The first and largest is the National Soil Characterization Database (NSCD), produced and updated by the U.S. Department of Agriculture (USDA 1994). The second is the World Inventory of Soil Emission Potential Database (WISE), compiled by the International Soil Reference and Information Centre (Batjes and Bridges 1994, Batjes 1995). The NSCD database characterizes 5307 profiles with site descriptions in the United States and elsewhere. The WISE database includes soil profiles from 69 countries, mainly in the Americas, Asia, Africa, and Australia, and emphasizes tropical regions. In both databases, soil physical and chemical measurements are recorded by horizon. These databases seek to characterize the diversity of agricultural and non-agricultural soils and together cover temperate and tropical biomes and, to a lesser extent, boreal systems. A third database from the Canadian Forest Service emphasizes Canadian forest and tundra soils (Siltanen et al. 1997).

We used profiles in the databases that included information on taxonomic classification, geographic location, vegetation, and land use. Geographic coordinates and elevation were included for all soils in the WISE database and for most in the NSCD. NSCD profiles lacking geographic coordinates but belonging to a U.S. county smaller than 2500 km² were assigned the geographical coordinates of the county center; this size threshold matched the resolution of the climate database described later.

The databases present SOC on a gravimetric basis. These values were transformed to a volumetric basis using accompanying values of bulk density. Only soil profiles having complete bulk density data were included in the analysis, with the exception of data gaps in a single horizon, where bulk density was interpolated from adjacent intervals. SOC content was also corrected for the volumetric gravel content in each horizon. Profiles with less than three suitable measurements of organic carbon in the first meter were eliminated from the analysis because there was insufficient detail to characterize the vertical distribution of SOC. Surface litter layers were also eliminated for all analyses. Because soil profiles were described by horizon, depth intervals in the first meter had variable thicknesses. To remove this variation, SOC content (absolute C mass) and mean SOC density (volumetric proportion) were interpolated at fixed depth intervals of 20 cm in the first meter and at 100-cm intervals at greater depths. The percentages of sand and clay in the first meter were also obtained for each profile.

We obtained climatic data for each soil site from a

global database developed by the International Institute for Applied Systems Analysis (IIASA) that presents mean monthly values of temperature and precipitation at a resolution of 0.5 × 0.5 degrees for all terrestrial systems (Leemans and Cramer 1990). Temperatures in the IIASA database were adjusted for a particular soil profile according to any elevation difference for the whole pixel (a lapse rate of 0.006°C/m; Barry 1981). Fewer than 15% of the profiles had an elevation difference >500 m and a temperature correction >3°C. Not all soil profiles in the database had descriptions of current land use and vegetation type. We identified 1271 profiles under agricultural use and 802 under natural vegetation, with descriptions that ranged in detail from a single physiognomic reference to a list of dominant species.

Controls of the vertical distribution of SOC

We examined associations for the vertical distribution of SOC, climate, soil texture, and vegetation type. We characterized the vertical distribution of SOC for five 20-cm intervals in the first meter and two 100-cm intervals in the second and third meters, adjusting the increment with depth because deeper profiles typically had fewer sample increments. In order to compare the relative vertical distribution of SOC independently of total SOC content, we calculated relative SOC contents for each interval by dividing the SOC content of the interval by the total SOC content in the first meter of the profile.

In this analysis, profiles, from agricultural soils were eliminated because of the potential effects of plowing on the vertical distribution of SOC. All profiles subject to strong intrazonal or azonal factors with a dominant effect on the vertical dynamics of soils were also removed. These included 11 fluvial soils (where frequent deposition of sediments alters the profile), 15 vertic soils (where expansion and cracking produce vertical turnover), and 82 soils with bedrock at a depth of <1 m. The selection yielded 694 soil profiles associated with natural vegetation that were used in this analysis.

We evaluated the association between total SOC in the first meter, and the absolute and relative contents of SOC by depth with mean annual temperature (MAT), mean annual precipitation (MAP), and clay and sand content in the first meter. To evaluate the effect of vegetation on the vertical distribution of SOC, we grouped soil profiles into grasslands, shrublands, and forests. In some cases, the databases included these categories explicitly; in others, a different physiognomic nomenclature or list of dominant species was available. Any herbaceous-dominated community was considered a grassland. Communities described as brush, chaparral, scrub, shrubsteppe, or shrub desert (those dominated by non-tree woody species) were considered shrublands. Any tree-dominated community, including woodlands, was considered forest. Sites with mixed

TABLE 1. Performance of the functions used to describe and extrapolate soil organic carbon profiles. Models describe either the cumulative content of soil organic carbon (Y) or soil organic carbon density (C) as a function of depth (d).

Model†	Equation‡	Flat distribution §	Significance cases (%)	Mean predictive error (kg/m ²)¶	
				0–30 cm	100–200 cm
Log–log, cumulative	$\log Y = K \log d + I$	$K = 1$	84	0.42	3.91
Log–linear, cumulative	$\log Y = K d + I$	$K = 1$	76	1.23	13.83
Log–log, non-cumulative	$\log C = S \log d + I$	$S = 0$	84	0.99	2.00
Log–linear, non-cumulative	$\log C = S d + I$	$S = 0$	76	1.73	10.37
Beta	Y (proportional) = $1 - \beta^d$	$\beta = 1$	63	12.13	44.50

† Logarithm transformations are base 10.

‡ Each function has a single slope parameter that describes how steep the distribution of soil organic carbon is, independent of total carbon content. The beta model used relative cumulative values, whereas the other models can use either absolute or relative values without affecting the slope. The slope parameters K , S , and β characterize relative rates of decrease with depth, and the intercept I characterizes the absolute content of an individual soil profile.

§ Slope values for a flat distribution, in which soil organic carbon density is constant with depth.

|| Percentage of soil profiles in which there was a significant ($P < 0.05$) fit for the model with actual data for 0–100 cm.

¶ Ability of the model to predict organic carbon content at 0–30 cm and 100–200 cm depths, expressed as the mean predictive error (MPE = $(\sum_n [\text{observed}_i - \text{predicted}_i]^2)/n^{0.5}$).

vegetation types such as savannas or grass–shrub steppes were not used in this analysis, but were included in analyses of global C budgets.

We first compared the vertical distribution of SOC among vegetation types globally and then isolated potential climatic effects by grouping soils within ranges of mean annual temperature and precipitation. We used 12 categories resulting from three MAT ranges (0–10°C, 10–20°C, and 20–30°C) and four MAP ranges (0–250 mm, 250–500 mm, 500–1000 mm, 1000–1500 mm in cold and temperate zones, and 250–500 mm, 500–1000 mm, 1000–1500 mm, >1500 mm in the tropics). Not all vegetation types were represented in each climatic range, either because they rarely occurred in some climates (e.g., forests in arid climates) or because they were poorly represented in the database (e.g., pure grasslands in tropical climates).

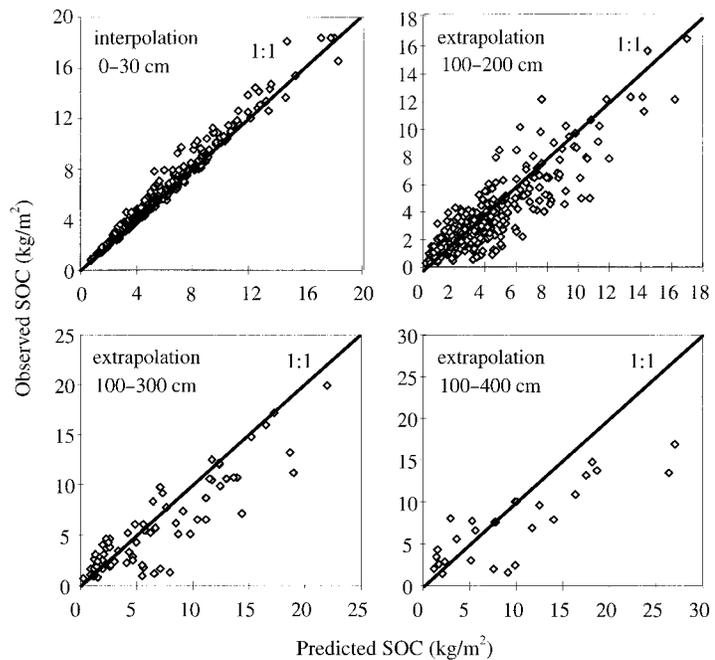
Estimates of deep SOC

To estimate global SOC storage at depth, we first characterized the vertical distribution of SOC and then evaluated functions to extrapolate SOC content at depth. To characterize mathematically the vertical distribution of SOC, we evaluated five functions that relate SOC density or cumulative content with depth in the first meter of soil (Table 1). We used simple, flexible functions that capture the relative slope of depth profiles (i.e., independently of total SOC content) with a single parameter. The “beta” model was previously used for vertical root distributions (Gale and Grigal 1987, Jackson et al. 1996, 1997) and is able to fit the steepest decreases with depth. The cumulative log–log model was used previously to describe SOC profiles (Zinke et al. 1978). We also evaluated a modification where depth was not log-transformed. These two functions had the advantage of integrating SOC values from the surface down to a given depth, but had the statistical disadvantage of non-independence between horizons

for curve fitting. The last type of model used log-transformed carbon densities rather than cumulative content, and depth was considered either directly or as a log-transformed variable. For these models, we estimated SOC content by integrating the functions in 20-cm intervals. Polynomial functions have been used to represent SOC distributions (e.g., Arrouays and Pelissier 1994), but they require more than one parameter and curtail the available degrees of freedom (commonly low in soil profile data sets).

To compare different models, we examined the percentage of soil profiles that fitted the data significantly for the first meter; the highest number of significant associations was found for the log–log function (Table 1). We also evaluated the agreement between actual SOC content and model interpolations for the 0–30 cm depth range, and between actual SOC content and model extrapolations for the 100–200 cm depth range. The agreement between predicted and observed values was calculated by the mean predictive error, where MPE = $(\sum_n [\text{observed}_i - \text{predicted}_i]^2/n)^{1/2}$. The predictive errors of the interpolations for the 0–30 cm interval and the extrapolations for the 100–200 cm interval were lowest when the log–log function was used (Table 1). The ability of this model to predict SOC storage at increasing depths was also evaluated. For this purpose, we used only those profiles that showed a significant fit of the model for the 0–100 cm interval ($P < 0.05$) and had SOC data below the first meter. We used the model parameters obtained from the 0–100 cm interval to extrapolate the function to greater depth and to compare SOC content with actual data. The performance of the extrapolations was evaluated by regression analysis of predicted and observed values through comparison with the 1:1 relationship (Dent and Blackie 1979) and by the MPE. Relative contributions of the differences between the mean predicted and mean observed values (Ubias), slope bias (Uslope), and un-

FIG. 1. Prediction of soil organic carbon content, with each data point representing an individual soil profile. The prediction is based on a model that fits organic carbon content (C) and depth (d) in the first meter of the soil according to the equation: $\log C = (S \log d) + i$, where the slope of the model (S) characterizes the relative rate of decrease with depth and the intercept (i) characterizes the absolute C content. An interpolation of carbon content for the 0–30 cm depth interval and extrapolations for the 100–200 cm, 100–300 cm, and 100–400 cm depth intervals are presented. In all cases, there is a significant association between predicted and observed values ($P < 0.0001$; linear minimum squares regression).



explained variance (U_e) to the overall departure from the 1:1 relationship were evaluated using Theil's partial inequality (Smith and Rose 1995). The regressions of predicted and observed SOC values for the 100–200 cm, 100–300 cm, and 100–400 cm depth intervals were significant, with $r^2 > 0.7$ (Fig. 1). The intercepts of these regressions did not differ from 0 but the regression slopes were significantly < 1 , indicating an overestimation by the log–log model. The mean predictive errors for SOC extrapolations down to the second, third, and fourth meter were 2.0, 2.86, and 4.32 kg/m^2 , respectively. Theil's partial inequality analysis indicated that errors were dominated by unexplained variation in the 100–200 cm ($U_e = 69\%$, $U_{\text{bias}} = 12\%$, $U_{\text{slope}} = 19\%$) and 100–300 cm extrapolations ($U_e = 64\%$, $U_{\text{bias}} = 12\%$, $U_{\text{slope}} = 24\%$), and by the slope in the 100–400 cm extrapolation ($U_e = 37\%$, $U_{\text{bias}} = 21\%$, $U_{\text{slope}} = 42\%$). For this and other reasons, we limited the depth of our estimates to three meters.

To integrate the data from individual profiles into a global estimate of deep SOC content, we grouped soils in 11 biomes following the classification of Whittaker (1975). We used this scheme to allow a direct comparison of biome and global SOC profiles with root distribution profiles in Jackson et al. (1996, 1997). The 802 profiles under natural vegetation were classified according to vegetation descriptions. The set of 1271 agricultural profiles was incorporated in the biome "crops." Boreal systems in the NSCD and WISE databases were poorly represented, with few profiles, typically from high-elevation sites. To improve the representation of northern biomes in the global SOC budget, we included profiles from the Canadian Forest Ser-

vice database for forest and tundra soils (Siltanen et al. 1997). We selected profiles sampled to the C or regolithic horizon, which added 617 boreal forest and 31 tundra profiles to the analysis.

Mean SOC content in the first meter, its proportional distribution in 20-cm intervals, and the mean slope parameter for the SOC depth function were calculated for each biome. For deep SOC estimates (100–300 cm) with the SOC depth function, we used only those soil profiles with complete carbon data for the first meter (2062 profiles). The profiles excluded had shallow bedrock or other limitations for development (188 profiles), or incomplete sampling above the first meter because of either a shallow water table (94 profiles) or shallow horizon differentiation (377 profiles). Within the set of profiles, those with a significant ($P < 0.05$) fit to the SOC-depth model were considered (1456 profiles). Deep SOC storage was estimated by extrapolating the average SOC-depth functions of each biome to the 100–200 cm and 200–300 cm depth intervals. To check biome estimates of SOC, we compared modeled data for 100–200 cm with actual estimates based on soils with SOC data in the 100–200 cm interval. As previously noted, actual data in these deeper intervals were not used to fit the initial models. As a measure of error for our SOC estimates, we calculated the standard deviation of values for each 1-m interval and for the entire 3-m profile. Error estimates for the 0–1 m depth interval were represented by the standard deviation of SOC content. Error estimates in the 1–2, 2–3, and 0–3 m intervals were based on the standard deviation of SOC and the mean predictive error of the log–log model.

TABLE 2. Associations of soil organic carbon (relative and absolute amounts by depth interval) with climate and soil texture. Numbers presented are r^2 values between SOC content and mean annual temperature (MAT), mean annual precipitation (MAP), and the percentage of clay or sand in the first soil meter.

Dependent variable	Independent variables			
	MAT	MAP	Clay	Sand
Absolute SOC content in the top 1 m	-0.16***	0.25***	0.14***	-0.33***
Absolute SOC content by depth (cm)				
0–20	-0.17***	0.33***	0.07*	-0.28***
20–40	-0.16***	0.20***	0.10**	-0.28***
40–60	-0.12**	0.12***	0.14***	-0.27***
60–80	-0.09*	0.09*	0.20***	-0.28***
80–100	-0.08*	...	0.19***	-0.25***
100–200	...	0.19*	0.25**	-0.28***
200–300	0.61***	...
Relative SOC content by depth (cm)				
0–20	-0.11**	0.35***	-0.07*	...
20–40	...	-0.16***
40–60	0.11**	-0.24***	0.10**	...
60–80	0.18***	-0.27***	0.06*	0.08*
80–100	0.08*	-0.38***
100–200	0.19*	0.20*
200–300	0.35*

Notes: Only non-agricultural soils are considered. The total number of profiles in each correlation ranged from 637 to 694 in the top meter, 114 to 130 in the second meter, and 19 to 30 in the third meter.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ellipses indicate that differences are not significant.

RESULTS

Controls of the vertical distribution of SOC

As shown by previous authors, the amount of soil organic carbon in the first meter was significantly correlated with climate and soil texture globally ($P < 0.001$, Table 2). SOC content was highest in wet and cold conditions and in fine-textured soils, but there remained a large amount of unexplained variation (Table 2). A stepwise regression model of total SOC in

the first meter, including mean annual precipitation, temperature, and clay and sand content as factors, achieved an r^2 of 0.28 ($P < 0.001$); the strength of the relationship increased when the dependent variable was SOC content in the top 20 cm ($r^2 = 0.36$, $P < 0.001$). When the same associations were examined by depth, the relative importance of climate and texture changed. The association of SOC content with precipitation and temperature was closest in the top 20 cm of the soil and decreased for deeper intervals. In contrast, the cor-

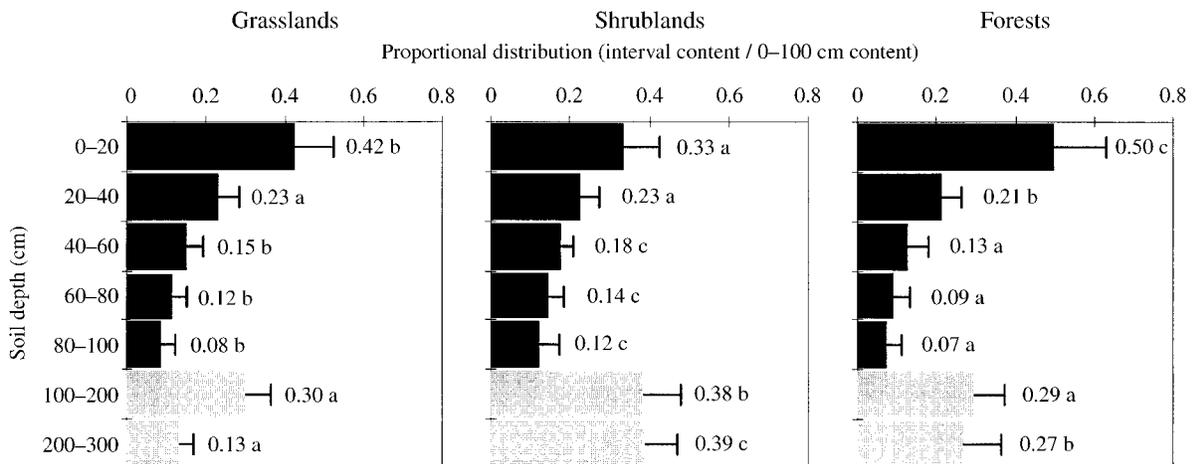


FIG. 2. Profiles of soil organic carbon distributions associated with dominant plant functional types (mean + SD). Grasslands are sites dominated by grasses and other herbaceous plants; shrublands include brush, shrub steppe, and scrub vegetation; forests are dominated by trees, including woodlands. Black bars indicate the proportional distribution of total organic carbon in the first soil meter in 20-cm intervals. These values were obtained by averaging the actual proportional values of individual soils. Bars in the first meter sum to one. Gray bars indicate the proportion of additional carbon in the 100–200 cm and 200–300 cm layers; the number at their right shows their contribution relative to the first meter. Values below the first meter were obtained from a smaller number of soils. Letters indicate significant differences among vegetation types at each depth interval (t test, $P < 0.05$).

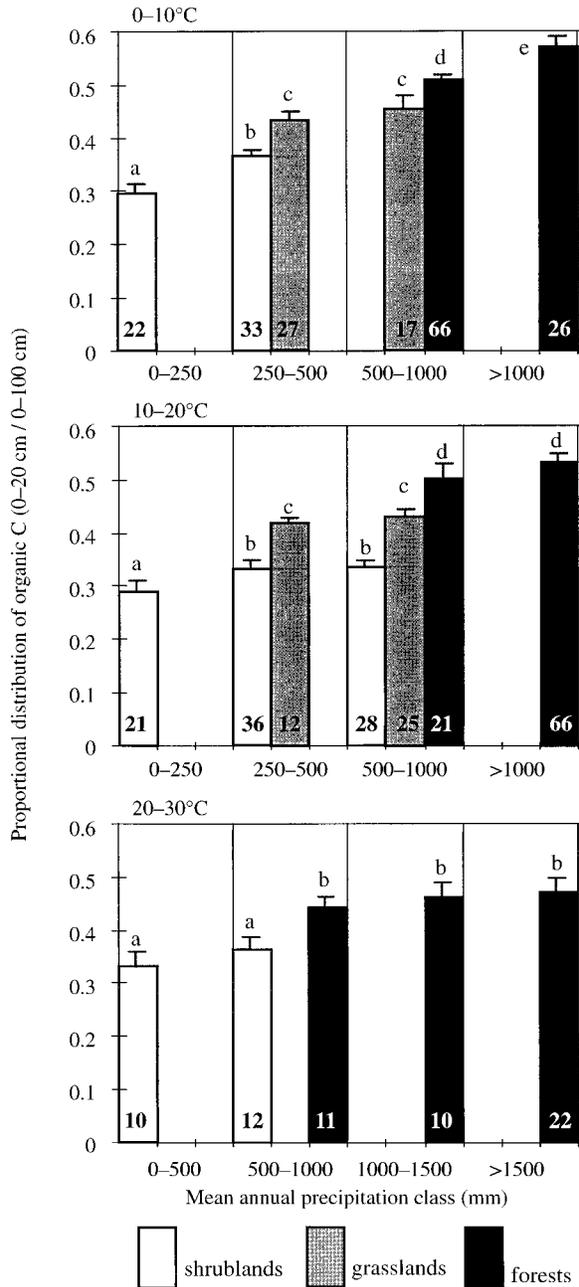


FIG. 3. The vertical distribution of soil organic carbon as a function of dominant plant functional type and climate. Soil carbon distribution is represented by the proportional contribution of the 0-20 cm layer to total carbon in the first meter. Sites were grouped in 12 climatic ranges based on four precipitation \times three temperature intervals. Within each climatic range, sites were classified as grassland, shrubland, or forest. Any class having <10 sites was discarded from the analysis. Line bars show $+1$ SE. Numbers within the bars indicate the number of samples considered in each class. Letters show significant differences ($P < 0.05$) among all classes within the same temperature range.

relation between SOC and clay content was highest in deeper intervals (Table 2). Sand content was negatively correlated with SOC content across all depths. The relative distribution of SOC with depth was shallower in wet and cold climates and in coarse-textured soils (Table 2). The proportion of SOC in the top 20 cm (relative to the first meter) increased with increasing precipitation (i.e., became shallower) and decreased slightly with temperature (Table 2). The stepwise regression model for the proportion in the top 20 cm had an r^2 of 0.32 ($P < 0.001$).

Plant functional types significantly altered the vertical distribution of SOC. The relative distribution of SOC in the first meter of soil was deepest in shrublands, intermediate in grasslands, and shallowest in forests (e.g., 33%, 42%, and 50% of all SOC in the top 1 m was contained in the uppermost 20 cm; Fig. 2). The relative SOC content in the second meter was higher in shrublands than in grasslands or forests. In the third meter, relative SOC content was highest in shrublands, intermediate in forest, and lowest in grasslands (Fig. 2). In shrublands, the amount of SOC in the second and third meters was 77% of that in the first meter, whereas in forests and grasslands, the totals were 56% and 43%, respectively. Globally, the vertical distribution of SOC had a slightly stronger association with vegetation than with climate, but the opposite was true for the amount of SOC (for the relative proportion of SOC in the top 20 cm, $r^2 = 0.29$ for MAT and MAP, and $r^2 = 0.32$ for vegetation as a ranked variable (shrublands, 1; grasslands, 2; forests, 3); $r^2 = 0.22$ when the total amount of SOC in the first meter was compared with climate, but only $r^2 = 0.16$ when compared with vegetation type; $P < 0.001$ in all cases).

To control for the effects of climate on vegetation, we grouped soil profiles in climatic ranges and compared vegetation types within each range. The proportion of SOC in the top 20 cm varied from 29% in cold arid shrublands to 57% in cold humid forests (Fig. 3).

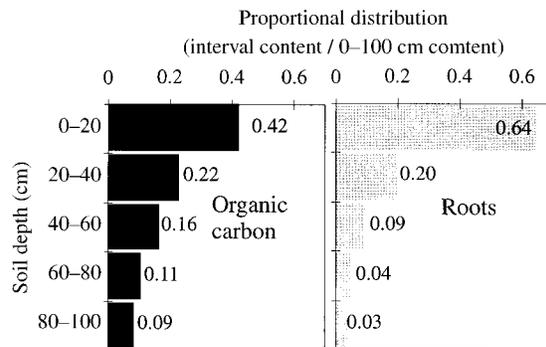


FIG. 4. Globally averaged profiles for organic carbon and root distributions in the first meter of soil. Bars indicate the relative proportion of carbon or roots in the first meter by 20-cm intervals. Estimates for root distributions are from Jackson et al. (1996); see Table 4.

TABLE 3. Global summary of soil organic carbon (SOC) content (mean, with 1 SD in parentheses), storage, and vertical distribution.

Biome [†]	No. samples [‡]	Land area [†] (10 ¹² m ²)	SOC content (kg/m ²) by depth (m)				Total SOC storage (10 ¹⁵ g) by depth (m)			
			0–3	0–1	1–2	2–3	0–3	0–1	1–2	2–3
Boreal forest	648, 118	12	12.5 (8.8)	9.3 (7.0)	2.4 (2.9)	0.8 (2.1)	150	112	29	10
Crops	1271, 837	14	17.7 (12.9)	11.2 (7.7)	3.8 (4.2)	2.7 (3.4)	248	157	53	38
Deserts	285, 161	18	11.5 (8.2)	6.2 (3.4)	2.9 (3.2)	2.4 (3.4)	208	112	52	44
Sclerophyllous shrubs	62, 38	8.5	14.6 (7.9)	8.9 (3.9)	3.3 (3.0)	2.4 (2.0)	124	76	28	20
Temperate deciduous forest	60, 41	7	22.8 (13.6)	17.4 (10.8)	3.3 (3.7)	2.1 (2.4)	160	122	23	15
Temperate evergreen forest	123, 85	5	20.4 (12.0)	14.5 (8.4)	3.6 (3.7)	2.3 (2.6)	102	73	18	12
Temperate grassland	121, 83	9	19.1 (10.9)	11.7 (6.6)	4.2 (3.7)	3.2 (2.8)	172	105	38	28
Tropical deciduous forest	29, 24	7.5	29.1 (14.6)	15.8 (9.2)	7.4 (4.4)	5.8 (3.3)	218	119	56	44
Tropical evergreen forest	36, 30	17	27.9 (8.9)	18.6 (10.4)	5.4 (3.1)	3.9 (2.2)	474	316	92	66
Tropical grassland/savanna	35, 27	15	23.0 (19.9)	13.2 (8.7)	5.5 (6.1)	4.2 (5.1)	345	198	83	63
Tundra	51, 12	8	18.0 (15.2)	14.2 (14.1)	2.4 (3.1)	1.4 (2.1)	144	114	19	11
Global average	2721, 1456	121					2344	1502	491	351

[†] Biome classification and land area values are based on Whittaker (1975) and Jackson et al. (1997).

[‡] The first number of samples refers to the total set of soil profiles used for the 0–1 m SOC calculation, and the second number refers to the subset of soil profiles used for deep SOC content estimates, based on a log–log extrapolation function adjusted to the top meter.

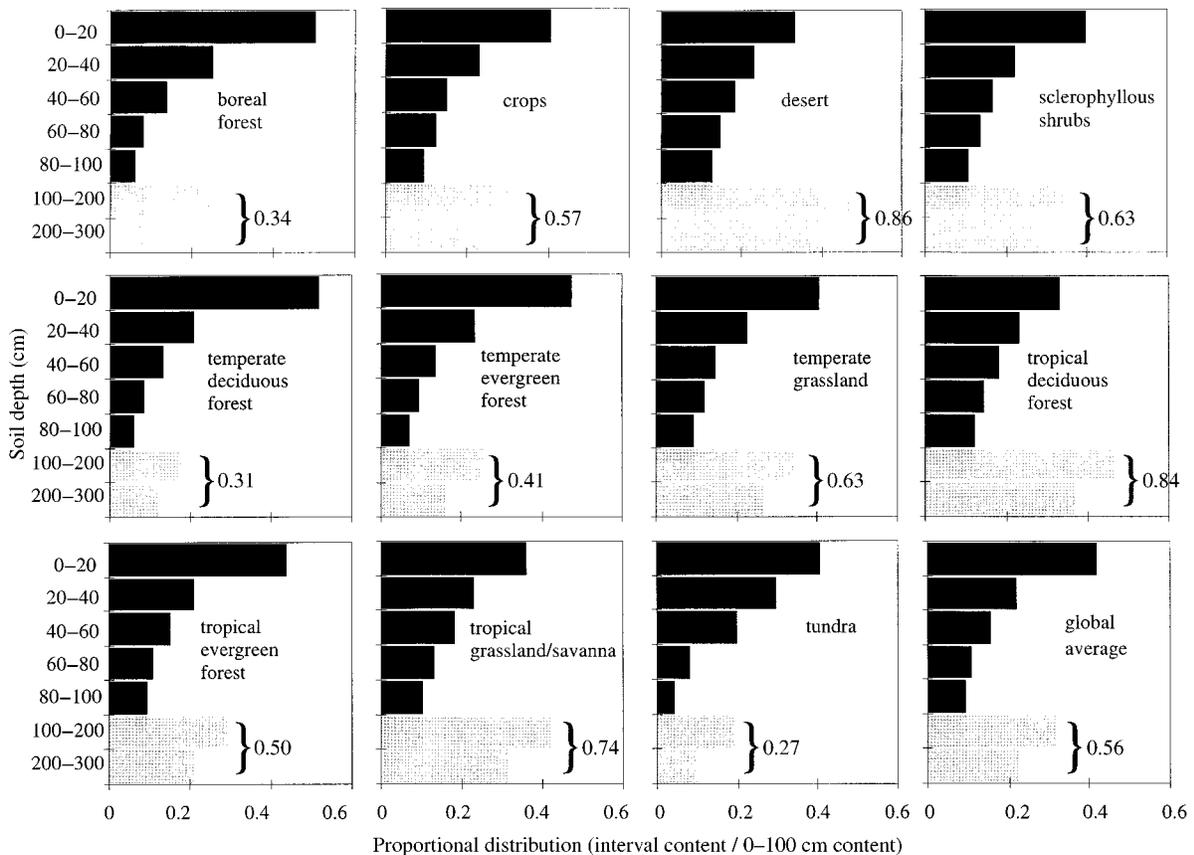


FIG. 5. Profiles of soil organic carbon distributions by biome. Black bars indicate the relative proportion of total organic carbon in the first meter of soil in 20-cm intervals (the sum of bars in the first meter is 1). Estimates were obtained by averaging proportional values for individual soils. Gray bars indicate the proportion of carbon added when the 100–200 cm and 200–300 cm intervals are considered, and the number at their right shows their combined contribution relative to the first meter. These values were obtained by averaging the extrapolations of the log–log model for each soil profile; see Table 3 for details.

TABLE 4. Global summary of the vertical distribution of soil organic carbon and root biomass in the first meter of soil. SOC and root biomass distributions are shown as percentages of the first-meter total found in successive 20-cm intervals. The last column indicates the proportion of the ecosystem biomass that is above ground.

Biome†	Soil organic carbon (%) by depth (cm)					Root biomass (%) by depth (cm)					Propor. above ground‡		
	No. samples	0–20	20–40	40–60	60–80	80– 100	No. sam- ples	0–20	20–40	40–60		60–80	80– 100
Boreal forest	648	50	25	13	7	5	5	81	10	5	2	1	0.76
Crops	1271	41	23	15	12	9	6	62	21	10	4	3	0.91
Desert	285	33	22	18	15	13	9	47	28	16	5	4	0.28
Sclerophyllous shrubs	62	39	22	16	13	10	11	62	20	10	4	4	0.45
Temperate deciduous forest	60	52	21	13	8	6	11	55	26	10	5	2	0.85
Temperate evergreen forest	123	47	23	13	9	7	14	57	24	9	5	2	0.81
Temperate grasslands	121	41	23	15	12	9	17	70	17	9	3	1	0.21
Tropical deciduous forest	29	33	23	18	14	12	5	72	20	3	1	1	0.75
Tropical evergreen forest	36	44	21	15	11	9	14	68	17	7	5	3	0.84
Tropical grassland/savanna	35	36	23	18	13	10	14	57	24	9	6	3	0.59
Tundra	51	40	29	19	7	5	11	80	15	1	0	0	0.13
Global average	2721	41	23	16	11	9	117	64	20	9	4	3	0.60

† The biome classification scheme is based on Whittaker (1975) and Jackson et al. (1997).

‡ Vertical distributions of root biomass and proportion of total ecosystem biomass located aboveground are based on data in Jackson et al. (1996).

Within climatic ranges, SOC distributions were always deepest in shrublands, intermediate in grasslands, and shallowest in forests ($P < 0.05$ for all analyses). For shrublands, the relative distribution of SOC was significantly deeper in arid conditions (0–250 mm/yr) than in semiarid conditions (250–500 mm/yr), whereas grasslands did not differ in the vertical distribution of SOC across climates. The most important changes in forests were across temperature ranges. In humid forests, the proportion of SOC located in the top 20 cm decreased significantly from 57% in cold climates to 43% in tropical climates ($P < 0.05$).

Global estimates of SOC with depth

Global SOC storage based on 2721 soil profiles grouped by biome was 1502 Pg of C for the first soil meter. The relative distribution in five successive 20-cm intervals was 41, 23, 16, 11, and 9% (Fig. 4). Extrapolated estimates of deep SOC storage, based on 1456 soil profiles, yielded 491 Pg of C in the second meter and 351 Pg C in the third meter. These values increased estimated total SOC storage by 33% and 23%, respectively, compared to the top meter (Table 3).

The vertical distribution of SOC was deepest in deserts and tropical deciduous forests and shallowest in temperate deciduous forests (Fig. 5, Table 4). Incorporating SOC estimates and the area of biome coverage globally showed that the main contributors to SOC storage at 100–300 cm depths were tropical evergreen forests (with 158 Pg C) and tropical grasslands and savannas (with 146 Pg C). Modeled global and biome SOC storage for the 100–200 cm interval models were similar to those based on the subset of soils with actual SOC values at this depth interval ($r = 0.91$, $P < 0.01$).

SOC had a deeper relative distribution than did root biomass, globally and in all biomes (Fig. 4, Table 4). The top 20 cm of soil had almost two-thirds of the roots, on average, but less than half of the SOC in the first meter of soil (Fig. 4). There was no association at the biome level between the relative contents of SOC and roots in the top 20 cm.

DISCUSSION

We hypothesized that vegetation, through patterns of allocation, would be the major determinant of the relative vertical distribution of SOC. We found significant changes in SOC profiles among vegetation types (Figs. 2 and 3), which can be explained, in part, by differences in root distributions and above- and belowground allocation patterns. Root distributions affect the vertical placement of C in the soil, and above- and belowground allocation affects the relative amount of C that eventually falls to the soil surface from shoots. In a global review of root distributions, grasses had the shallowest root profiles, trees were intermediate, and shrubs had the deepest profiles (Jackson et al. 1996). Our SOC analysis showed a similar result for shrub-dominated systems, but the order for tree- and grass-dominated systems was reversed. This can be explained by higher relative aboveground allocation for trees than for grasses and shrubs. For example, temperate grasslands exhibit an average root : shoot ratio as high as 3 or 4 (Sims and Coupland 1979, Risser et al. 1981, Jackson et al. 1996), whereas the global average for temperate forests is ≈ 0.26 (Jackson et al. 1996, Cairns et al. 1997). The quality of carbon inputs, often characterized by lignin content, is another important control of decomposition rates (Menteemeyer 1978, Melillo et al. 1982, Austin and Vitousek 1998), and may contribute to observed

differences for forests and grasslands. Woody above-ground inputs and relatively low decomposability in forests could increase SOC storage in surface soils compared to grasslands.

The relative distribution of SOC with depth was slightly correlated with climate, with SOC distributed more deeply as precipitation decreased and temperature increased (Table 2). The association with precipitation can be largely accounted for by the replacement of vegetation types along precipitation gradients (Fig. 3). This suggests that it may be vegetation type rather than the direct effect of precipitation that determines changes in the relative vertical distribution of SOC along rainfall gradients, a hypothesis that needs further testing. Nevertheless, precipitation clearly has a direct role regionally and globally in the amount of SOC stored (e.g., Burke et al. 1989). It is interesting that, although precipitation and climate were the best predictors of total SOC in the top 20 cm of soil, clay content was the best predictor in deeper layers. This result may be due to the increased proportion of slower cycling SOC pools at depth (Paul et al. 1997, Trumbore 2000); such C pools are strongly associated with clay particles and noncrystalline minerals that stabilize and protect organic matter (Paul 1984, Torn et al. 1997).

In contrast to precipitation, the positive association between SOC vertical distributions and temperature was important within vegetation types, as illustrated by the increase of SOC depth from cold to tropical forests (Fig. 3). This pattern agrees with the observation that the ratio of litter to mineral soil carbon decreases from temperate to tropical forests (Jenny 1950), and suggests that mean annual air temperature may have a proportionally higher effect on the decomposition of shallow SOC than on deep SOC. This is also supported by our observation of a decreasing correlation between SOC content and temperature with depth. The effects of temperature in the analysis might have been even more pronounced if a climate database with finer resolution were available.

The correlative approach that we used does not prove a causal effect of vegetation on SOC, but trends in the vertical distribution of SOC under different vegetation types were consistent across climates and continents. There are a number of examples in the literature in which SOC vertical patterns differ after vegetation change. In New Zealand grasslands, the introduction of pine plantations produced shallower SOC profiles after 20 yr (Parfitt et al. 1997). The introduction of an exotic grass species in the savannas of Colombia substantially increased SOC storage (Fisher et al. 1994). Ecosystem simulations in complex landscapes containing forests, savannas, and grasslands with an explicit representation of root distributions suggest that SOC pools are particularly sensitive to root distributions of grasses (Daly et al. 2000). New data covering transitions among grasslands, shrublands, and forests, com-

bined with improved modeling of belowground processes, are needed to address the controlling mechanisms of the patterns presented here. Temporal factors are also likely to play an important role.

SOC pools with slow turnover rates can carry the imprint of previous vegetation for centuries to millennia, as revealed by carbon isotopes (Dzurec et al. 1985, McPherson et al. 1993, Connin et al. 1997, Ehleringer et al. 2000). A high proportion of these pools may dilute the association between SOC profiles and vegetation types if the vegetation had changed previously at some of the sites analyzed here. Because the relative proportion of slow and passive SOC pools generally increases with depth (Desjardins et al. 1994, Trumbore et al. 1996, 2000, Paul et al. 1997), a larger decoupling between current vegetation and SOC pools should be expected for deeper soil layers (e.g., Tieszen and Pfau 1998).

SOC storage in the top 3 m of soil, to our knowledge estimated for the first time, was 2344 Pg C. The addition of the 100–300 cm depth interval augmented the global SOC estimate by 842 Pg C, more carbon than is contained in the atmosphere (Schlesinger 1997). Our estimate of global SOC in the second soil meter (491 Pg) is considerably lower than the only previous estimate for this depth (911 Pg; Batjes 1996). Batjes estimated SOC content by averaging profiles under FAO soil taxonomic units. For his analysis, SOC in the second meter was estimated using only those profiles with actual data down to 2 m (12% of the profiles used for the first meter). A bias toward high SOC content in that subset of soils may explain the discrepancy, particularly in two soil units of high SOC content. For histosols and podzols, the addition of the second meter added 180% and 80%, respectively, to organic carbon stocks in the first meter of the earlier analysis. The discrepancy with our estimates, and the large area of these soil units in tundra and boreal forests, highlight deep soil layers in boreal regions as a source of uncertainty in current estimates. The inclusion of the large Canadian Forest Service database improved our SOC storage estimates for the top meter in boreal forest and tundra, and resulted in substantially lower SOC estimates in these biomes compared to previous global budgets (e.g., Post et al. 1982), but were similar to a previous soil carbon inventory of boreal systems (Apps et al. 1993). There are almost no SOC data below 1 m in boreal ecosystems, making deep SOC estimates there uncertain.

The standard deviation of SOC content is large, as observed in other global SOC budgets. Within the biomes of our study, the average coefficient of variation (cv) of SOC content in the first meter is 64%, in close agreement with the average cv in previous budgets that grouped profiles based on soil taxonomic orders (79%, calculated from Batjes 1996) or bioclimatic zones (65%, calculated from Post et al. 1982). This variability

implies that other factors, perhaps local ones, are probably important, and that the grouping of SOC data into large, aggregated units may mask meaningful variation.

If the variation in SOC content is the only source of uncertainty in the calculations, our estimate of global SOC storage for the 0–1 m depth interval has an approximate error of 1502 ± 320 Pg C (mean ± 1 SD). For the deeper intervals, the uncertainty of extrapolation also needs to be included (mean predictive error of the log–log models), which yields approximate errors of 491 ± 150 , 351 ± 130 , and 2344 ± 480 Pg C for the 1–2, 2–3, and 0–3 m depth intervals, respectively. These error estimates are coarse at best, and do not include any potential biases of nonrandom sampling within each soil database (i.e., profiles not taken randomly within a biome).

The proposed values of deep SOC storage may be inflated because we did not consider bedrock limitations to soil depth. A global characterization of this factor is lacking, as existing global databases of soil depth are based on the position of the C-horizon rather than on actual physical barriers (e.g., FAO 1995). Some indication of a potentially small magnitude of shallow bedrock as a source of SOC overestimation is that only 7% of the set of profiles recorded a bedrock limitation. However, a sampling bias against soils overlaying bedrock may exist in the databases. Constraints to soil depth need further consideration in analyses of deep soil carbon storage. Overall, the effect of excluding all soil profiles with no data down to at least 1 m (those with bedrock limitations, a shallow water table, and shallow horizon development) and those profiles with a nonsignificant fit to our log–log model were small. The inclusion of the first group, assuming zero SOC below 1 m, reduced the estimates for the second and third meter to 412 and 301 Pg of C, respectively. Incorporating the second group of profiles (those without a significant fit to the log–log model, and assuming the average relative SOC profile of the corresponding biome) had no substantive effect on estimates.

Our data provide an interesting comparison between the vertical distribution of SOC and roots. When compared at global (Fig. 4) or biome levels (Table 4), roots are distributed more shallowly than is SOC. This pattern was originally described in humid grasslands (Weaver et al. 1935) and was recently confirmed in semiarid grasslands (Gill et al. 1999). If aboveground biomass is added to the surface soil layer, then the difference between SOC and biomass becomes even larger. Why is SOC distributed more deeply than biomass? Potential explanations include: (1) decreasing SOC turnover with depth, resulting in higher SOC accumulations per unit of C input in deep soil layers; (2) increasing root turnover with depth, causing higher C inputs per unit of standing root biomass in deep soil layers; (3) SOC leaching from upper to lower layers; and (4) vertical mixing by soil organisms. There is

substantial support for the first explanation. Radiocarbon evidence from soils of the Great Plains of North America (Paul et al. 1997) and from boreal, temperate, and tropical forests (Trumbore 2000; see also Allen et al. 2000) show decreasing SOC turnover rates with depth. Changes in root tissue quality with depth, caused by larger and woodier structures in deeper soil layers or lower nutrient concentrations, could also contribute to the observed pattern (e.g., Pregitzer et al. 1998, Gordon and Jackson 2000). To our knowledge, there is no published evidence for the second explanation; an extensive review of root life-span patterns does not report any trend associated with depth (Eissenstat and Yanai 1997). The last two explanations cannot be discarded completely, but may play minor roles. Organic carbon migrates in the soil as a result of leaching (Dosskey and Bertsch 1997), and soil organisms can mix large amounts of soil (Jenny 1981, Paton et al. 1995). Both mechanisms result in C enrichment below the surface and C dilution in shallow layers. Along climatic gradients, leaching and mixing tend to increase with precipitation (Paton et al. 1995, Dosskey and Bertsch 1997). If leaching and mixing by organisms were dominant factors in the vertical distribution of SOC, then SOC should be deeper as precipitation increases; we found the opposite to be true. An intense and deeper biological mixing in the tropics resulting from a more diverse set of organisms might contribute to deeper SOC profiles there compared to temperate and cold forests (Paton et al. 1995).

The patterns of SOC presented here may contribute as an input or as an independent validation for ecosystem biogeochemistry models. Not all models specify soil depth or consider carbon dynamics below the top 30 cm of soil (e.g., Raich et al. 1991, Running and Gower 1991, Potter et al. 1993), but models that include multiple soil layers and that vary the distribution of roots may benefit from more detailed descriptions of soil carbon pools and the environmental factors that control them at depth (Daly et al. 2000).

That the soil apparently stores a large pool of carbon below the first meter raises important issues for global carbon budgets and for carbon sequestration strategies (Batjes 1996, IGBP 1998). On the one hand, relatively deep soil layers may be unimportant regardless of size, because of fairly slow carbon turnover, making them relatively insensitive to changes in climate or management. On the other hand, some proportion of deep SOC probably has a relatively fast turnover and might act as a carbon source if temperature increases. Changes in vegetation type could also play an important role. Introducing relatively deeply rooted vegetation into shallow-rooted systems might store carbon deep in the soil, acting as a potential C sink for centuries. Potential examples include shrub encroachment of grasslands or afforestation of areas dedicated to annual crops or pasture. Loss of plant functional types with deeper roots

might have the opposite effect. Such changes in vegetation are increasingly common (e.g., Jackson et al. 2000), both intentionally and unintentionally, and the contrast between root and SOC profiles supports the idea that the deep soil might act as a carbon reservoir. The fate of new carbon added to deep soil, however, can be complex and may not necessarily follow the average cycling pattern of the total SOC pool (e.g., Trumbore et al. 1995). In summary, the information presented here, combined with a better understanding of how different SOC fractions turn over with depth (Trumbore 2000), may (1) improve soil carbon models, (2) help us understand the consequences of vegetation change, and (3) help determine more efficient strategies for land use and vegetation management to ameliorate rising atmospheric CO₂ levels.

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LITERATURE CITED

- Allen, A. S., J. A. Andrews, A. C. Finzi, R. Matamala, D. D. Richter, and W. H. Schlesinger. 2000. Effects of free-air CO₂ enrichment (FACE) on belowground processes in a *Pinus taeda* forest. *Ecological Applications* **10**:437–448.
- Alvarez, R., and R. Lavado. 1998. Climate, organic matter and clay content relationships in the Pampa and Chaco soils, Argentina. *Geoderma* **83**:127–141.
- Amundson, R. G., O. A. Chadwick, and J. M. Sowers. 1989. A comparison of soil climate and biological activity along an elevational gradient in the eastern Mojave Desert. *Oecologia* **80**:395–400.
- Apps, M. J., W. A. Kurz, R. J. Luxmoore, L. O. Nilsson, R. A. Sedjo, R. Schmidt, L. G. Simpson, and T. S. Vinson. 1993. Boreal forest and tundra. *Water, Air, and Soil Pollution* **70**:39–53.
- Arrouays, D., and P. Pelissier. 1994. Modeling carbon storage profiles in temperate forest humic loamy soils of France. *Soil Science* **157**:185–192.
- Austin, A. T., and P. M. Vitousek. 1998. Nutrient dynamics on a rainfall gradient in Hawai'i. *Oecologia* **113**:519–529.
- Barry, R. G. 1981. *Mountain weather and climate*. Methuen, London, UK.
- Batjes, N. H., editor. 1995. *A homogenized soil data file for global environmental research: a subset of FAO, ISRIC and NRCS profiles (Version 1.0)*. Working Paper and Preprint 95/10, ISRIC, Wageningen, The Netherlands.
- Batjes, N. H. 1996. Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science* **47**:151–163.
- Batjes, N. H., and E. M. Bridges. 1994. Potential emissions of radiatively active gases from soil to atmosphere with special reference to methane: development of a global database (WISE). *Journal of Geophysical Research* **99**:16479–16489.
- Burke, I. C., C. M. Yonker, W. J. Parton, C. V. Cole, K. Flach, and D. S. Schimel. 1989. Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. *Soil Science Society of America Journal* **53**:800–805.
- Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. *Oecologia* **111**:1–11.
- Carter, M. R., D. A. Angers, E. G. Gregorich, and M. A. Bolinder. 1997. Organic carbon and nitrogen stocks and storage profiles in cool, humid soils of eastern Canada. *Canadian Journal of Soil Science* **77**:205–210.
- Connin, S. L., R. A. Virginia, and C. P. Chamberlain. 1997. Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. *Oecologia* **110**:374–386.
- Daly, C., D. Bachelet, J. M. Lenihan, R. P. Neilson, W. Parton, and D. Ojima. 2000. Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications* **10**:449–469.
- Dent, J. B., and M. J. Blackie. 1979. *Systems simulation in agriculture*. Applied Science, London, UK.
- Desjardins, T., F. Andreux, B. Volkoff, and C. C. Cerri. 1994. Organic carbon and ¹³C contents in soils and soil size-fractions, and their changes due to deforestation and pasture installation in eastern Amazonia. *Geoderma* **61**:103–118.
- Dokuchaev, V. V. 1883. *Russian chernozem*. St. Petersburg Evdokimova (1883).
- Dosskey, M. G., and P. M. Bertsch. 1997. Transport of dissolved organic matter through a sandy forest soil. *Soil Science Society of America Journal* **61**:920–927.
- Dzurec, R. S., T. W. Boutton, M. M. Caldwell, and B. N. Smith. 1985. Carbon isotope ratios of soil organic matter and their use in assessing community composition changes in Curlew Valley, Utah. *Oecologia* **66**:17–24.
- Ehleringer, J. R., N. Buchmann, and L. B. Flanagan. 2000. Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications* **10**:412–422.
- Eissenstat, D. M., and R. D. Yanai. 1997. The ecology of root lifespan. *Advances in Ecological Research* **27**:2–60.
- Eswaran, H., E. van den Berg, and P. Reich. 1993. Organic carbon in soils of the world. *Soil Science Society of America Journal* **57**:192–194.
- FAO. 1995. *Digital soil map of the world and derived soil properties (version 3.5)*. Food and Agriculture Organization, Rome, Italy.
- Fisher, M. J., I. M. Rao, M. A. Ayarza, C. E. Lascano, J. I. Sanz, R. J. Thomas, and R. R. Vera. 1994. Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature* **371**:236–238.
- Gale, M. R., and D. F. Grigal. 1987. Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research* **17**:829–834.
- Gill, R. A., I. C. Burke, D. G. Milchunas, and W. K. Lauenroth. 1999. Relationship between root biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado. *Ecosystems* **2**:226–236.
- Gordon, W. S., and R. B. Jackson. 2000. Nutrient concentrations in fine roots. *Ecology* **81**:275–280.
- Hilgard, E. 1906. *Soils, their formation, properties, compositions, and relations to climate and plant growth in the humid and arid regions*. Macmillan, New York, New York, USA.
- IGBP (International Geosphere Biosphere Programme) Terrestrial Carbon Working Group. 1998. *The terrestrial carbon cycle: implications for the Kyoto Protocol*. *Science* **280**:1393–1394.
- Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. A global analysis of

- root distributions for terrestrial biomes. *Oecologia* **108**: 389–411.
- Jackson, R. B., H. A. Mooney, and E.-D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences, (USA)* **94**:7362–7366.
- Jackson, R. B., H. J. Schenk, E. G. Jobbágy, J. Canadell, G. D. Colello, R. E. Dickinson, C. B. Field, P. Friedlingstein, M. Heimann, K. Hibbard, D. W. Kicklighter, A. Kleidon, R. P. Neilson, W. J. Parton, O. E. Sala, and M. T. Sykes. 2000. Belowground consequences of vegetation change and their treatment in models. *Ecological Applications* **10**: 470–483.
- Jenny, H. 1941. *Factors of soil formation*. McGraw-Hill, New York, New York, USA.
- Jenny, H. 1950. Causes of high nitrogen and organic matter content in temperate and tropical soils. *Soil Science* **69**: 63–69.
- Jenny, H. 1981. *The soil resource*. Springer-Verlag, New York, New York, USA.
- Kern, J. S. 1994. Spatial patterns of soil organic carbon in the contiguous United States. *Soil Science Society of America Journal* **58**:439–455.
- Leemans, R., and W. P. Cramer. 1990. The IIASA database for mean monthly values of temperature, precipitation and cloudiness of a global terrestrial grid, WP-90–41. IIASA, Luxenburg-Austria.
- McPherson, G. R., T. W. Boutton, and A. J. Midwood. 1993. Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA. *Oecologia* **93**:95–101.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**:621–626.
- Menteemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* **59**:465–472.
- Nakane, K. 1975. Dynamics of soil organic matter in different parts on a slope under evergreen oak forest. *Japanese Journal of Ecology* **25**:205–216.
- Oades, J. M. 1988. The retention of organic matter in soils. *Biogeochemistry* **5**:33–70.
- Parfitt, R. L., H. J. Percival, R. A. Dahlgren, and L. F. Hill. 1997. Soil and solution chemistry under pasture and radiata pine in New Zealand. *Plant and Soil* **191**:279–290.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in grasslands. *Soil Science Society of America Journal* **51**:1173–1179.
- Paruelo, J. M., E. G. Jobbágy, O. E. Sala, W. K. Lauenroth, and I. C. Burke. 1997. Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications* **8**:194–206.
- Paton, T. R., G. S. Humphreys, and P. B. Mitchell. 1995. *Soils, a new global view*. Yale University Press, New Haven, Connecticut, USA.
- Paul, E. A. 1984. Dynamics of soil organic matter. *Plant and Soil* **76**:275–285.
- Paul, E. A., R. F. Follet, S. W. Leavitt, A. Halvorson, G. A. Peterson, and D. J. Lyon. 1997. Radiocarbon dating for determination of soil organic pool sizes and dynamics. *Soil Science Society of America Journal* **61**:1058–1067.
- Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger. 1982. Soil carbon pools and world life zones. *Nature* **298**:156–159.
- Potter, C. S., J. T. Randerson, C. B. Field, P. A. Matson, P. M. Vitousek, H. A. Mooney, and S. A. Klooster. 1993. Terrestrial ecosystem production: A process model based on global satellite and surface data. *Global Biogeochemical Cycles* **7**:811–841.
- Pregitzer, K. S., M. J. Laskowski, A. J. Burton, V. C. Lessard, and D. R. Zak. 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* **18**:665–670.
- Raich, J. W., and C. S. Potter. 1995. Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles* **9**:23–36.
- Raich, J. W., E. B. Rastetter, J. M. Melillo, D. W. Kicklighter, P. A. Steudler, B. J. Peterson, A. L. Grace, B. Moore III, and C. J. Vorosmatry. 1991. Potential net primary productivity in South America: application of a global model. *Ecological Applications* **1**:399–429.
- Risser, P. G., E. C. Birney, H. D. Blocker, S. W. May, W. J. Parton, and J. A. Wiens, editors. 1981. *The true prairie ecosystem*. (US/IBP synthesis series, vol. 16). Hutchinson Ross, Stroudsburg, Pennsylvania, USA.
- Running, S. W., and S. T. Gower. 1991. Forest-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology* **9**:147–160.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* **69**:40–45.
- Schlesinger, W. H. 1977. Carbon balance in terrestrial detritus. *Annual Review of Ecology and Systematics* **8**:51–81.
- Schlesinger, W. H. 1997. *Biogeochemistry, an analysis of global change*. Academic Press, San Diego, California, USA.
- Siltanen, R. M., M. J. Apps, S. C. Zoltai, R. M. Mair, and W. L. Strong. 1997. A soil profile and organic carbon data base for Canadian forest and tundra mineral soils. Canadian Forestry Service, Edmonton, Canada.
- Sims, P. L., and R. T. Coupland. 1979. Producers. Chapter 5. Pages 49–72 in R. T. Coupland, editor. *Grassland ecosystems of the world: Analysis of grasslands and their uses*. Cambridge University Press, Cambridge, UK.
- Smith, E. P., and K. A. Rose. 1995. Model goodness-of-fit analysis using regression and related techniques. *Ecological Modelling* **77**:49–64.
- Spain, A. V., R. F. Isbell, and M. E. Probert. 1983. Soil organic matter. Pages 551–563 in CSIRO, Melbourne, editor. *Soils: An Australian viewpoint*. CSIRO, Melbourne. Academic Press, London, U.K.
- Tiessen, H., E. Cuevas, and P. Chacon. 1994. The role of soil organic matter in sustaining soil fertility. *Nature* **371**:783–785.
- Torn, M. S., S. E. Trumbore, O. A. Chadwick, P. M. Vitousek, and D. M. Hendricks. 1997. Mineral control of soil organic carbon storage and turnover. *Nature* **389**:170–173.
- Trumbore, S. E. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* **10**:399–411.
- Trumbore, S. E., O. A. Chadwick, and R. Amundson. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science* **272**: 393–396.
- Trumbore, S. E., E. A. Davidson, P. Barbosa de Camargo, D. C. Nepstad, and L. A. Martinelli. 1995. Belowground cycling of carbon in forests and pastures of eastern Amazonia. *Global Biogeochemical Cycles* **9**:515–528.
- USDA. 1994. *National Soil Characterization Data*. Soil Survey Laboratory, National Soil Survey Center, Soil Conservation Service, Lincoln, Nebraska, USA.
- Weaver, J. E., V. H. Houghen, and M. D. Weldon. 1935. Relation of root distribution to organic matter in prairie soil. *Botanical Gazette* **96**:389–420.
- Webb, W. L., S. Szarek, W. K. Lauenroth, R. Kinerson, and M. Smith. 1978. Primary production and water use on native forest, grassland, and desert ecosystems. *Ecology* **59**: 1239–1247.

- Whittaker, R. H. 1975. *Communities and ecosystems*. Macmillan, London, UK.
- Woodwell, G. M., F. T. Mackenzie, R. A. Houghton, M. Apps, E. Gorham, and E. Davidson. 1998. Biotic feedbacks in the warming of the Earth. *Climatic Change* **40**:495–518.
- Zinke, P. J., S. Sabhasri, and P. Kundstadter. 1978. Soil fertility aspects of the Lua forest fallow system of shifting cultivation. Pages 134–159 *in* P. Kundstadter, E. C. Chapman, and S. Sabhasri, editors. *Farmers in the forest*. University Press of Hawaii, Honolulu, Hawaii, USA.