



Fine Root and Soil Organic Carbon Depth Distributions are Inversely Related Across Fertility and Rainfall Gradients in Lowland Tropical Forests

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ABSTRACT

Humid tropical forests contain some of the largest soil organic carbon (SOC) stocks on Earth. Much of this SOC is in subsoil, yet variation in the distribution of SOC through the soil profile remains poorly characterized across tropical forests. We used a correlative approach to quantify relationships among depth distributions of SOC, fine root biomass, nutrients and texture to 1 m depths across 43 lowland tropical forests in Panama. The sites span rainfall and soil fertility gradients, and these are largely uncorrelated for these sites. We used fitted β parameters to characterize depth distributions, where β is a numerical index based on an asymptotic relationship, such that larger β values indicate greater concentrations of root biomass or SOC at depth in the profile. Root β values ranged from 0.82 to 0.95 and were best predicted by soil pH and extractable potassium (K) stocks. For

example, the three most acidic ($\text{pH} < 4$) and K-poor ($< 20 \text{ g K m}^{-2}$) soils contained $76 \pm 5\%$ of fine root biomass from 0 to 10 cm depth, while the three least acidic ($\text{pH} > 6.0$) and most K-rich ($> 50 \text{ g K m}^{-2}$) soils contained only $41 \pm 9\%$ of fine root biomass at this depth. Root β and SOC β values were inversely related, such that a large fine root biomass in surface soils corresponded to large SOC stocks in subsoils (50–100 cm). SOC β values were best predicted by soil pH and base cation stocks, with the three most base-poor soils containing $34 \pm 8\%$ of SOC from 50 to 100 cm depth, and the three most base-rich soils containing just $9 \pm 2\%$ of SOC at this depth. Nutrient depth distributions were not related to Root β or SOC β values. These data show that large surface root biomass stocks are associated with large subsoil C stocks in strongly weathered tropical soils. Further studies are required to evaluate why this occurs, and whether changes in surface root biomass, as may occur with global change, could in turn influence SOC storage in tropical forest subsoils.

Key words: Panama; Base cations; Potassium; Soil pH; Dissolved organic carbon (DOC); Root depth distribution.

Received 16 May 2020; accepted 12 September 2020;
published online 13 October 2020

Electronic supplementary material: The online version of this article (<https://doi.org/10.1007/s10021-020-00569-6>) contains supplementary material, which is available to authorized users.

Daniela F. Cusack conceived of and designed the study, performed research, analyzed data, and wrote the paper; Benjamin L. Turner helped design the study, performed research, and helped write the paper.

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HIGHLIGHTS

- Root depth distributions in 43 tropical forests were predicted by pH and exchangeable potassium.
- Soil carbon stocks in subsoils were greatest in infertile, base cation-poor soils.
- Root and soil carbon depth distributions were inversely related across sites.

INTRODUCTION

Tropical forests contain some of the largest soil organic carbon (SOC) stocks on Earth, making them broadly important in the global carbon (C) cycle (Jobbagy and Jackson 2000). Soil below 30 cm depth can contribute over half of forest SOC stocks (Rumpel and Kogel-Knabner 2011), with deep SOC typically having longer turnover times than surface SOC, and consisting of C protected from decomposition in organo-mineral associations (Schoening and Kogel-Knabner 2006; Chaopricha and others 2010; Schmidt and others 2011). Despite the importance of subsoil SOC for long-term C storage, predictors of the distribution of SOC through the soil profile remain poorly characterized in tropical forests.

Humid tropical forests also contain some of the largest fine root biomass stocks among biomes globally (Jackson and others 1996), and there is evidence that roots are the primary source of subsoil SOC, as opposed to leaf litter. Studies using correlative approaches and stable isotope tracers from root tissue into soil have found: (a) root turnover transfers organic matter directly into the soil profile, where decomposition rates decline with depth and deep roots are the primary source for deep SOC stocks (Rasse and others 2005; Pries and others 2018); (b) root tissue is generally more complex, less bioavailable and retained for longer periods in soil than leaf tissue, as indicated by greater retention of isotopically labeled root versus leaf litter over decadal timescales (Lorenz and others 2007; Bird and others 2008; Pries and others 2017); (c) fine root biomass stocks are positively correlated with SOC stocks to about 1 m depth, as seen across tropical landscapes in the Canary Islands and Panama (Mora and others 2014; Cusack and others 2018). These relationships suggest that root depth distributions might directly influence subsoil C storage in tropical forests, with in situ retention of root material down the soil profile.

Given the apparent contribution of fine roots to SOC in tropical forests, factors influencing root depth distribution, such as moisture and nutrient availability, could provide indirect control over SOC depth distributions. Few studies have examined root depth distributions in humid tropical forests, but studies of root stocks provide some insight. For example, fine root biomass stocks in the upper 1–2 m of soil have been inversely related to soil phosphorus (P) and/or base cation availability across lowland tropical forest edaphic gradients in Queensland, Costa Rica and Panama (Cavelier 1992; Maycock and Congdon 2000; Espeleta and Clark 2007; Cusack and others 2018). These trends support the idea that plant C allocation into absorptive fine root biomass declines when nutrients are plentiful (Bloom and others 1985), with absorptive fine roots generally concentrated in shallow soils (McCormack and others 2015). Thus, infertile soils may promote greater fine root biomass at shallow depth to take up scarce nutrients, which may in turn be reflected in shallow SOC depth distributions.

In contrast to nutrient availability, soil moisture has been positively related to fine root biomass stocks in humid tropical forests. For example, fine root biomass stocks declined during dry periods in seasonal Malaysian and Brazilian forests (Green and others 2005; Metcalfe and others 2008), and fine root biomass increased during wetter months and years in a Costa Rican rainforest (Espeleta and Clark 2007). Root turnover and production rates in surface soils were also greatest during wet periods in an Amazon rainforest (Cordeiro and others 2020). Thus, greater stocks and production of fine roots in relatively wetter tropical forests may contribute to larger SOC stocks, although few studies have assessed the effect of moisture on root depth distributions. One study of 62 tree seedling species in the Amazon found deeper root distributions in drier forests (Markesteijn and Poorter 2009), so dry forests may have relatively greater root tissue contributions to subsoil C stocks. Thus, nutrient availability and moisture patterns may control the vertical distribution of root biomass across tropical forest landscapes, with subsequent effects on subsoil C storage.

Other ecosystem properties may also influence SOC depth distributions, potentially overwhelming the influence of root inputs. In particular, soil weathering, clay content and sorptive capacity are important for subsoil C storage because of their influence on the formation of organo-mineral associations (Angst and others 2018). Accordingly, clay content was a significant predictor of SOC

stocks to 1 m depth across 50 forest sites in Panama (Cusack and others 2018). Also, soil hydrology and drainage can influence the transfer of C from the soil surface to subsoil via dissolved organic C (DOC) leaching (for example, Sanderman and Amundson 2008). If mineralogical and hydrological soil properties are more important than root depth distributions as drivers of subsoil C storage, then root and SOC depth distributions could be decoupled.

Broad-scale geographic studies can help us understanding the relative strengths of root depth distributions versus other ecosystem properties for predicting subsoil C storage in tropical forests. Globally, humid and wet tropical forests span a wide range in rainfall (2000 to > 8000 mm year⁻¹ mean annual precipitation [MAP]) (Holdridge and others 1971), dry season duration (0–5 months) (FAO 2012), and orders of magnitude in soil nutrient availability (Beinroth and others 1996; Holzman 2008; Quesada and others 2010; Quesada and others 2011; Turner and Engelbrecht 2011). To better understand relationships among depth distributions of SOC, fine root biomass, nutrients, and soil texture we collected soils to 1 m depth across 43 distinct lowland moist tropical forests in Panama. The sites span gradients of rainfall and fertility, where soil fertility and rainfall are not or weakly correlated, and include five orders in Soil Taxonomy. We used this observational approach to test the hypotheses that: (1) SOC depth distributions are positively related to fine root depth distributions, (2) fine root depth distributions reflect availability and depth distributions of scarce rock-derived nutrients in tropical forests, and (3) drier sites have relatively more SOC at depth than wetter sites, reflecting deeper root depth distributions. We predicted that root depth distributions would be the primary predictor of subsoil C stocks, with a secondary influence of soil clay content.

METHODS

Study Sites

We studied 43 1-ha plots in lowland tropical forests across the Isthmus of Panama maintained by the Smithsonian Tropical Research Institute (STRI), where forests span a wide range in soil fertility (Turner and Engelbrecht 2011; Condit and others 2013; Cusack and others 2018; Turner and others 2018), and a distinct rainfall gradient from 1750 mm year⁻¹ mean annual precipitation (MAP) on the Pacific coast to about 4000 mm year⁻¹ MAP on the Caribbean coast (Pyke and others 2001; Engelbrecht and others

2007). Rainfall at each of our study sites was calculated using the nearest long-term rainfall data from Panama Canal Authority (ACP) sites as described previously (Engelbrecht and others 2007), noting that these calculations tend to underestimate rainfall measured by STRI for Caribbean sites (STRI 2020). Variation in soil nutrient availability is related primarily to lithology and is therefore decoupled from rainfall in the geologically complex central Panama region (Stewart and others 1980; Pyke and others 2001; Turner and Engelbrecht 2011), providing an opportunity to isolate the influence of rainfall from soil properties. The forests have a tropical monsoon climate, and the wetter Caribbean coast has a shorter dry season (~ 115 days) compared with the drier Pacific coast (~ 150 days). The mean annual temperature across sites is 26 °C and mean monthly temperature varies by < 1 °C during the year (Windsor and others 1990).

Soil parent materials include volcanic (basalt, andesite, agglomerate, rhyolitic tuff) and marine sedimentary (limestone, calcareous sandstone, siltstone, mudstone) lithologies, contributing to the formation of five soil orders in the USDA Soil Taxonomy system of classification (Soil Survey Staff 1999; Cusack and others 2018). Infertile acidic soils across the sites typically have 1:1 layer kaolinitic clays and are richer in metal oxides, while fertile neutral pH soils have 2:1 layer smectitic clays (Messmer and others 2014).

All plots were in lowland tropical forests (10–410 m above sea level) and included a range of secondary and old growth forests. Aboveground biomass does not vary significantly among sites or according to rainfall or soil fertility (Pyke and others 2001; Cusack and others 2018). Tree community composition does vary markedly across the rainfall and fertility gradients, driven in large part by species-specific affinities for moisture and P (Engelbrecht and others 2007; Condit and others 2013; Turner and others 2018).

Fine Root Biomass and Soil Collections

We quantified SOC, fine root biomass, nutrient content, metals and soil texture to 1 m depth in 1-ha plots at each site using samples from within plots and soil profile pits outside each plot. The upper meter of soil includes SOC stocks well below the main rooting zone for these forests (< 50 cm) (Cusack and others 2018) and allows comparison with other studies of root and SOC depth profiles across other sites and ecosystems (Jackson and others 1996). Samples were collected during the

~ 8-month wet season to avoid changes in SOC concentrations that can occur during the dry season (Turner and others 2015). The majority of the plots were sampled during 2008 and 2009, with additional plots sampled between 2010 and 2015. This approach provided a spatially extensive measure of fine root biomass, SOC, and nutrient stocks, but did not account for seasonal and inter-annual fine root biomass variation, which can be substantial in forest ecosystems (Vogt and others 1998).

Soil cores were taken to 1 m depths in quadrats in the four corners and the center of each 1-ha plot (5 root profiles per plot), in increments of 0–10 cm, 10–20 cm, 20–50 cm and 50–100 cm. The 0–10 cm and 10–20 cm samples were taken with a constant volume corer (5 cm diameter), and deeper samples taken with an auger (6.25 cm diameter). To account for greater variation in fine root biomass and SOC at the surface versus at depth, eight additional soil samples from 0 to 10 cm depth were collected from alternate 20 × 20 m quadrats within the 1-ha plots using the constant volume corer (that is, 13 surface samples in total per plot). Live fine roots (< 2 mm diameter) were removed exhaustively from each soil sample by hand (until no more visible roots remained), washed on a 250- μ sieve, oven-dried for 3 days at 60 °C and weighed. Hand-sorting fine roots from soil tends to slightly underestimate biomass compared with wet sieving, but was used here to preserve soil for comparison of root biomass with characteristics of the surrounding soil. We focused on fine roots because these generally represent first- and second-order absorptive roots and turn over more rapidly (for example, lifespan < 2 years) compared to higher order coarse roots (for example, > 2 mm diameter, lifespan up to 10 years) (McCormack and others 2015). As a result, fine roots likely contribute a more constant flux of organic matter to mineral soils than longer-lived coarse roots.

Leaf litter on the soil surface, which typically decays completely during the wet season in this region (Wieder and Wright 1995), was removed prior to sampling. The ephemeral nature of the litter layer and the absence of a true organic horizon means that fine roots are rare in the litter layer, and at one of our sites comprised < 3% of the root biomass from 0 to 10 cm depth (Rodtassana and Tanner 2018). This paucity of fine roots in the litter layer contrasts with some wetter tropical forests where a persistent organic horizon can contain abundant fine root mats (Vance and Nadkarni 1992; Guevara and Romero 2007). Exclusion of the litter layer was therefore unlikely to significantly

influence total fine root biomass stocks to one-meter depth.

On each root-free soil sample, we measured total C, total nitrogen (N), total soil P, resin-extractable phosphate, potassium sulfate (K_2SO_4)-extractable ammonium, nitrate, dissolved organic C (DOC), and total dissolved N (TDN), Mehlich-III extractable base cations and extractable aluminum (Al), soil pH in water, particle size distribution and bulk density as described previously (Turner and Engelbrecht 2011; Condit and others 2013; Cusack and others 2018; Turner and others 2018). Extractable DOC was used as an indication of relatively soluble and mobile C. Extractable Al was included because prior work has indicated Al toxicity to plant growth and potential negative effects on canopy greenness for these sites (Zemunik and others 2018; Fisher and others 2020), so could potentially affect belowground productivity. Stocks for live fine root biomass, SOC and nutrients at each depth increment were calculated on an area basis using bulk density measured by constant volume core (upper 20 cm) or from soil profile pits (Table S11).

To compare depth profiles for fine root biomass and SOC stocks, we fitted a depth coefficient β to raw depth increment data for each site (Table S12), where β is a numerical index of depth distribution based on the asymptotic equation $Y = 1 - \beta^d$, where d = depth and Y = the cumulative proportion of fine root biomass or SOC from the surface to depth d (Gale and Grigal 1987). Larger β values correspond to a greater proportion of fine root biomass or SOC at depth (50–100 cm), while smaller β values indicate a greater proportion of fine root biomass or SOC in the soil surface (0–10 cm). One site on a Mollisol (Campo Chagres) was an outlier because of shallow bedrock (< 50 cm). This site was therefore excluded from statistical analyses, but is shown on graphs for comparison, and as a representation of other tropical forests that also occur on shallow, fertile soils.

Statistical Analyses

We used initial backward stepwise linear regressions to identify significant predictors of the root depth coefficient (hereafter Root β) and SOC depth coefficient (hereafter SOC β). Predictors included MAP, dry season moisture deficit, aboveground biomass, soil order, total nutrient stocks to 1 m (total P, total N, resin-extractable phosphate, nitrate, ammonium, TDN, extractable base cations individually and total extractable base cations [TEB]), extractable Al, average pH and average soil

texture to 1 m depth. We also assessed the relationship between Root β and SOC β and included Root β values in the stepwise test for SOC β (above). The stepwise model selection process sought to minimize Bayesian information criterion (BIC) values. This approach identifies significant factors and provides a penalty for adding parameters (Schwarz 1978), thus identifying the minimum adequate general linear model. We then ran the identified model and included only significant factors selected by the stepwise regressions.

Using the significant factors in the identified models above, we ran post hoc regressions and Fisher's least significant difference (LSD) tests to further explore relationships among the factors. For post hoc tests, significant effects of K and pH on Root β , and TEB on SOC β , were explored by grouping sites into four levels of K, pH and TEB, such that the range of nutrient availability or pH was divided roughly equally, with the highest level representing the top 10% quantile of data (that is, to separate out extremely fertile sites). Thus, sites were assigned to extractable K groupings of: 5–20 g/m² ($n = 22$), > 20–50 g/m² ($n = 12$), > 50–100 g/m² ($n = 5$), and > 100–300 g/m² ($n = 4$); pH groupings of: 3–4 ($n = 3$), 4–5 ($n = 11$), 5–6 ($n = 20$), and 6–7 ($n = 9$). For TEB, the lower three levels had no significant variation in SOC β , so we used just two TEB levels, with the upper level still representing the top 10% quantile of data: 0–3 kg/m² ($n = 33$), and > 3–6 kg/m² ($n = 10$). For these analysis, we show fine root biomass and SOC depth increment data, rather than β values, to clarify the vertical patterns according to these groupings.

We also explored significant relationships using structural equation modeling (SEM) path analysis to statistically assess the goodness of fit of our hypothesized relationships among factors influencing Root β and SOC β . We used soil chemical and physical factors, aboveground biomass, and rainfall as exogenous factors, and Root β and SOC β as endogenous factors. We used SEM modification indices to add or remove specific pathways from the model. An initial model included extractable P, clay concentrations and rainfall as exogenous factors, but these were removed because of poor model similarity to the saturated model. The final default model (that is, our model) was tested for overall similarity to the saturated model (that is, ideal model) using common metrics of comparison (that is, no significant difference from saturated model, Chi square $p > 0.05$, GFI > 0.9, NFI > 0.9, RMSEA < 0.05). The model used 42 observations, excluding the site with shallow bedrock.

Where necessary, values were log transformed to meet assumptions of normality (for example, total P, resin-extractable P, extractable potassium (K), DOC). Averages are reported ± 1 standard error, and significance levels are reported at $p < 0.05$. Pearson's correlation coefficients are reported for post hoc correlations, and means separations letters are shown for Fisher's LSD ($p < 0.05$). General linear models were performed using 13.0.0 JMP Pro software (SAS Institute Inc. 2016), and SEM path analysis was performed using SPSS AMOS 23 software (IBM 2015).

RESULTS

Predictors of Fine Root Depth Distributions

There was substantial variation in Root β among the 43 sites. The minimum adequate model for predicting Root β values included soil order, pH and extractable K, with Root β positively correlated to both soil pH ($R^2 = 0.52$, Figure 1A) and extractable K ($R^2 = 0.55$, Figure 1B). Thus, the most shallow root distributions were generally in acidic, K-poor Ultisols and Oxisols (for example, Cardenas, $\beta = 0.888$, pH 3.70, $K = 5.8$ g K/m²), whereas the most even root depth distributions were in neutral, K-rich Mollisols, Alfisols and Inceptisols (for example, PNM, $\beta = 0.956$, pH 6.79, $K = 80.9$ g K/m²). The Mollisol on shallow bedrock had a much shallower root depth distribution than all other sites because there was no soil below 50 cm (Campo Chagres, $\beta = 0.819$, pH 6.70, $K = 8.4$ g K/m², Tables 1, SI1, and SI2).

Post hoc tests revealed that sites with soil pH < 4 ($n = 3$) had greater proportions of fine root biomass stocks at shallow depth, with $76 \pm 5\%$ of root biomass in the upper 10 cm of the profile, versus $46 \pm 4\%$ at this depth for sites with pH above 6 ($n = 9$, Figure 2A). Similarly, sites with extractable $K < 20$ g K/m² ($n = 22$) had $58 \pm 2\%$ of fine root biomass in the upper 10 cm, versus $46 \pm 5\%$ of fine root biomass at this depth in sites with extractable $K > 100$ g K/m² ($n = 5$, Figure 2B). For example, the three most acidic (pH < 4) and K-poor (5–20 g K/m²) soils had $76 \pm 5\%$ of fine root biomass in the upper 10 cm of the profile (Albrook, Cardenas and Campo Chagres), compared to only $41 \pm 9\%$ of fine root biomass in the upper 10 cm in the three least acidic (pH 6–6.8), most K-rich sites (50–300 g K/m², P23, Caritas and PNM, Table SI2). Acidic and K-poor soils also had greater total fine root biomass stocks relative to more neutral, K-rich soils (Figure 2A,

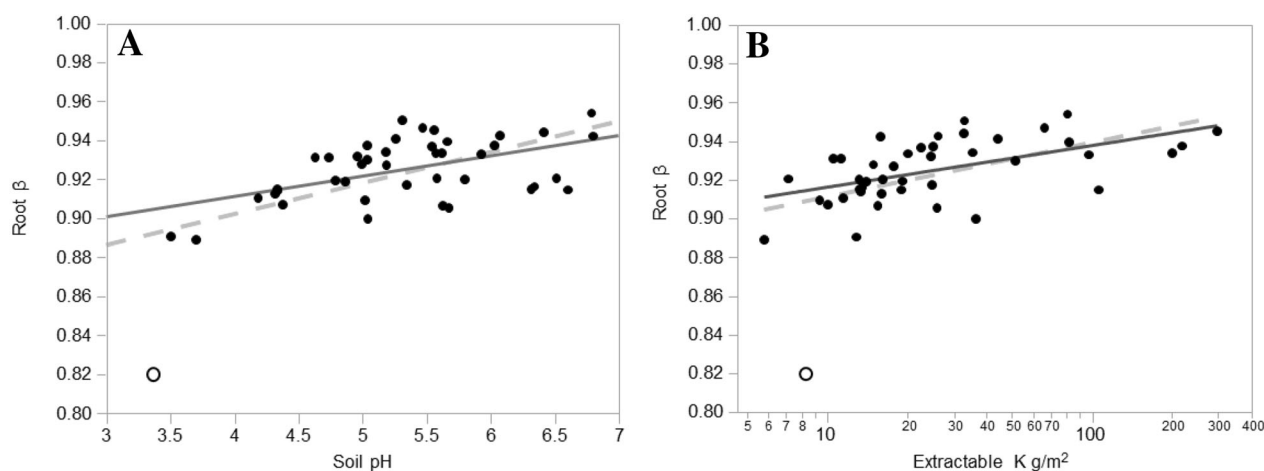


Figure 1. The strongest predictors of Root Biomass β values were (**A**) average soil pH ($R^2 = 0.17$ or 0.52 without shallow-soil outlier shown as open circle), and (**B**) total extractable K^+ ($R^2 = 0.26$ or 0.55 without shallow-soil outlier shown as open circle) to 1 m depths. Regression fits including the shallow-soil outlier site are shown in dashed line ($n = 43$), and excluding the outlier site are shown in solid line ($n = 42$). Smaller Root Biomass β values indicate greater relative proportions of fine root biomass in surface soils, as observed in more acidic and K-poor soils.

B). Soil pH and extractable K stocks to 1 m were significantly but weakly correlated with each other across sites ($R^2 = 0.17$).

Predictors of Soil Organic C Depth Distributions

There was also substantial variation in SOC β values among the 43 sites. The minimum adequate model for predicting SOC β included total extractable bases and soil pH to 1 m. The strongest predictor was a negative relationship for total extractable bases with SOC β ($R^2 = 0.72$, Figure 3A), followed by a negative relationship for soil pH with SOC β ($R^2 = 0.58$, Figure 3B). The most even SOC depth distributions were in base cation-rich, neutral pH Inceptisols and Mollisols (for example, Las Pavas 2, SOC $\beta = 0.954$, TEB = 3.09 kg/m^2 , pH = 6.0), while the greatest proportions of C in subsoils at 50–100 cm depth were in a base cation-poor, acidic Ultisols (for example, Cardenas, SOC $\beta = 0.979$, TEB = 0.03 kg/m^2 , pH = 3.7, Tables 1, SI1, and SI2).

Post hoc tests revealed that base-poor soils had $20 \pm 2\%$ of SOC at 50–100 cm depth (TEB < 3 kg/m^2 , $n = 33$), whereas base-rich soils had only $13 \pm 1\%$ of SOC at this depth (TEB $3.01\text{--}6 \text{ kg/m}^2$, $n = 10$, Figure 4A). For example, the three most base-poor soils (< 0.07 kg-TEB/m^2) had $34 \pm 8\%$ of SOC stocks at 50–100 cm depth (P25, Albrook, Cardenas), compared with only $9 \pm 2\%$ of SOC at this depth in the three most base-rich soils (> 5.6 kg-TEB/m^2 , P17, P21, P23, Table SI1). Patterns for extractable DOC were similar to and even

stronger than for SOC, with greater extractable DOC at depth in base-poor soils (Figure 4B). Also, base-poor soils had larger total SOC and DOC stocks relative to base-rich soils (Figure 4A, B). Somewhat surprisingly, clay content, which had a large range across these sites (22–82%, Table SI1), was not related to SOC β .

Relationships Between Fine Root and Soil Organic C Depth Distributions

Overall, SOC β and Root β values were negatively correlated ($R^2 = 0.29$, Figure 3C), such that shallower root depth distributions corresponded to greater proportions of SOC in deeper soil. At the same time, total stocks of fine root biomass were significantly positively correlated to total SOC stocks to 1 m depth ($R^2 = 0.53$, $n = 43$) and to extractable DOC stocks to 1 m depth ($R^2 = 0.57$, $n = 43$). Among soil depths, fine root biomass was strongly correlated to SOC and DOC at the 10–20 cm depth ($R^2 = 0.42$ and 0.45 , respectively) and to DOC at 0–10 cm depth ($R^2 = 0.41$).

The SEM path analyses supported the above results, indicating that smaller Root β values (that is, shallower root distributions) corresponded to larger SOC β values (deeper SOC distributions). Soil K and pH were the exogenous factors most related to Root β , and TEB was the exogenous factor most related to SOC β values (Figure 5). Additional factors did not improve the fit of the model to the data. This final SEM model was not significantly different ($p = 0.19$) from the “ideal saturated

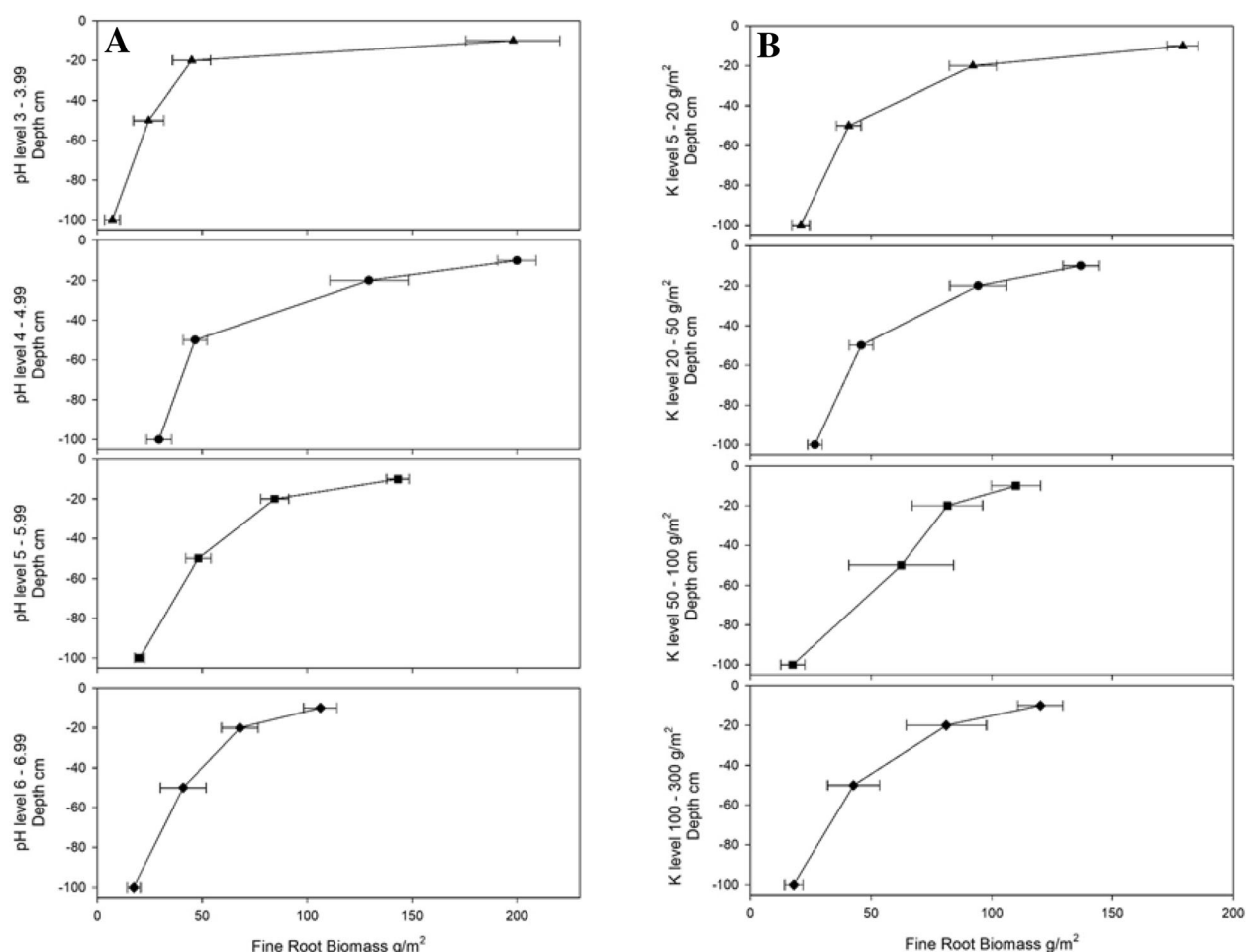


Figure 2. The depth distributions of fine root biomass are shown across: **(A)** soil pH groupings, from the most acidic sites (top left panels, triangles $n = 3$, circles $n = 11$), to nearly neutral sites (bottom left panels, squares $n = 20$, diamonds $n = 9$), with acidic soils having greater fine root biomass overall and a greater proportion of biomass in surface soils, reflecting smaller Root Biomass β values at these sites; **(B)** extractable K levels, from K-poor sites (top right panels, triangles $n = 22$, circles $n = 12$), to K-rich sites (bottom right panels, squares $n = 4$, diamonds $n = 5$), with K-poor soils having greater fine root biomass overall and a greater proportion of biomass in surface soils, reflecting smaller Root Biomass β values at these sites.

model" (Chi square 8.7, $df = 6$), indicating a good fit for the data.

Fine Root and Soil Organic C Depth Distributions Among Soil Orders

Post hoc tests indicated that Ultisols contained a significantly greater proportion of fine root biomass in the surface soil (that is, smaller Root β values) compared to other soil orders (Table 1). Ultisols had $59 \pm 6\%$ of fine root biomass at 0–10 cm depth ($n = 5$), while Oxisols, Mollisols, Inceptisols, and Alfisols all had less ($53 \pm 4\%$, $n = 7$; $53 \pm 12\%$, $n = 4$; $54 \pm 2\%$, $n = 16$; and $48 \pm 3\%$, $n = 11$, respectively; Figure 6A).

For SOC depth distributions, Oxisols and Ultisols contained significantly greater proportions of SOC

at 50–100 cm depth (that is, larger SOC β values) relative to other soils (Table 1). Ultisols had $32 \pm 5\%$ ($n = 5$) of SOC at 50–100 cm depth, and Oxisols had $24 \pm 2\%$ ($n = 7$) at this depth (Table S11). Inceptisols, Alfisols and Mollisols all had smaller SOC stocks at this depth ($16 \pm 2\%$, $n = 16$; $14 \pm 2\%$, $n = 11$; $11 \pm 4\%$, $n = 4$, respectively, Table S11). Similar patterns among soil orders were even stronger for extractable DOC depth distributions (Figure 6B). Ultisols had $43 \pm 3\%$ ($n = 5$) of extractable DOC at 50–100 cm depth, and Oxisols had $27 \pm 3\%$ ($n = 7$) at this depth, whereas Inceptisols, Alfisols and Mollisols had less ($26 \pm 2\%$, $n = 16$; $23 \pm 4\%$, $n = 11$; $15 \pm 5\%$, $n = 4$, respectively, Table S11).

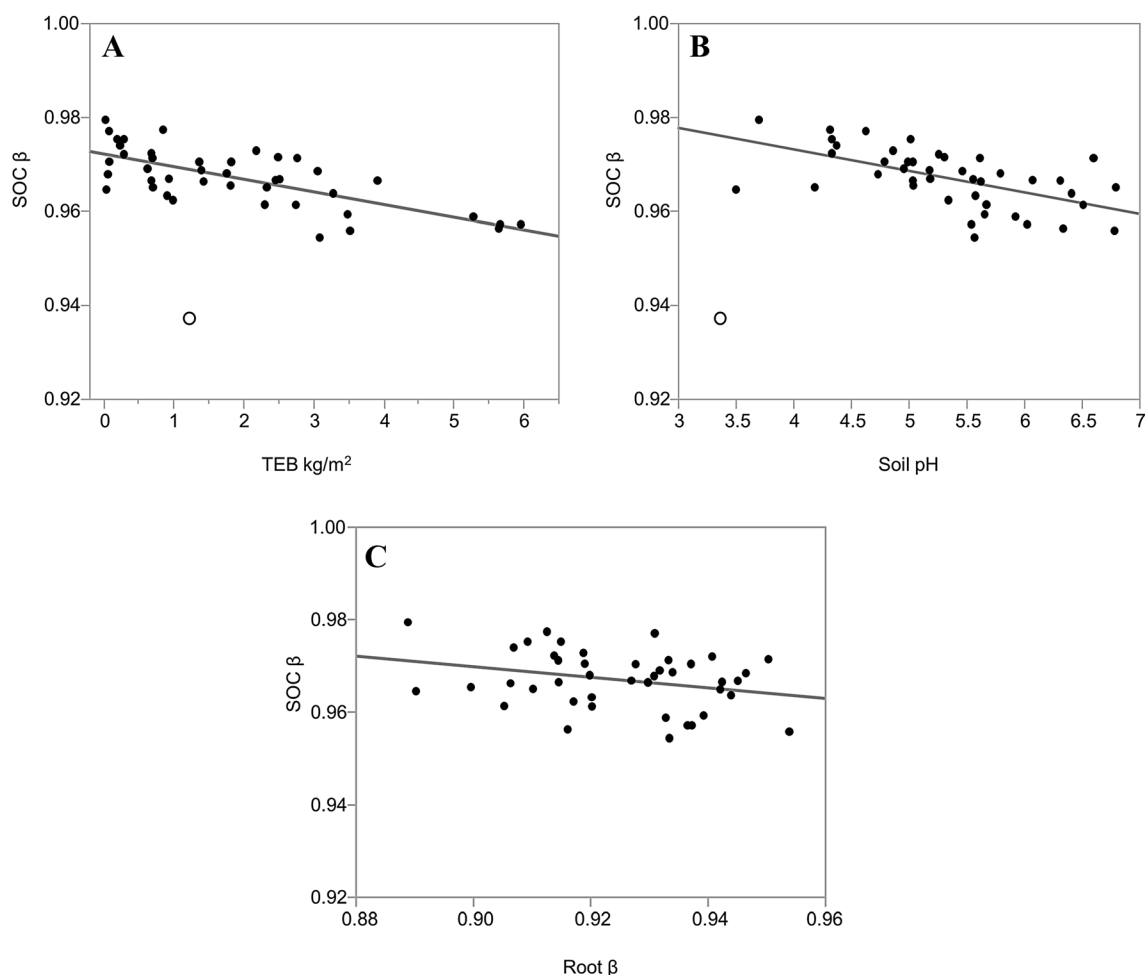


Figure 3. The strongest predictors of SOC β profile coefficients to 1 m were: **(A)** total extractable base cations (TEB) to 1 m ($R^2 = 0.72$, $n = 42$); **(B)** average soil pH to 1 m depth ($R^2 = 0.58$, $n = 42$); **(C)** Root β values ($R^2 = 0.29$, $n = 42$). An outlier site with shallow bedrock is shown with an open circle in **A** and **B**, and was excluded from analyses. Larger SOC β values indicate greater relative proportions of SOC in deeper soils, apparent here in sites with smaller TEB stocks, more acidic soils, and shallow root depth profile values (smaller β).

Soil orders also varied in the chemical characteristics that were the best predictors of Root β and SOC β among sites. Ultisols and Oxisols had the most acidic pH to 1 m, smaller stocks of extractable K and smaller stocks of total extractable bases relative to other soil orders (Table 2).

Nutrient Depth Distributions

Nutrient depth distributions were not correlated with Root β or SOC β , despite the importance of total soil nutrient stocks in the above analyses. Nutrient depth distributions varied with soil fertility in a different way, in that fertile soils, which had the most even depth distributions for fine root biomass and SOC, had the most uneven depth distributions for nutrients. Fertile soils generally

contained a greater proportion of their nutrient stocks in subsoil (50–100 cm), while infertile soils had more even nutrient depth distributions (Table S11). For example, K-rich soils had the largest proportion of K at 50–100 cm depth (Figure 7) and base-rich soils had the largest proportions of total extractable bases at 50–100 cm depth (Figure 8).

DISCUSSION

Depth distributions of fine root biomass and SOC were inversely related across the lowland tropical forests of central Panama, with the largest surface root biomass and subsoil C stocks in infertile soils. These results suggest that while turnover of surface roots may provide an important input of organic

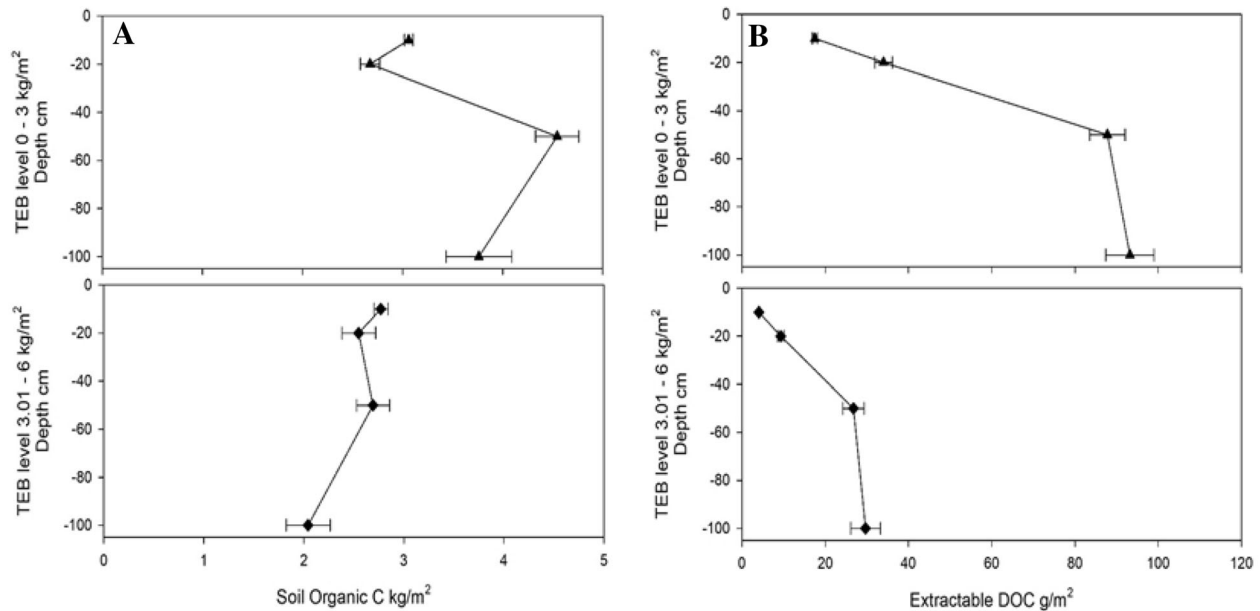


Figure 4. Depth distributions of (A) SOC stocks and (B) extractable DOC are shown relative to total extractable base cations (TEB) levels, with larger overall SOC stocks and extractable DOC at depth in TEB-poor sites (top panels, triangles $n = 33$) versus TEB-rich sites (bottom panels, diamonds $n = 10$), reflecting larger SOC β values at these sites.

matter to soils, it is likely that subsoil properties, rather than in situ retention of fine root detritus, control deep soil C storage in these forests.

Predictors of Fine Root Depth Distributions

Root β values in central Panama were similar to values reported for tropical forests elsewhere. The range of Root β across our sites (0.88–0.95, excluding the shallow-soil outlier at 0.82) is similar to that for *terra firme* forests in the Central Amazon (0.86–0.97) (Noguchi and others 2014) and slightly lower than a global average for tropical evergreen and deciduous forests of 0.96 (Jackson and others 1996). The large landscape-scale variation in Root β values across our sites is also comparable with the large variation in root biomass across forest types in Puerto Rico (Yaffar and Norby 2020).

Our data support growing evidence for the importance of base cations, particularly K, in driving root distribution and dynamics in humid tropical forests. In a long-term fertilization experiment at one of our infertile, mid-rainfall sites (Gigante), fine root biomass and productivity at 0–10 cm depth declined in response to long-term K addition (Yavitt and others 2011; Wurzbarger and Wright 2015). This coincides with our observation that K scarcity is related to greater fine root biomass in surface soils across lowland Panama forests and

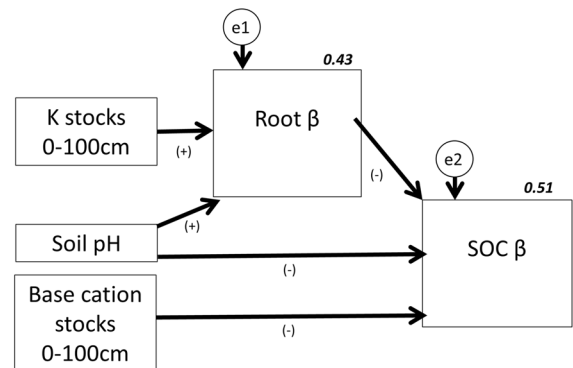


Figure 5. A structural equation model path analysis for the relationships between exogenous factors (soil K stocks, base cation stocks, and pH to 1 m depths) and endogenous factors (Root β and SOC β , where larger values indicate greater concentrations at depth) is shown. Bold values in italics above each endogenous factor show the squared multiple correlation for that factor, giving the amount of variation in that factor accounted for by all of its predictors (that is, R^2). The sign below each arrow shows the direction of the relationship, all of which are significant ($p < 0.05$). Correlations among exogenous factors were significant in this analysis (see text). Factors in rectangles represent measured values, and circles represent unmeasured error terms (e1 and e2) for each endogenous factor. Our model was not significantly different ($p = 0.19$) from the “ideal saturated model” (Chi square 8.7, $df = 6$), indicating a good fit for the data.

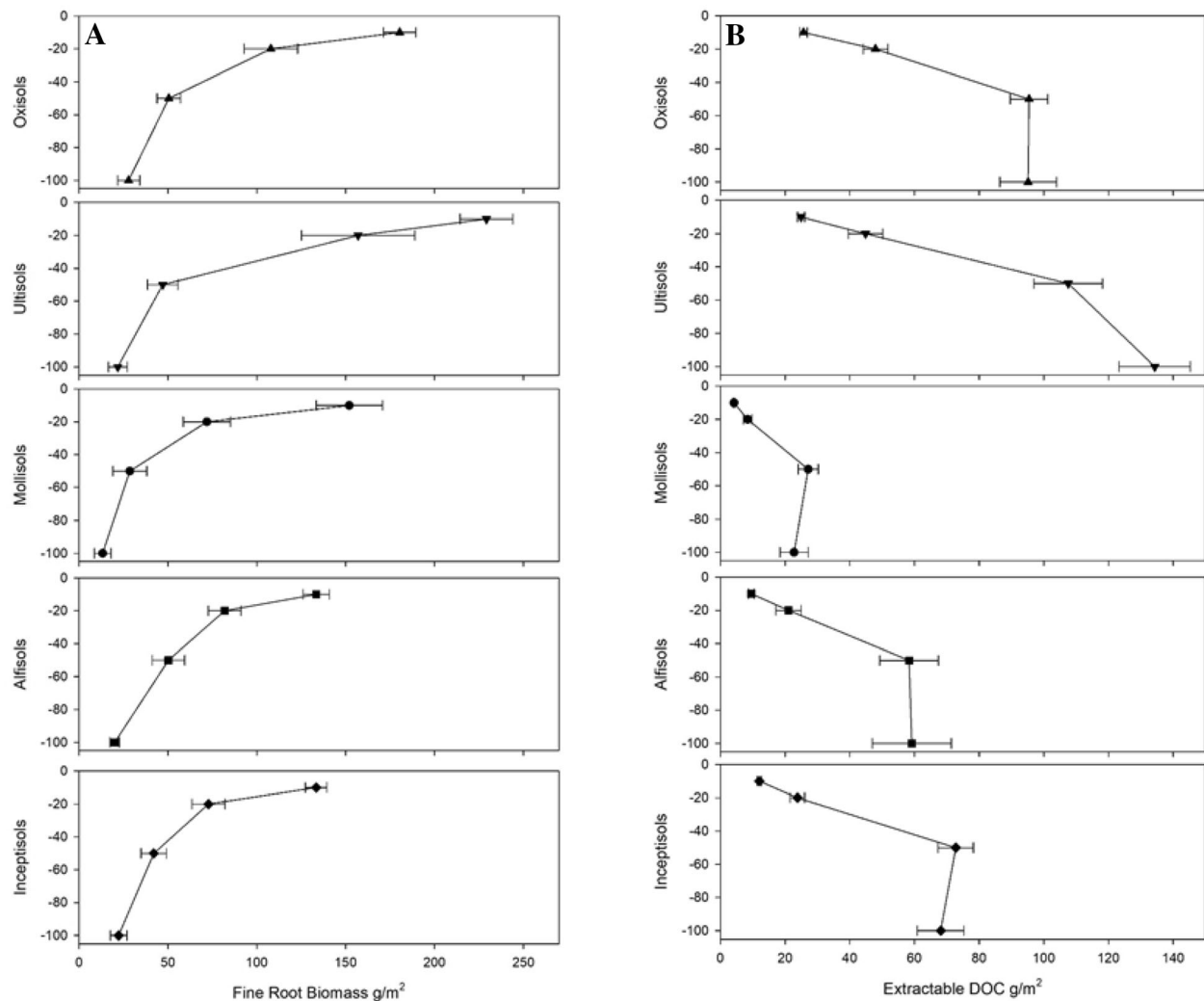


Figure 6. Variation among soil orders is shown for: **(A)** fine root biomass, and **(B)** extractable DOC. There were generally larger stocks overall, greater proportions of fine root biomass in surface soils (0–20 cm), and larger stocks of DOC at depth (50–100 cm) in more acidic, nutrient-poor orders like Oxisols (top panels, triangles), and Ultisols (second panels, triangles). Oxisol $n = 7$, Ultisol $n = 5$, Mollisol $n = 4$, Alfisol $n = 11$, Inceptisol $n = 16$.

suggests that plant allocation of C to roots may be controlled by K availability. Studies in rainforests of Borneo, Costa Rica and Colombia also found that forest stands on infertile and acidic soils (for example, poor in P, K, and/or Ca) had greater surface root biomass stocks compared with more fertile and/or neutral pH soils (Berish 1982; Gower 1987; Espeleta and Clark 2007; Jimenez and others 2009; Kochsiek and others 2013). Interestingly, the Bornean study also found that greater local availability of K corresponded to greater root biomass and greater growth rates over small spatial scales, contradicting the broader-scale pattern in the study and possibly indicating root foraging for K. Similarly, a study in *terra firme* Amazonian forests found that surface fine root growth was stimulated by

addition of the most locally limiting nutrient (N or P) (Cuevas and Medina 1988). Also, surface fine roots in an Oxisol in the Venezuelan Amazon had rapid uptake of added isotopically labeled P and Ca (Stark and Jordan 1978), suggesting that proliferation of fine root biomass at the surface serves to rapidly take up scarce nutrients released during litter decomposition. Together, the above results are consistent with a paradigm in which plants invest in fine roots on infertile soils (Panama, Borneo), root growth is stimulated by local increases in scarce nutrients (Borneo, Amazon), and nutrient addition reduces plant investment in fine root biomass (Panama fertilization experiment).

In addition to root biomass, root productivity and turnover are crucial for the transfer of root C into

Table 1. Average Organic C Profiles, Including Root β , SOC β , Fine Root Biomass (< 2 mm Diameter), SOC Stocks and Extractable DOC to 1 m Depth are Shown Among Soil Orders \pm One Standard Error

Soil order	N	Root beta*	Soil organic C beta*	Fine root biomass to 1 m g/m ²	Soil organic C to 1 m kg/m ²	DOC to 1 m g/m ²
Inceptisol	16	0.924 \pm 0.003 a	0.966 \pm 0.002bc	259.6 \pm 33.3b	12.4 \pm 0.9a	170.3 \pm 22.8b
Alfisol	11	0.932 \pm 0.004a	0.965 \pm 0.001c	287.7 \pm 32.8b	13.6 \pm 1.0a	142.2 \pm 45.2bc
Mollisol	4	0.934 \pm 0.030a	0.957 \pm 0.007abc	253.7 \pm 53.0b	12.0 \pm 2.1a	41.6 \pm 11.9c
Ultisol	5	0.909 \pm 0.008b	0.971 \pm 0.003ab	435.9 \pm 107.2a	13.0 \pm 0.8a	287.3 \pm 47.8a
Oxisol	7	0.922 \pm 0.005 ab	0.972 \pm 0.001a	363.4 \pm 24.5ab	14.3 \pm 1.5a	266.1 \pm 15.3a

*One Mollisol site had shallow bedrock (Campo Chagres) and so was excluded in statistical analyses for Beta distributions ($n = 3$ for these analyses). Letters indicate significant differences among orders down each column using Fisher's LSD test ($p < 0.05$).

Table 2. Average Soil Chemistry to 1 m Depths is Shown Among Soil Orders \pm One Standard Error, Including Significant Predictors of Root and Soil Organic C Beta Values

Soil order	N	K g/m ²	TEB kg/m ²	Soil pH
Inceptisol	16	45.2 \pm 12.6a	2.3 \pm 0.4a	5.31 \pm 0.16bc
Alfisol	11	72.9 \pm 29.0a	2.7 \pm 0.5a	5.73 \pm 0.14b
Mollisol	4	31.1 \pm 16.8ab	2.5 \pm 0.5a	6.72 \pm 0.04a
Ultisol	5	12.5 \pm 2.2b	0.1 \pm 0.05b	4.21 \pm 0.26d
Oxisol	7	18.6 \pm 4.5ab	0.6 \pm 0.2b	4.97 \pm 0.18c

Letters indicate significant differences among orders down each column using Fisher's LSD test ($p < 0.05$).

SOC. Productivity and turnover of surface roots was greater than for deeper roots across Amazonian forests (Girardin and others 2013; Cordeiro and others 2020), indicating that the large surface fine root biomass in our infertile sites may have been more important than deep roots as an input to SOC stocks. Potential variation in root turnover rates across our fertility gradients is unclear. Temperate forests on acidic, N-poor soils can have slower fine root turnover and longer residence times compared with more fertile temperate sites (Nadelhoffer and others 1985; Pregitzer and others 1995; Godbold and others 2003; Aragao and others 2009), which would lead to a slower flux of root tissue inputs to soils. In contrast, fine root turnover may increase with P scarcity, in part because P resorption from roots appears to be greater than N resorption, so plant P losses are not as great as N losses with root turnover. For example, P-scarce tropical shrublands in Australia had faster surface root turnover compared with P-rich sites (Laliberte and others 2015), and an infertile sandy soil in the Colombian Amazon had greater surface root productivity compared with a more fertile loamy soil (Jimenez and others 2009). Root productivity and turnover may be particularly susceptible to global change, with feedbacks to climate likely if SOC stocks change in parallel (Cusack and others 2016; Cusack and

Marin-Spiotta 2019a, b). Understanding root production and turnover across the Panama forest fertility and rainfall gradients is a crucial next step for linking surface root biomass stocks to subsoil C storage.

Somewhat surprising in our study was the lack of a relationship between P availability and fine root depth distributions. Phosphorus plays a key role in many ecological relationships across these lowland Panama forests, including variation in tree growth rates, hydrolytic enzyme activities, microbial biomass, microbial gene expression and shifts in the distribution of tree species and mycoheterotrophic plants (Condit and others 2013; Turner and Wright 2014; Prada and others 2017; Sheldrake and others 2017; Turner and others 2018; Yao and others 2018). Similarly, soil P is a strong determinant of plant community composition and root productivity across Amazonian forests (Aragao and others 2009). Also, a previous study across 15 of the Panama sites found that extractable phosphate was the best predictor of the magnitude of seasonal soil respiration change (Cusack and others 2019a, b), which could have indicated a root flush with rewetting in P-rich sites. However, since resin phosphate was not related to root depth distributions (this study) or total root biomass stocks in these forests (Cusack and others 2018), the relationship

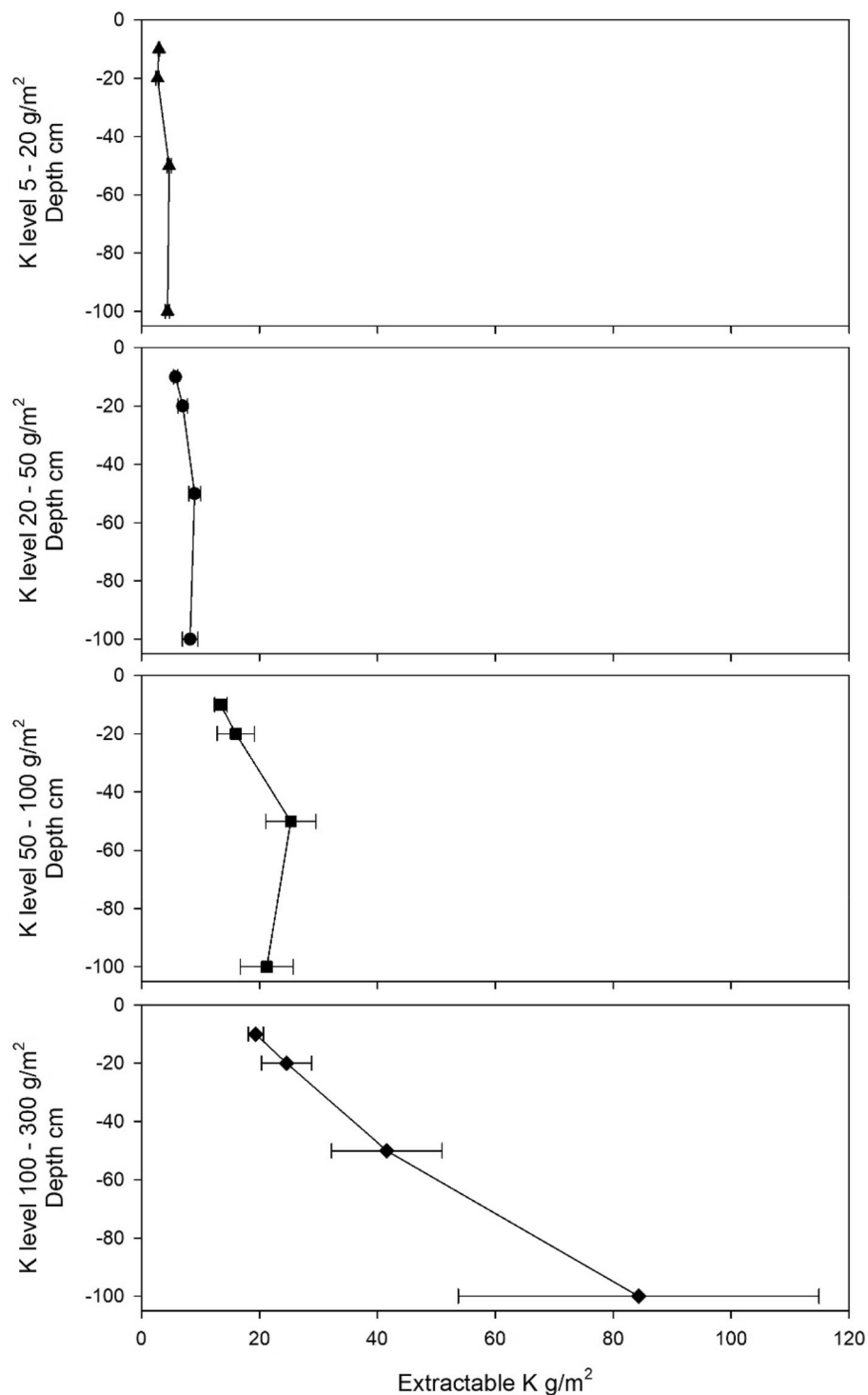


Figure 7. Potassium (K) depth profiles showed greater proportions at depth in nutrient-rich sites (bottom panels), and more even depth distributions in more nutrient-poor sites (top panels) triangles $n = 22$, circles $n = 12$, squares $n = 4$, diamonds $n = 5$.

between phosphate availability and seasonal soil respiration shifts may be due primarily to changes in soil microbial activity. Thus, although P influences tree species distributions and plant growth

rate across these sites, it did not predict root depth distributions, suggesting that the “top down” control of tree species over root depth distributions was relatively unimportant. Rather, other soil

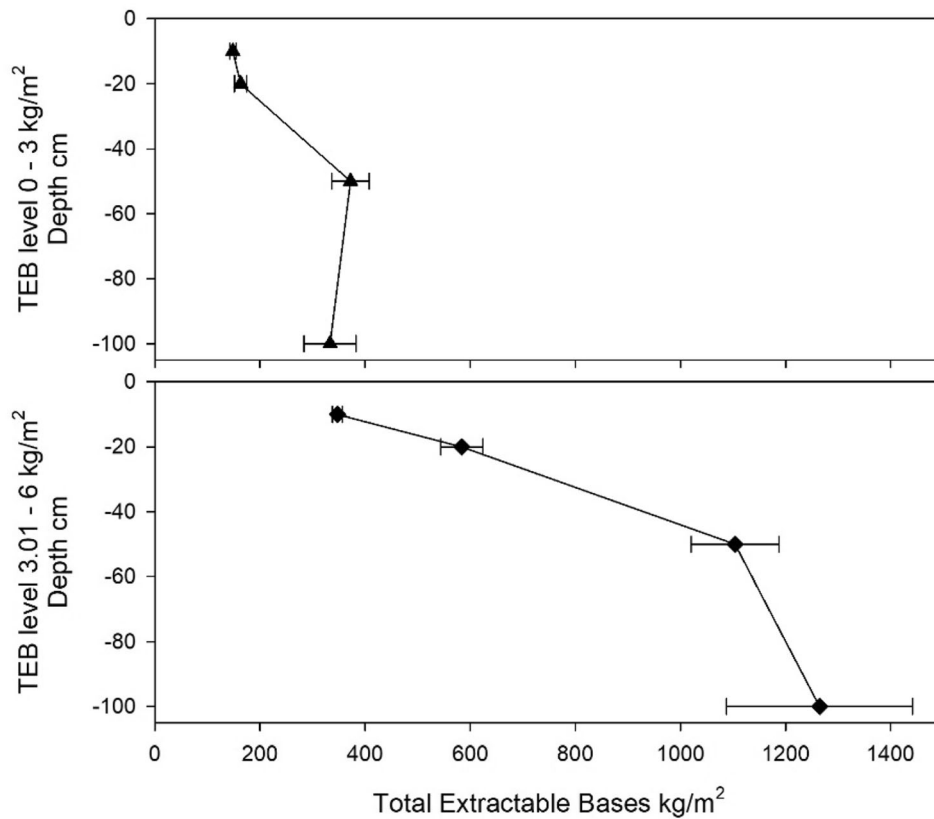


Figure 8. Total extractable base (TEB) depth profiles showed greater proportions at depth in nutrient-rich sites (bottom panel, diamonds $n = 10$), and more even depth distributions in more nutrient-poor sites (top panel, triangles $n = 33$).

properties like base cations, which do not appear to strongly control tree species assemblage at these sites (Turner and others 2018), drive root depth distributions.

The lack of a direct relationship between P availability and fine root biomass stocks or root depth distributions may point to the importance of mycorrhizal fungi in obtaining P for these tropical trees (Schachtman and others 1998), reducing the need for investment in fine root biomass in response to P scarcity. In contrast, K and other base cations are more easily accessed directly by roots, in part because base cations are typically more mobile and soluble than P and diffuse more easily to the rhizosphere (Schachtman and Schroeder 1994; Smith and Read 2008). Thus, K may be a stronger control over fine root biomass and depth distributions across these sites because roots “outsource” uptake of P to mycorrhizal fungi. Further study is needed to isolate the relationships among nutrient availability, mycorrhizal association, and root contributions to subsoil C storage at these sites.

Also somewhat surprising was the lack of a relationship between rainfall and fine root depth distributions, despite the nearly twofold increase in

MAP across sites, and the approximate 30% decline in dry season duration. Previously, rainfall was found to be a significant albeit relatively weak positive predictor of SOC stocks at these sites (Cusack and others 2018), but this relationship does not appear to be mediated by root depth distributions. At one of our mid-rainfall sites, dry season irrigation did not affect root depth distributions (Yavitt and Wright 2001), suggesting that root depth distributions do not respond to short-term changes in moisture in these forests. The positive effect of rainfall on SOC stocks across these sites may be related more to weathering and/or changes in soil sorptive properties at high rainfall, rather than to effects on root depth distribution.

We did not attempt to characterize the more spatially heterogeneous distribution of coarse root biomass and depth distributions. In a nearby plantation, coarse root biomass and morphological traits for five native Panama species were related primarily to species and neighborhood tree size, rather than to soil traits like moisture and nutrients (Madsen and others 2020). Because plant species distributions across these Panama lowland forests are strongly spatially structured (Pyke and others

2001), future investigation into how coarse root biomass and turnover vary among sites and with depth could provide further insight to patterns in subsoil C storage.

Predictors of SOC Depth Distributions

For these Panama forests, SOC depth distributions were not positively correlated with fine root depth distributions, which has been found in other studies. Across ten lowland tropical Andisols, fine root depth distributions were positively related to SOC depth distributions (Mora and others 2014), which the authors attributed to in situ retention of root detritus in mineral soils. In a global dataset, fine root depth distributions were also positively associated with SOC depth distributions, although SOC had deeper distributions relative to roots in wet forests, suggesting slower turnover of SOC versus roots at depth, and/or vertical transport of DOC from the rooting zone into deeper soils (Jobbagy and Jackson 2000). In contrast, another review across ecosystem types found that root depth distributions were poorly related to SOC depth distributions, even though total stocks of fine root biomass and SOC were positively related (Rasse and others 2005), more similar to our study. Thus, there appears to be a divide, both within tropical forests and among other ecosystems, between sites where in situ root biomass retention drives SOC depth distributions, versus sites where root biomass contributes to SOC stocks but SOC depth distributions are controlled by other factors.

Our statistical and structural equation models point to the importance of soil acidity for promoting subsoil C storage at these sites. Acidity promotes precipitation of organo-metal complexes, increases adsorption of DOC onto mineral surfaces and increases the mobility of Al, which can inhibit soil decomposer activity via toxicity, all promoting accumulation of SOC (Kemmitt and others 2006; Scheel and others 2008; Kunito and others 2016). For example, subsoil C storage across Canary Island and Ecuadorian Andisols was positively related to soil acidity and available Al (Tonneijck and others 2010; Mora and others 2014). At our sites, there is evidence that soil acidity and associated Al toxicity inhibit biological activity. High levels of extractable Al are associated with reduced tree growth at one of our mid-rainfall sites on moderately acidic soils (Zemunik and others 2018) and declines in canopy greenness among these Panama forests was associated with variation in extractable Al (Fisher and others 2020). We found no direct relationship between Al with SOC depth

distribution, which might be related to overestimation of the available “free” Al^{3+} pool in our Mehlich-3 extractions (Jansen and others 2002). Still, the positive relationship between soil acidity and subsoil C storage suggests that Al toxicity to decomposers influences subsoil C accumulation, in addition to direct effects of acidity on organic matter precipitation and sorption on mineral surfaces.

The negative relationship between base cation availability and subsoil C storage across the Panama sites is somewhat counterintuitive. Typically, base cations and Ca^{2+} in particular increase sorption of organic matter to smectitic and kaolinitic clays via “cationic bridging,” leading to a positive relationship between base cations and SOC retention in mineral soils (Roychand and Marschner 2014; Singh and others 2016). Here the opposite pattern occurred. Base cation concentrations reflect soil weathering status and sesquioxide formation, which we did not measure directly. Over the course of bedrock weathering and soil formation, base cations are lost in large quantities following desilication, at the same time that secondary clays and sesquioxides are formed at depth (for example, B and C horizons), which promote SOC sorption (Oh and Richter 2005). Further characterization of subsoil physical and chemical properties across these sites may provide greater insight to the direct mechanisms driving variation in subsoil C storage.

Soil Properties that Can Promote Deep C Storage

While clay content was a positive, albeit relatively weak, predictor of SOC stocks to 1 m depth (Cusack and others 2018), clay was not related to SOC depth distributions. Clay content has been positively correlated to subsoil SOC stocks in a global data set, while climate predicted surface SOC stocks (Jobbagy and Jackson 2000). Similarly, temperate forests with abundant soil clay and iron oxide content often have larger subsoil C stocks with older radiocarbon dates relative to less weathered soils, presumably because of greater organic matter sorption onto extensive mineral surface area provided by clays (Rumpel and others 2002; Eusterhues and others 2003; Angst and others 2018). In contrast, dense subsoil clay, as found in some sites of the Central Amazon, can impeded deep root growth and reduce C inputs to subsoil (Noguchi and others 2014). Across 147 Amazonian sites, clay was only a significant predictor of SOC stocks from 0 to 30 cm depth among strongly weathered soils, whereas SOC storage in less weathered soils was

more related to interactions between Al precipitation, soil pH and litter quality (Quesada and others 2020). Our soils contain a broad range (22–88%) of clay content to 1 m depth, yet clay was not related to subsoil SOC storage. Like in the Amazon study, SOC storage mechanisms may vary among soil orders across the Panama lowlands.

Subsoil mineralogy could contribute to the landscape-scale variation we observed in SOC depth distributions. Mineralogy among our sites was kaolinitic in the more infertile, strongly weathered acidic soils, and smectitic in the more fertile, higher pH soils. This difference is broadly related to soil parent material, with soils developed on volcanic lithologies yielding kaolinite-rich soils, and soils developed on marine sedimentary lithologies yielding smectite-rich soils. Sorption of DOC is greater on smectitic versus kaolinitic clays in laboratory settings (Saggar and others 1996; Dontsova and Bigham 2005), opposite of the patterns we observed across the Panama forest soils. Actual sorption rates of C to different minerals in the field, however, are strongly influenced by specific surface area and concentrations of sesquioxides (for example, Al oxides) and electrolytes (for example, Ca^{2+}) (Singh and others 2016). Also, the influence of organic chemistry on sorption and turnover time can differ among mineralogies. For example, a study across seven savanna sites found no difference in the quantity of mineral-associated SOC between kaolinitic and smectitic clays, but kaolinitic soils sorbed more polysaccharides and had faster C turnover times, while smectitic soils sorbed more aromatic compounds and had slower C turnover times (Wattel-Koekkoek and others 2001; Wattel-Koekkoek and others 2003). Again though, this cannot explain the larger subsoil C stocks we observed in kaolinitic soils.

Vertical transport of C from the soil surface to depth via particulate movement, DOC leaching, and/or microbial recycling can also drive variation in subsoil C storage (Michalzik and others 2003), potentially via cracks, macropores and/or leaching (Rumpel and Kogel-Knabner 2011). A Hawaiian study showed that vertical transport of organic particulates and DOC from the surface to subsoils via cracks in shrink-swell clays accounted for large deep SOC stocks (Marin-Spiotta and others 2011), and this could play a role in some of the Panama sites with smectitic clays that shrink and swell seasonally. Dissolved organic C transported in soil water can be efficiently sorbed onto subsoil mineral surfaces in strongly weathered tropical soils, as observed in Puerto Rican forests below 30 cm

depth (McDowell 1998; Cusack and others 2011). Root-derived organic matter can directly contribute to organo-mineral associations in soils below the main rooting zone, as demonstrated with molecular data from mesic temperate forests (Rumpel and others 2002; Angst and others 2018). Alternately, microbial uptake and recycling of organic matter can eventually contribute microbial necromass to subsoil C stocks (Pries and others 2018), although in some cases reduced C inputs from the surface to subsoils can suppress microbial decomposer activity, reduce priming effects and promote greater subsoil SOC storage (Fontaine and others 2007). Because vertical transport would supply relatively young C into subsoils (Ota and others 2013), radiocarbon data for deep soils at these Panama sites could provide insight to the importance of vertical transport.

CONCLUSION

Overall, these results from 43 lowland seasonal tropical forests showed that Root β and SOC β values were inversely related, suggesting that concentration of fine root biomass in surface soils may contribute to SOC stocks, although other soil properties likely control subsoil C storage (50–100 cm). Soil acidity and nutrient scarcity, in particular lack of K, appear to drive proliferation of fine roots in surface soils, while subsoil properties appear to drive retention of SOC in these sites. Further mechanistic studies are needed to elucidate links between surface roots and deep SOC, including measurements of fine root turnover and exudation rates, organic matter in leachate and macropore flow, microbial recycling, the contribution of coarse roots to deep SOC and the influence of mineralogy and other physiochemical subsoil properties for retaining C in subsoil. The short- and longer-term sensitivity of subsoil C storage to changes in surface root dynamics could improve prediction of future climate-forest feedbacks for the humid tropics.

ACKNOWLEDGEMENTS

Funding was provided by NSF GSS Grant No. BCS-1437591 and DOE grant DE-SC0015898 to D. F. Cusack. We thank Julio Rodriguez, Didimo Urena and David Brassfield for field support, Dayana Agudo, Aleksandra Bielnicka, Dianne de la Cruz, Tania Romero and Irene Torres for laboratory support, and Carley Tsiamas for research support. Data are available in tables, figures and SI. We would like to thank Peter Vitousek and two

anonymous reviewers for very helpful comments that improved the paper.

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