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Root Characteristics Vary with Depth Across Four Lowland Seasonal Tropical Forests

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Abstract

Fine roots are key to ecosystem-scale nutrient, carbon (C), and water cycling, yet our understanding of fine root trait variation within and among tropical forests, one of Earth's most C-rich ecosystems, is limited. We characterized root biomass, morphology, nutrient content, and arbuscular mycorrhizal fungal (AMF) colonization to 1.2 m depths across four distinct lowland Panamanian forests, and related root characteristics to soil C stocks. We hypothesized that: (H1) Fine root characteristics vary consistently with depth across seasonal tropical forests, with deeper roots exhibiting more exploratory traits, such as for deep water acquisition; (H2) fine root characteristics vary among tropical forests mainly in surface soils, where resource availability also varies. We found consistent variation with depth across the four forests, including decreased root biomass, root tissue density, and AMF, and increased specific root length. Among the forests, there was variation in some fine root characteristics, including greater surface root biomass and lower SRL in the wettest forest, and smaller fine root diameter in the driest forest. We also found that root characteristics were related to total soil C stocks, which were positively related to root biomass and negatively related to specific root length. These results indicate emergent properties of root variation with depth across tropical forests, and show site-scale variation in surface root characteristics. Future work could explore the flexibility in root characteristics under changing conditions such as drought.

Key words: roots; morphology; chemistry; biomass; radiocarbon; traits; soil; nutrients; carbon; 13C NMR.

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Highlights

- Across four distinct seasonal tropical forests, fine root biomass and root tissue density declined with depth, while specific root length increased. Fine root diameter increased with depth in the driest tropical forest, and other fine root characteristics varied among the forests, particularly in shallow soils.
- Soil carbon stocks to 1 m depth were positively correlated with fine root biomass and negatively correlated with specific root length.
- These results indicate that there are emergent patterns in root characteristics as they vary with depth across tropical forests, whereas site-scale variation appears mostly related to resource acquisition strategies in surface soils.

Introduction

Fine roots play a crucial role in the biogeochemical cycling of nutrients, water and carbon (C), and provide a primary input of biomass to soil C. Some of the largest stocks of both root biomass and soil C exist in tropical forests, (Jackson and others 1996; Cusack and others 2018a; Crowther and others 2019), and these ecosystems have the largest net primary production (NPP) globally (Field and others 1998; Jobbagy and Jackson 2000; Hengl and others 2017), with over one-third of NPP potentially allocated to roots (Aragao and others 2009; Malhi and others 2011; Cordeiro and others 2020; Huaraca Huasco and others 2021). Despite the ecosystem-scale and global importance of tropical fine roots, our understanding of fine root characteristics among and within tropical forest sites, and how these relate to soil C, is still very limited.

Variation in fine root characteristics is important to explore among tropical forest sites, which can often occur across landscape-scale variation in soil moisture and nutrient availability. For example, mean annual precipitation (MAP) in moist and wet tropical forests ranges from 2,000 to over 8,000 mm (Holdridge and others 1971), with dry seasons ranging from 0 to 5 months (FAO 2012). Water availability in tropical forests can also vary greatly with depth and time, with moisture in surface soils declining sharply during dry seasons (Cusack and others 2019; Spanner and others 2022), and forests in some regions depending on water tables for water uptake during dry periods (Nepstad and others 1994; Andrade and others 2005; Fan and others 2017). Soil fertility variation is also common, such as a more than 250-fold difference in soil available phosphorus (P) and base cations across the Panamanian lowlands and the Amazon Basin (Turner and Engelbrecht 2011; Cusack and others 2018a; Quesada and others 2020), with nutrients also varying differently by depth across different forests (Cusack and Turner 2020). Despite these large environmental gradients within and among tropical forests, little is known about overall variation in root characteristics, or whether there are emergent patterns among tropical forest for fine root characteristics.

Whether or not there are emergent ecosystems characteristics depends to some degree on whether site-scale differences swamp broader biome-scale patterns. For example, site-scale variation in soil resources has been related to shifts in plant biomass allocation above versus belowground, and among plant structures (that is, the ''optimal partitioning theory'', Bloom and others 1985). Specifically, infertile soils generally have more surface root biomass compared with fertile soils for greater soil exploration and resource acquisition, such as observed across 50 Panamanian forests with strong soil moisture and nutrient variation (Cusack and others 2018a; Cusack and Turner 2020).

Beyond biomass allocation, root morphology can also vary with soil resources. For example, larger specific root length (SRL) in more infertile or dry soils potentially increases soil exploration, since longer, thinner roots represent less biomass investment per volume of soil explored (Cusack and others 2021a; Freschet and others 2021b). Fine root SRL increased with experimental drought in an Amazonian forest (Metcalfe and others 2008). Similarly, SRL increased in low-fertility soils in local-scale gradients in Brazil (Metcalfe and others 2008; Zangaro and others 2008), indicating larger soil exploration. However, SRL decreased with low soil base saturation and soil P in a primary tropical forest in China (Hogan and others 2020), and with low fertility in a fertilization experiment in Panama (Wurzburger and Wright 2015). In contrast, SRL did not in response to fertilization in Brazil (Lugli and others 2021), or showed mixed responses to different nutrients in a pantropical review, such as larger SRL in low P soils, but smaller SRL in low base saturation soils (Addo-Danso and others 2020). These results indicate complex responses to soil fertility that deserves further research. Also, results for root morphology are primarily from surface soils (< 30 cm), so we know much less about morphological root traits in deeper tropical forest soils.

The biomass of fine roots can have downstream effects on soil C storage, since root mortality is a primary input of new C to soils (Rasse and others 2005; Jackson and others 2017; Dijkstra and others 2021), as seen in a broadscale positive relationship between fine root biomass and soil C stocks to 1 m depths across the Panamanian lowlands (Cusack and others 2018a; Cusack and Turner 2020). Root characteristics in addition to biomass, such as SRL, could influence soil C stocks because high SRL roots have less dense, thinner structures which might be more easily decomposed, or alternatively could promote soil aggregate production through physical entanglement of soil particles (Poirier and others 2018). Thus, exploring root morphological and tissues quality effects on soil C storage could improve our predictions of landscape-scale patterns.

To address these gaps in our understanding of how tropical ecosystems are structured, we assessed patterns in community-scale root characteristics and soil C stocks across four distinct lowland Panamanian forests. We used 32 plots across the four forests sampling roots in depth increments to 1.2 m depths. The forests were representative of regional-scale variation in rainfall, dry season length, and soil fertility across the Isthmus of Panama, with soil fertility and rainfall uncorrelated (Cusack and others 2018a). We hypothesized that: (H1) There is consistent variation in fine root characteristics with depth among tropical forests, with deeper fine roots exhibiting less conservative, more exploratory traits (for example, high SRL), such as for deep soil water acquisition during dry periods. (H2) Variation in fine root characteristics among tropical forests occurs mainly in the soil surface, where site-scale differences in nutrient availability and moisture are also greatest. We also predicted that root biomass and tissue characteristics (for example, root tissue density [RTD]) would be positively related to soil C stocks.

Methods

Study Sites

Fine roots were collected across four distinct lowland tropical forests in central Panama. The forests represent regional variation in MAP and soil fertility, and were located near a subset of ~ 50 long-term 1-ha forest dynamics plots maintained by the Smithsonian Tropical Research Institute, with three sites in the Barro Colorado Nature Monument (BCNM, Cusack and others 2018a). Fertile and infertile sites were identified based on prior measures of resin-extractable P and total extractable base cations to 1 m (Table 1). The sites included Gigante Peninsula in the BCNM (GIG, 2350 MAP, infertile, Oxisol), plot 12 in the BCNM (P12, 2600 MAP, infertile, Ultisol), plot 13 in the BCNM (P13, 2600 MAP, fertile, Alfisol, BCNM), and Sherman Crane in the Bosque Protector San Lorenzo (SC, 3421 MAP, infertile, Oxisol, Table 1, Figure 1).

All sites were classified as tropical moist forests (Holdridge and others 1971) with a mean annual temperature of 26°C (Windsor 1990). Aboveground biomass did not vary significantly among sites or across the broader rainfall and soil fertility gradients (Pyke and others 2001; Cusack and others 2018a). Across the Panamanian lowlands, there was more than a 250-fold variation in soil extractable P and base cations (Turner and Engelbrecht 2011; Turner and others 2018; Cusack and others 2021b). Our sites represented a subset of this variation with tenfold variation in resin P and 24-fold variation in base cations to 1 m depth and a 1.5-fold increase in MAP (Table 1). Tree species composition shifted across the broader rainfall and fertility gradients of the Isthmus, predominantly influenced by species-specific affinities for moisture and P (Engelbrecht and others 2007; Condit and others 2013; Turner and others 2018), and the four forests used here were typical of this rapid turnover in tree species (Cusack and others 2023a). In each of the four forests, we collected root samples in 10-cm depth increments to 1.2 m from 8 plots (n = 8/site, total plots = 32) during late 2017 through 2018 during periods when soils were wet (late wet season through transition to dry season, see below), with further details for the sites described previously (Dietterich and others 2022; Cusack and others 2023b).

Root Collection

Root biomass stocks to a depth of 1.2 m were collected using a 5-cm diameter hand auger. These collections coincided with the subsequent installation of minirhizotron tubes into the resulting holes, which were installed at a 45° angle to the soil surface (Norby and others 2004). Since soils were sampled at an angle, we collected cores in 14.1 cm length intervals so that the true vertical depths were in 10-cm intervals. Soil samples were collected from one hole per plot (10 × 10 m), and plots were located > 10 m apart in each forest (n = 8 per site). Soils were then stored in plastic bags at 4°C until processing within one year of collection. Soils were collected in September 2017

Table 1. Site Characteristics for the Four Tropical Forests Used in This Study (Cusack and others 2018a).

Site	Latitude north	Longitude east	Soil order	Fertility	MAP (mm)	Profile clay to 1 m depth (%)	Above ground biomass (Mg / ha) > 10 cm dbh	SOC to 1 m depth (kg/m^2)	Total N to 1 m depth (kg/m^2)	Total P to 1 m depth (g/m^2)	Resin-extractable P AEM Pi to 1 m depth (g/m^2)	DOC to 1 m depth (g/m^2)	Total extractable bases to 1 m depth (kg/m^2)
GIG	9.09918	−79.8540	Oxisol	Infertile	2350	86.129	201.8	19	2.01	152.95	0.25	318.32	1.37
P12	9.17936	−79.8296	Ultisol	Infertile	2600	52.298	212.8	19	1.45	241.66	0.33	267.33	0.63
P13	9.18788	−79.821	Alfisol	Fertile	2600	49.228	260.2	12	1.01	204.13	1.58	65.32	5.29
SC	9.28087	−79.9747	Oxisol	Infertile	3421	78.217	304.9	13	1	233.59	0.15	375.3	0.22

(P12), December 2017 (P13), February 2018 (SC), and October 2018 (GIG). These dates correspond to the late wet season for P12, P13 and GIG, and the transition to the dry season in SC (Paton 2023a, b). In total, we collected 384 samples across sites and depths.

Additional root samples were collected from each plot to measure AMF colonization by taking sequential cores from 0 to 10 cm and 10 to 20 cm depth in three locations per plot using a 3.81 cm diameter constant volume corer. Collection dates for AMF samples were September 2018 (P12, P13, and SC) and December 2018 (GIG) during the wet season. Fine roots were separated from the soil and stored in plastic cassettes in tap water at 4°C until staining for colonization counts (see below).

Root Processing

The wet weight of all field samples was measured, then subsamples of 3–4 g of root-free, fresh soil were oven-dried at 105°C until constant weight to calculate the moisture content and dry weight of soil for each depth increment.

Fresh soils were then gently rinsed through a 0.25-mm-diameter sieve to remove soil from roots, and roots were then cleaned by hand using paint brushes and water. Roots were divided into fine roots (< 2 mm in diameter) and coarse roots (> 2 mm in diameter) using a caliper. In general, the coarse roots collected in our cores were no larger than 3 mm, such that we collected a relatively small-diameter portion of the coarse root stock. Although most research uses this threshold for fine roots, it varies across the literature (Fantozzi and others 2024). Therefore, we refer to roots > 2 mm as ''coarse'' roots. Fine roots were then separated into live or dead using visual and mechanical assessments. Live roots were determined based on having more turgid tissues that were not easily broken, and the cortex and periderm could not be separated easily (Freschet and others 2021a). Live fine roots were then scanned to assess morphology (see below), and dried at 60°C until constant weight to measure root biomass per sample. Root biomass per mass of soil was then calculated using dry root and dry soil mass per sample (g-biomass/kg-dry-soil). We calculated cumulative root biomass to 1.2 m depth in mg/cm^2 by dividing the fine root biomass sum for the whole soil profile by the soil core surface ground area. We also calculated standing root biomass C stocks (mg C/cm^2, see below).

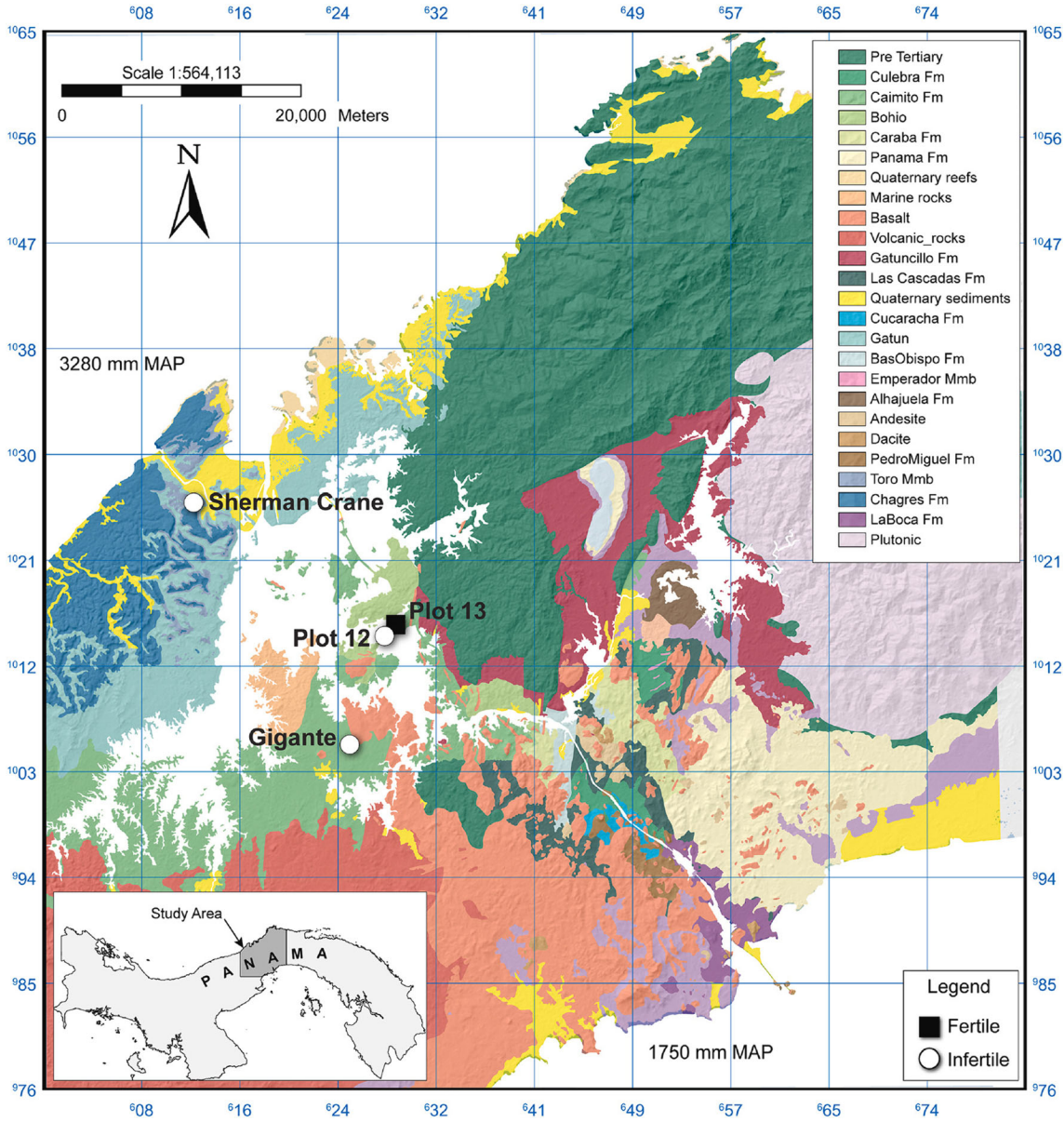

Figure 1. Four lowland tropical forest study sites are shown along a rainfall gradient on the Isthmus of Panama. Geological substrates and formations (Fm, shown in different colors) give rise to large variation in soil fertility, which is not correlated with the rainfall gradient. Rainfall increases from 1750 mm mean annual precipitation (MAP) on the Pacific coast to > 3200 on the Caribbean coast, with sites for this study ranging from 2350 (Gigante) to 3400 (Sherman Crane). Soil fertility for the study sites is shown as fertile (black squares) or infertile (white circles). Citation: Geología de la República de Panamá, digitalizada del mapa Geológico de Panamá, 1:250,000 preparado por el Ministerio de Comercio e Industrias, Dirección General de Recursos Minerales, año 1990. Ministerio de Comercio e Industrias, Dirección General de Recursos Minerales, año 1990. Site details are presented in Table 1.

Root Morphology, Chemistry and AMF Colonization

Live fine root samples were scanned fresh at 800 dpi on a 9800XL plus-Microtek-TMA 1600 II scanner. Images were then analyzed using WinRHIZO (WinRHIZO Regular, Regent Instruments, Canada) to determine SRL, specific root area (SRA), RTD, and mean root diameter; SRL (cm * mg^{-1}) was calculated as root length per dry mass; SRA (cm^2 * mg^{-1}) as root surface area per dry mass; and RTD (g * cm^{-3}) as root dry mass per volume.

After oven drying, live root tissues were finely cut into fine pieces that resembled powder for elemental C and N analysis on a Carlo-Erba

NA1500 at the Environmental Stable Isotope Laboratory at Duke University, USA. Root chemistry was analyzed for all depths in 4–5 plots per site, with site selection for these analyses depending on tissue availability.

For standing fine root C stocks, we multiplied mg-biomass by site-average fine root %C. For this, fine root %C was averaged across depths to obtain a whole soil profile average %C with its mean and SE across plots for each site reported in Table 2. In order to compare with other studies, we also calculated the measurements to Mg C/ha using the surface area of the collection auger.

To further explore differences in deep root characteristics among sites, we also measured radiocarbon content (fraction modern [FM] and $\Delta^{14}C$) and $\delta^{13}C$ on live deep roots (> 80 cm depth) for a subset of plots where tissues were available (n = 5 for GIG, P12 and P13, n = 4 for SC). Roots were prepared for analysis by sealed-tube combustion to CO_2 in the presence of copper oxide (CuO) and silver (Ag), cryogenically purified, and reduced to graphite on Fe powder in the presence of H_2 (Vogel and others 1984). The $\delta^{13}C$ values were measured on a split of purified CO_2 at the Stable Isotope Geosciences Facility at Texas A&M University on a Thermo Scientific MAT 253 Dual Inlet Stable Isotope Ratio Mass Spectrometer. The ^{14}C samples were measured as graphite on the 10 MV Van de Graaff FN or the 1MV NEC Compact accelerator mass spectrometer at Lawrence Livermore National Laboratory (Broek and others 2021). The ^{14}C values were corrected for mass dependent fractionation using measured $\delta^{13}C$ values and are reported here as $\Delta^{14}C$ corrected to the year of analysis of 2022 or 2023 (Stuiver and Polach 1977) and as fraction modern, also referred to as FM or $F^{14}C$ (Reimer and others 2004).

We also analyzed a subset of dried and ground root samples (n = 6 per site) from 0 to 10 cm depths to explore the organic chemistry of live fine roots among the forests, using the same four sample plots as the radiocarbon analyses. Composite pulse multi-cross polarization ^{13}C NMR experiments were conducted on the using a 300 MHz Bruker Avance III NMR spectrometer (Bruker BioSpin, Billerica, MA) at Baylor University (Waco, TX), using the method of Duan and Schmidt-Rohr (2017). The pulse program employed eleven contact pulses of 1.1 ms each, a proton repolarization time of 0.8 s and the 4 mm sample rotor was operated at a magic angle spinning (MAS) frequency of 12 kHz. Resulting spectra were assessed for the relative contributions of seven C functional groups by integrating the signal magnitude on the δ–scale (ppm). Carbon functional groups are followed in parentheses by some of the many common C compounds in which they occur: (1) alkyl 0 to 45 ppm (for example, waxes, other lipids); (2) *N*-alkyl + methoxyl (hereafter *N*-alkyl) 45 to 60 ppm (for example, proteins, peptides,); (3) O-alkyl 60 to 95 ppm (for example, cellulose, other carbohydrates); (4) di-O-alkyl 95 to 110 ppm (for example, hemicellulose); (5) aromatic 110 to 145 ppm (for example, lignin, tannin); (6) phenolic 145 to 165 ppm (for example, acids, tannin (Min and others 2015); and (7) amide + carboxyl 165 to 215 ppm (for example, chitin, proteins, peptides, and hemicellulose) (Li and others 2015). To assess tissue quality, we calculated a lignin/N ratio by multiplying the lignin content of the roots, determined as 26.9% of root C using the molecular mixing model (Baldock and others 2004), by the root C/N ratio.

For AMF colonization, roots were cleared and stained using standard protocols modified for field-collected tropical roots (Giovannetti and Mosse 1980; Koske and Gemma 1989; INVAM 2023). Roots were cleared in 10% KOH at ~ 60°C for 7 days and bleached in ~ 3% household H_2O_2 at room temperature for 30–60 min, until appropriately cleared. Roots were then thoroughly rinsed in tap water, acidified in 1% HCl for 30–60 min. Next, they were stained with 0.05% trypan blue in 10:9:1 glycerol: deionized water: 1% HCl at ~ 60°C for 30–60 min until appropriately stained, rinsed again in tap water, and stored in tap water at 4°C until visual scoring under a microscope was completed. AMF colonization was estimated as the percentage of root length containing AMF structures using the gridline-intersect method (Giovannetti and Mosse 1980), and colonization was calculated as the proportion of scorable intersections in which AMF structures were observed for each plot and soil depth.

Soil C Stocks

We used previously reported soil C stocks (Cusack and others 2018b; Cusack and Turner 2020) to explore relationships with the root characteristics collected here. Briefly, soil cores were collected from five locations within each 1-hectare plot in depth increments of 0–10 cm, 10–20 cm, 20–50 cm, and 50–100 cm. The top 20 cm was sampled with a 5-cm-diameter constant volume corer, while deeper samples were taken using a 6.25-cm-diameter auger. An additional eight surface samples (0–10 cm) were collected, totaling 13 surface samples per plot. The soil samples were air-dried for

Table 2. Root Characteristics Compared Among Sites for Each Response Variable for the Whole Soil Profile from 0 to 1.2 m Depth, Using Summed Values for Biomass, and Average Values for Other Traits.

Site	Live fine root biomass (g/kg-dry-soil) *#	Dead fine root biomass (g/kg-dry-soil) *#	Coarse root biomass (g/kg-dry-soil) *	Dead/total fine root biomass ratio	SRL (cm/mg) *	SRA (cm^2/mg) *	RTD (g/cm^3) *	Diameter (mm) *#	N content (%) *#	C content (%)	C/N ratio *#
GIG	2.72 ± 0.45 B	1.49 ± 0.32 B	3.78 ± 1.44 B	0.35 ± 0.06 AB	1.77 ± 0.18 A	0.28 ± 0.03 B	0.39 ± 0.03 A	0.6 ± 0.02 B	1.1 ± 0.03 AB	40.87 ± 0.4 B	40.46 ± 0.78 B
P12	4.52 ± 0.73 AB	1.79 ± 0.42 B	3.95 ± 1.66 B	0.22 ± 0.02 B	1.75 ± 0.22 A	0.34 ± 0.03 A	0.21 ± 0.01 C	0.77 ± 0.02 A	0.93 ± 0.07 B	43.61 ± 0.97 A	50.46 ± 2.97 A
P13	2.64 ± 0.43 B	1.09 ± 0.12 B	7.97 ± 2.01 AB	0.29 ± 0.02 B	1.47 ± 0.12 A	0.31 ± 0.02 A	0.22 ± 0.02 C	0.73 ± 0.02 A	1.07 ± 0.11 A	42.82 ± 0.83 A	43.38 ± 3.58 B
SC	6.52 ± 1.65 A	3.91 ± 0.77 A	13.72 ± 3.15 A	0.44 ± 0.03 A	1.26 ± 0.25 B	0.26 ± 0.04 B	0.28 ± 0.02 B	0.8 ± 0.04 A	1.07 ± 0.05 AB	41.31 ± 0.44 B	41.72 ± 2.26 B

*Mean ± SE are given, with letters in columns giving significant differences among sites using Tukey's HSD test. Total fine root length and AMF results are shown in Table SI 5. If variable had also a depth effect, a * is given in the column header, and if there was interaction between site and depth # is given. All raw data by depth is provided in Table SI 1.*

10 days, sieved and ground in a ball mill. Total carbon was measured by combustion and gas chromatography with a Thermo Flash NC1112 Soil Analyzer. The C stocks were calculated in kg/m^2 using the average C concentrations, bulk density, surface area of the corer, and depth increments, up to 1 m.

Statistical Analyses

To assess variation of root characteristics with depth and across sites, we conducted a mixed model nested ANOVA for each root characteristic separately, nesting plots within the site, including a random effect of plot, and using site (categorical) and depth (continuous) as predictors. When there were site*depth interactions, we then applied post hoc Tukey's honest significant difference (HSD) means separation tests to explore differences among sites for each depth. If there was no interaction, Tukey HSD tests were run for the whole soil profile (0–1.2 m). Root characteristics for these analyses included live fine root biomass, dead fine root biomass, coarse root biomass, dead/total fine root biomass ratio, total fine root length, SRL, SRA, RTD, root diameter, AMF colonization, root %N, root %C, and root C:N ratios. All raw data are available in Table SI 1.

To assess coordination and tradeoffs in root characteristics across depths and sites, we used principal components analysis (PCA) and cluster analysis. For these analyses, we used data from all depth increments, as well as whole-profile data (summed root biomass and averages for other characteristics). All variables were scaled and centered prior to analysis. We followed these analyses with multiple analysis of variance (MANOVA) using all root characteristics as response variables, with post hoc Hotelling's T-squared test. We also created correlation matrices of all one-to-one comparisons to assess bivariate relationships among root characteristics.

For initial PCA, all characteristics were used, and then subsequent tests were conducted removing auto-correlated characteristics (|Pearson correlation coefficient| > 0.8 or $R^2 > 0.64$). For cluster analyses, we first identified clusters by depth, then by site, both using all available data 0–1.2 m, and then with additional tests including AMF for only 0–10 and 10–20 cm depths. Soil depths were included together in the same PCA or separately for each interval, and using averaged or summed total-profile values from 0–1.2 m. We repeated PCA and cluster analyses after removing fine root biomass to assess patterns in root morphology, and then per-

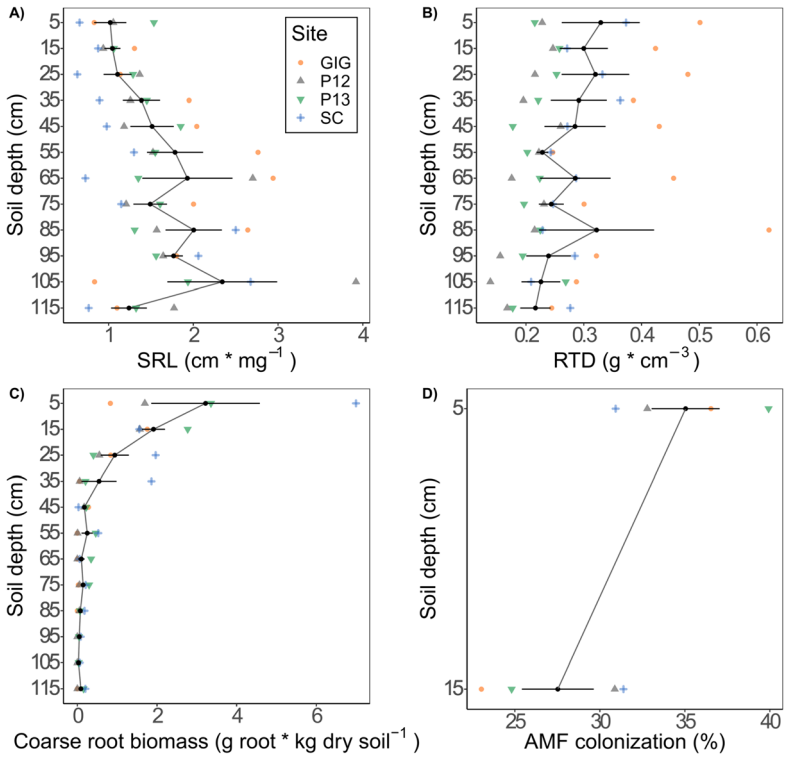

Figure 2. Root characteristics that varied significantly by depth consistently across all sites (no interaction with site) are shown, with depth on the y axis and root characteristic values on the x axis. Depth increments are presented as midpoints of depth intervals (that is: 5 cm for 0–10 cm depth interval). **a** Site and depth predicted SRL, without interaction; **b** Site and depth predicted RTD, without interaction; **c** Site and depth predicted coarse root biomass, without interaction; **d** Depth predicted AMF, without effect of site or interaction. The AMF data were collected only 0–10 and 10–20 cm depths. Black dots and bars represent mean ± SE across sites (n = 4 sites per depth). Colored markers show the average from 8 plots per site for each variable and depth. A similar figure for SRA, the only other root characteristic which also had significant effects of site and depth but not interaction, is in Figure SI 1.

formed additional tests adding root chemistry for available plots (Table SI 2).

The smaller datasets for deep root radiocarbon and δ^{13}C values as well as NMR data were analyzed separately using nonparametric Kruskal–Wallis test to assess differences among sites. Post hoc pairwise comparisons between all pairs of sites were conducted using the Wilcoxon method.

Root characteristics were assessed as predictors of soil C stocks across depth increments using forward stepwise model building. Response variables were total soil C (TC, g/kg) and dissolved organic C (DOC, mg C/kg), and we used all of the measured root characteristics for the initial model building exercise (Table SI 2). The final most parsimonious significant model is reported.

All data were assessed for normal distribution. Log transformations were applied when variables were non-normal and are reported in tables (Tables SI 3, SI 4). The significance level was $p < 0.05$, except for multiple comparisons we used Bonferroni corrections, and these significance levels are reported. Unless otherwise noted, we present mean ± standard error (SE).

Analyses were conducted in R studio version ''*Already Tomorrow*'' 4.3.0 (R-Core-Team 2023) or JMP 17.0 software (SAS Institute, 2023). The R *scales* package (Wickham 2022), cmdscale and dist functions were used for the cluster analysis; the *emmeans* package (Lenth 2023) and cld function were employed for pairwise comparisons of site means; the *ggfortify* package (Tang 2016) was utilized for the PCA analyses; the *lme4* package (Bates 2015) was applied for the mixed models; the stepAIC function from the *MASS* package (Venables 2002) was used for the stepwise model building. R codes are provided in Notes 1.

Results

We observed a set of root characteristics that varied consistently with depth across sites, whereas other characteristics had site and depth interactions, or varied by site without depth interactions.

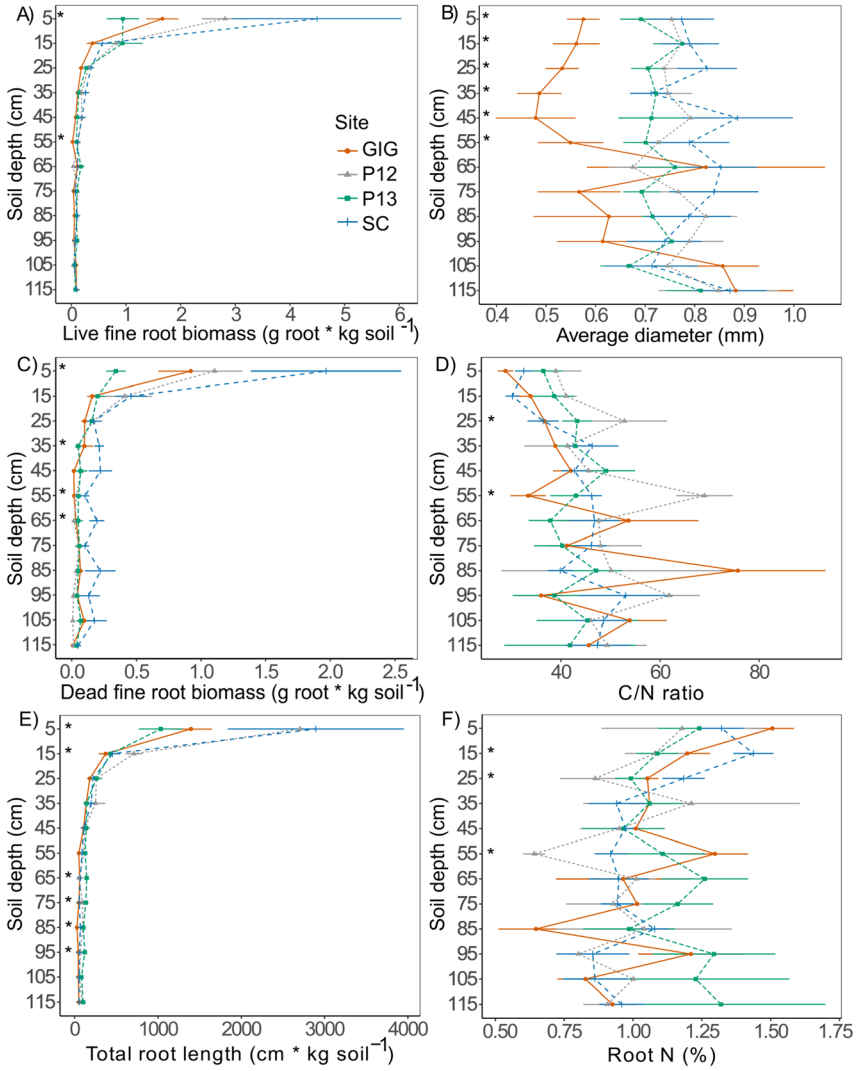

Figure 3. Root characteristics are shown by depth and site where there was a significant depth*site interaction. Soil depth is on the y axis and root characteristic values are on the x axis, with depth increments presented as midpoints of sampled depth intervals (that is: 5 cm for 0–10 cm depth). Asterisks (*) show significant means separation of sites within depths using Tukey's HSD test. Colored symbols and bars give mean ± SE for each site and depth (n = 8 plots per site).

Consistent Depth Effects on Root Characteristics Across Four Tropical Forests

Across all sites, we observed some consistent root patterns with depth, including for coarse and fine root biomass (live and dead), RTD, and AMF colonization, all of which decreased with depth, and SRL and SRA, which increased with depth (Figure 2, Figure SI 1, Table SI 3, Table SI 4). Thus, the relatively small stocks of deeper roots were longer and thinner, less dense, and had less AMF colonization, whereas the larger surface root stocks across the sites were shorter, denser, and had higher AMF colonization (Figure 2, Table SI 4). None of these root characteristics had an interaction of depth*site except live and dead fine root biomass (see below). Thus, these important root biomass, morphological and symbiotic characteristics varied with depth in a consistent manner across these tropical forest sites, regardless of local rainfall and soil fertility.

Interacting Effects of Site and Depth on Tropical Forest Root Characteristics

Another set of root characteristics also varied by depth, but without consistent trends among sites. This group included live and dead fine root biomass, total fine root length per sample, fine root diameter, fine root %N, and fine root C:N ratios, which all had significant site*depth interaction

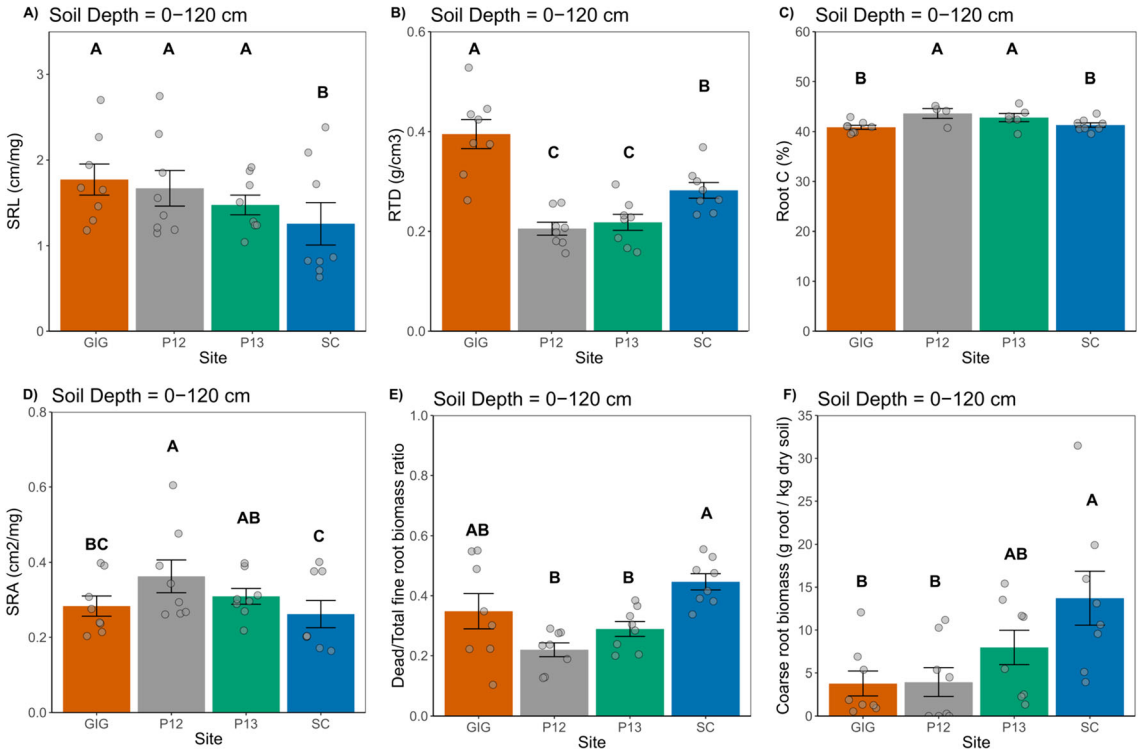

Figure 4. Average values for root characteristics are compared by site for the whole soil profile (0–1.2 m depth), only for root characteristics with no site * depth interactions. Sites are arranged in order of increasing MAP (GIG < [P12, P13] < SC). Data are mean ± SE (n = 8 per site). Letters show differences using Tukey's HSD means separation tests.

Table 3. Root biomass to 1.2 m depths is given as mg/cm^2, Summed for the whole soil profile (0–1.2 m), with means and standard errors (SE, n = 8 plots per site).

Site	Live fine root biomass (mg/cm^2)		Live fine root biomass (mg C/cm^2)		Dead fine root biomass (mg/cm^2)		Coarse fine root biomass (mg/cm^2)		Total biomass (mg/cm^2)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
GIG	34.9 **C**	5.1	14.3 **C**	2.1	19.6 **B**	3.9	64.3 **B**	25.0	118.8 **B**	23.6
P12	67.2 **AB**	6.3	29.3 **AB**	2.8	25.8 **B**	4.7	57.5 **B**	24.2	150.4 **B**	25.5
P13	41.4 **BC**	5.8	17.7 **BC**	2.5	16.9 **B**	1.9	123.1 **AB**	29.5	181.4 **AB**	32.0
SC	73.6 **A**	11.7	30.4 **A**	4.8	54.9 **A**	8.9	193.6 **A**	44.3	322.1 **A**	42.8

Letters give significant differences among sites using Tukey's HSD test. Total biomass values were calculated by summing root biomass across depth increments in grams, then dividing by the soil core surface area (5 cm diameter).

(Figure 3, Tables SI 3, SI 5). Separate regressions for each site for these root characteristics vs depth indicated that live and dead fine root biomass, and total fine root length, all decreased with depth at all sites, but there was significantly less surface fine root biomass and length in the most fertile site (P13) and more in the wettest, most infertile site (SC) (Figure 3, Tables SI 4, SI 5). Fine root diameter generally did not change with depth, except in the driest site, which had significantly smaller surface fine root diameter, which increased with depth (GIG, Figure 3, Table SI 4). Fine root %N generally decreased with depth, while C/N increased with depth, with the strongest changes at the driest and wettest sites (GIG and SC, Figure 3, Table SI 4). Also, variation of %N and C/N ratio across sites occurred mostly at the soil surface with different patterns depending on the depth. For

these characteristics with site*depth interactions, Tukey HSD tests indicated that the largest variation among sites was in surface to mid-depth soils (0–60 cm depth, Figure 3, Table SI 5).

Site-scale Variation in Root Characteristics Among Four Tropical Forests

The root characteristics that varied among the four forests without depth interactions were coarse root biomass, dead/fine root biomass ratio, SRL, SRA, RTD and %C (Figure 4, Table SI 5). Thus, together with the above results, all root characteristics measured in this study varied by site, except AMF colonization (Table 2, Tables SI 3, SI 5). For site-scale differences with no depth interaction, the wettest and most infertile site (SC), which was characterized by the largest surface fine root biomass (live and dead), also had overall more coarse roots, a larger proportion of dead/total fine roots, and generally shorter, thicker roots than other sites (lower SRL and SRA) (Table SI 5, Figures 3, 4). The driest site (GIG) was distinguished by having higher RTD overall (Figure 4, Table SI 5). Fine root %C was also lower in the driest and the wettest sites (GIG and SC) compared to the two mid-rainfall sites (P12 and P13, Figure 4, Tables 2, 3, SI 5).

We also observed a site effect for deep root radiocarbon content, even while other deep root characteristics were generally similar among sites (see cluster analyses below). Specifically, deep root (> 80 cm depth) radiocarbon averages varied significantly among sites (Chi-Square 8.69, DF = 3, $p = 0.03$). The most fertile site had the highest fraction modern and $\Delta^{14}C$ (P13: 1.09 ± 0.04 FM, or $\Delta^{14}C$ 81.62 ± 35.10‰), with the lowest fraction modern and $\Delta^{14}C$ in its paired infertile site (P12: 1.01 ± 0.006 FM, or $\Delta^{14}C$ 3.38 ± 6.66‰), and intermediate values for deep roots in the driest and wettest infertile sites (GIG: 1.05 ± 0.02, or $\Delta^{14}C$ 41.74 ± 24.47‰; SC: 1.04 ± 0.02 FM, or $\Delta^{14}C$ 35.85 ± 16.81‰, Table SI 6). Pairwise Wilcoxon comparisons indicated that the significant difference between sites was driven by P13 (fertile) versus P12 (paired infertile, Z = 2.4, $p = 0.01$). The within-site variation was generally large, except for P12, with overall values ranging from 0.99 to 1.22 FM and $\Delta^{14}C$ − 10.6 to 213.5 ‰, indicating a broad range of deep root ages. Using age conversions for modern radiocarbon values (Reimer and others 2004; Reimer and Reimer, 2024), the site-level

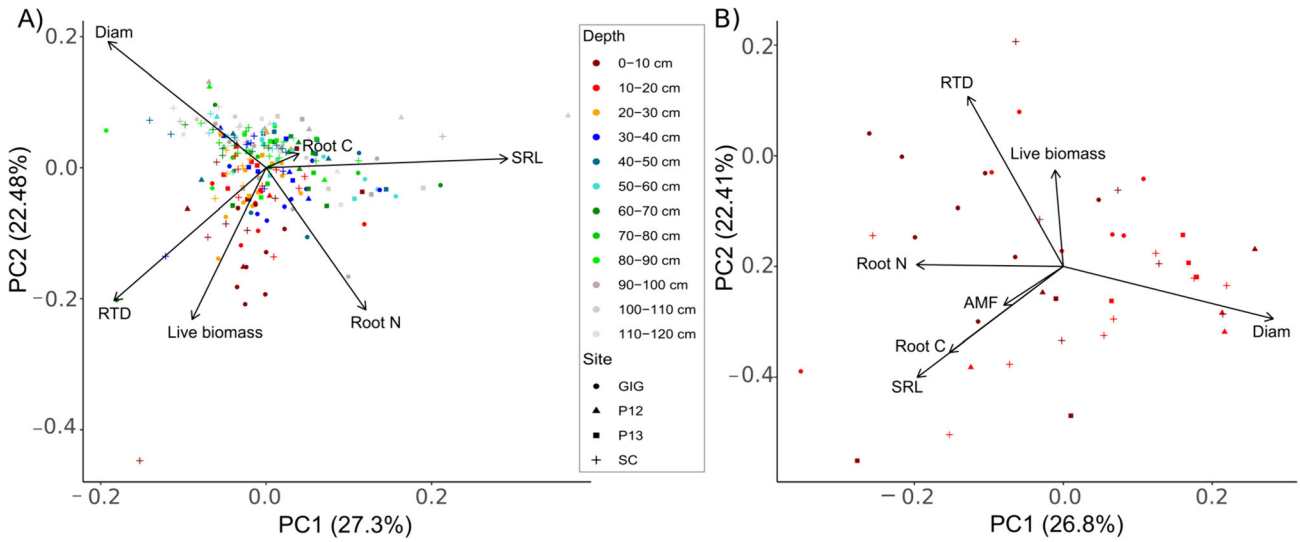

Figure 5. Tradeoffs in root characteristics are shown using principal components analyses (PCA) for 32 plots across four distinct tropical forests, including Gigante (GIG), plot 12 (P12), plot 13 (P13), and Sherman Crane (SC, details in Table 1) to 120 cm depths (10 cm increments shown in different colors). The percent variance explained by each component is shown on the axis. **A** PCA results using root data to 1.2 m depths in 10 cm increments for live fine root biomass (live biomass), specific root length (SRL), root tissue density (RTD), root diameter (Diam), root %N (Root N), and root %C (Root C). This analysis illustrates separation in root traits by depth along axis 2, with shallow roots in particular separating out (brown markers). Axis 1 shows a tradeoff for SRL and root %N versus diameter, RTD, and live root biomass. Root characteristics that were strongly auto-correlated with those shown were not used here (see Tables SI 14, SI 15 for details). **B** PCA results including AMF colonization to 20 cm depth with other characteristics to that depth show that AMF varied in the same direction as SRL and root %C, and AMF did not vary with diameter as had been expected. In this shallow depth analysis, the separation of the two depths is apparent on Axis 1.

averages indicate that deep roots from P12 are constructed from either very recent fixed C (past 5 years), or from C fixed during the 1950s. Values for GIG and SC are slightly older than 5 years, and P13 values suggest they grew from C that was fixed about 20 years ago. The $\delta^{13}C$ of deep roots did not vary among sites (Table SI 6).

The 13C NMR analysis of C functional groups and lignin/N ratios (tissue quality index) in surface live fine roots (0–10 cm) revealed no significant differences across the sites. There were significant differences in the fine root content of different C functional groups. Specifically, O-alkyls, which are indicative of carbohydrates such as cellulose, represented the largest proportion of root C. In contrast, amide + carboxyl C functional groups represented the smallest proportion of root C (Table SI 7).

Cluster Analyses

Cluster analyses of overall separations of root biomass and morphological characteristics among depths or among sites helped clarify where the largest differences in root characteristics were found.

First, clustering by depth revealed that root characteristics differed across depth intervals (Figure SI 2). The MANOVA results confirmed depth as a significant factor, with Hotelling's T-squared test showing distinct differences in 10 cm increments down to 60 cm, after which root characteristics remained relatively constant (Table SI 8). When fine root biomass was excluded from the analysis, surface roots still differed from deeper roots, though the surface layers became more similar to each other, and deeper layers continued to show similarity to each other (Table SI 8). This suggests that fine root biomass plays a key role in distinguishing root characteristics at different depths in the soil profile. Similar cluster analyses by depth conducted for each site separately indicated that the most root variation among surface depth increments was at the driest, infertile site (GIG), where each surface depth increment was unique down to 60 cm depth, whereas in the most fertile site (P13) only the surface 0–10 cm had unique root characteristics relative to the rest of the profile (Figure SI 3, Table SI 8).

Second, clustering by site showed separation among the four forests, with the strongest separation for the driest infertile site (GIG), followed by the wettest infertile site (SC, Figures SI 4, SI 5). The MANOVA results confirmed site as a significant factor (Table SI 9), with Hotelling's tests by depth increment confirming that the most distinct surface root characteristics were in the driest infertile site (GIG), with some separation also for the wettest infertile site (SC, Table SI 10). Similar results were found when considering only morphological variables and excluding fine root biomass (Table SI 11) or when including chemistry data that is not available for all sites and depths (Table SI 12). As indicated above, most variation in root characteristics was for surface soils, and this was where most separation among the sites occurred (Table SI 9; Figures SI 4, SI 5).

Principal Components Analysis of Root Characteristics in Tropical Forests

The first three axes of the PCA for live fine root biomass, SRL, RTD, diameter, %C and %N from 0 to 1.2 m depth explained 27, 22, and 19% of the variation in root characteristics, similar to the PCA axes for just 0–20 cm depth where we could in-

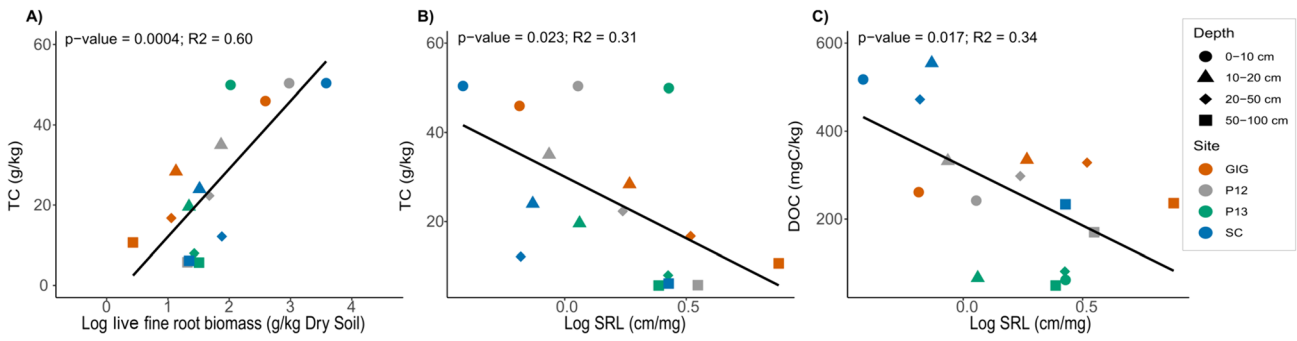

Figure 6. The strongest significant predictors of total soil C (TC) stocks selected using forward stepwise tests (Table SI 19) are shown, including a) live fine root biomass (g/kg-soil), and B) specific root length (SRL, cm/mg). Similarly, the most significant predictor of DOC (mg C/kg-soil) was SRL. One-way regression p values and R^2 are given on each figure, with symbols showing depth increments and colors representing the four forests.

clude AMF colonization (Figure 5, Table SI 13). The PC1 had strong opposite loadings for SRL (0.689) versus fine root diameter (− 0.450), PC2 had strong opposite loadings of fine root diameter (0.454) versus live fine root biomass (− 0.547), and PC3 had strong opposite loadings for RTD (− 0.295) versus root %C (0.737, Figure 5A, Table SI 13). It should be noted that fine root diameter did not load cleanly on either axis and instead showed moderate loadings on both PC1 and PC2, which limits clear inference in relation to diameter alone. For the PCA of 0–20 cm depth with AMF, the axis PC3 had strong opposite loadings for AMF (− 0.616) versus SRL (0.366, Figure 5B, Table SI 13). The PCA that added all root characteristics including auto-correlated factors also gave similar results (Figure SI 6, Tables SI 14, SI 15), as did the PCA with root biomass removed (Figure SI 7, Table SI 16), and the PCA considering root characteristics summed or averaged across the whole soil profile (Figure SI 8, Table SI 17).

We followed PCA with a further exploration of bivariate correlations (Figures SI 9, SI 10, Table SI 15), noting that relationships from PCA did not necessarily match these bivariate relationships. In there analyses, AMF was not significantly correlated with diameter or with any other root characteristics in the bivariate relationships (Figure SI 12).

Root Characteristics as Predictors of Soil C Stocks

Overall, we found that root characteristics were significant predictors of soil C stocks across depth increments. The forward stepwise model with the lowest Akaike Information Criterion (AIC) highlighted that depth, live fine root biomass, and SRL were significant predictors of total soil C (Table SI 19, Figure 6). For extractable dissolved organic C (DOC), SRL was the only significant predictor. Post hoc regressions showed that live fine root biomass was strongly positively correlated to soil C stocks (R^2 = 0.60, Figure 6a, Table SI 19); SRL was negatively correlated with soil C stocks (R^2 = 0.31, Figure 6b, Table SI 19); and SRL was negatively correlated to DOC (R^2 = 0.34, Figure 6c, Table SI 19). Thus, root biomass as well as fine root morphology predicted soil C stocks, with longer, thinner roots associated with smaller soil C and DOC stocks. Complete data shown in Table SI 20.

Discussion

Emergent Patterns in Tropical Forest Fine Root Variation with Depth

We identified emergent patterns of root characteristics with depth across four tropical forests. Our observation that live and dead fine root biomass and coarse root biomass declined with depth was similar to depth distributions identified in other tropical forest studies in Panama (Cusack and Turner 2020), Brazil (Cordeiro and others 2020), Puerto Rico (Yaffar and Norby 2020; Cabugao and others 2021), and more broadly across terrestrial ecosystems (Jackson and others 1996).

More novel here were the other morphological and symbiotic root characteristics that varied with depth consistently across the forests. We observed increased fine root SRL and SRA with depth, and declines in fine root RTD and AMF colonization. Deeper fine roots are more likely formed primarily for water acquisition, since surface soils tend to dry out seasonally in these Panama forests (Cusack and others 2019). Our data suggest that these tropical forests make fewer deep fine roots, and these are comprised of less dense, longer and thinner tissues, suggesting minimal investment for what are likely ephemeral, exploratory roots (Meinzer and others 1999; Andrade and others 2005).

Our consistent increases in SRL at depth across these four tropical forests contrasts with a broad-scale study comparing surface roots (0–20 cm) with deep roots (100–150 cm) across climatic zones (Prieto and others 2015), but agree with results to 3 m depths in a relatively dry Brazilian Eucalyptus plantation (1,360 mm MAP) (Maurice and others 2010) Thus, the increase in SRL with depth might be a property of drier tropical forests, where surface soils have moisture scarcity for prolonged periods.

The decline in RTD with depth that we observed is also indicative of reduced biomass investment per unit root at depth in these forests. Greater fine root RTD represents tissues that can resist desiccation and herbivory (Birouste and others 2014; Freschet and others 2021b), both of which are more prevalent in surface soils in seasonal tropical forests. Higher RTD had been associated with greater content of secondary compounds for protection against root grazers (Xia and others 2021), and a longer root lifespan (Freschet and others 2021b). Thus, this pattern for RTD with depth appears also be an emergent property of seasonal tropical forests, which should be confirmed at a broader set of sites.

Site-Scale Effects on Tropical Forest Root Characteristics

While we observed emergent patterns of root variation with depth across our four forests, some root characteristics varied with depth in certain forests but not in others. Generally, root %N declined with depth and C:N ratios increased, but there was site-scale variation in root chemistry across depths, with this pattern driven by the driest and wettest infertile sites (GIG and SC). This result might reflect the stronger reduction in soil N content with depth in infertile versus fertile Panamanian forests (Cusack and Turner 2020). The results from our infertile sites aligns with findings from Puerto Rican forests to 70 cm depths (Yaffar and Norby 2020) and across broader ecosystem types to 150 cm depths (Prieto and others 2015) which also observed a decrease in root %N with depth. Root %N is not directly linked to root function, and is likely more useful as an indicator of soil nutrient scarcity.

There were also root characteristics that varied among sites, primarily in shallow soils. For example, the most fertile forest had the least surface live and dead fine root biomass (0–10 cm), whereas the wettest, infertile forest had the most.

In terms of morphology, the driest forest had the smallest fine root diameter at 0–60 cm depth, with diameter increasing with depth uniquely in this forest. While root diameter is often related to greater hydraulic conductivity, smaller diameter could also be related to greater moisture uptake as it can reduce the apoplastic barrier for water to enter the xylem (Comas and others 2013).

Also, the driest forest had the highest overall RTD, whereas the wettest forest had the smallest overall SRL (0–120 cm). The greater RTD in the drier forest could help plants to conserve roots by increasing root lifespan, plant mechanical resistance and decreasing plant palatability (Freschet and others 2021b). Somewhat surprisingly, the wettest, most infertile forest had the smallest SRL, indicating, shorter, thicker roots with less exploration potential. This site also had the largest surface root biomass, suggesting that plants may not require high SRL for effective soil exploration due to the greater root mass.

We note that there was a lack of root morphological difference between the most fertile site (P13) versus its paired infertile site (P12), despite the fertile forest having $\sim 4.5 \times$ more soil resin-extractable P and $\sim 8 \times$ more extractable base cations, and our expectation that root morphology would be sensitive to soil fertility (Cusack and others 2021a). Thus, our site-scale differences point toward moisture as a more important influence on tropical forest root morphology.

Our radiocarbon data provided the main difference we observed for deep root characteristics among sites, and presented an interesting difference for the fertile forest versus infertile forests (in addition to less surface root biomass in the fertile forest). The largest deep root radiocarbon values were in the most fertile site (P13), with the lowest values in the paired infertile site (P12), indicating a difference in the average age of deep root biomass stocks. The low values for P12 suggest either very recent fixed C (past five years) or $\sim$ 75 year-old fixed C, depending on which side of the bomb curve the C indicate (that is, before versus after nuclear weapon testing in the 1950s) (Reimer and others 2004; Schuur and others 2016; Reimer and Reimer 2024). In contrast, dates from the fertile forest indicate ages of $\sim$ 20 years. It is most likely that the infertile site deep roots are modern, rather than 75 years old, following a model-data study in three temperate forests indicating deep root ages of 5–13 years (Gaudinski and others 2010). Thus, the fertile forest appears to invest in longer-lived deep roots compared with the infertile forests, possibly supported by the greater resource availability in this site.

In summary, we observed emergent patterns of root variation with depth for some root characteristics (fine root biomass, SRL, SRA, RTD, AMF), but more site-scale variation for other (root N, C/N ratio, diameter). Thus, we observed lower root biomass with thinner and longer roots and lower tissue density at deeper soil layers across forests, but increased root diameter with depth in the driest site.

Therefore, these results partially supported our first hypothesis that there is consistent variation in fine root characteristics with depth across tropical forests, with deeper fine root exhibiting more exploratory morphological traits. Our second hypothesis that variation in fine root characteristics among tropical forests is mainly in the soil surface was fully supported and the variation in these characteristics appeared to be more influenced by changes in moisture than soil fertility.

Panama Forest Fine Root Characteristics in the Context of the Broader Biome

Root Biomass Stocks Across Tropical Forests

Overall, root biomass and trait values in these four Panamanian forests were representative of pub-

lished data across broader seasonal tropical forests. The range of live fine root biomass in the four Panamanian forests from this study to 1.2 m depth (1.64 to 14.08 Mg/ha or 0.67 to 5.82 Mg C/ha) is consistent with data from other seasonal tropical forests. For example, in other Panamanian lowland forests, live root biomass stocks range from 1.14 to 7.70 Mg/ha to 1 m depth (Cusack and others 2018a; Cusack and Turner 2020). In Amazonian forests, live fine biomass ranges from 1.7 Mg C/ha to 6 m depth in a forest with a ~ 6-month dry season (Trumbore and others 2006) to 13.1 Mg/ha to 90 cm depth in a seasonal forest with a ~ 3-month dry season (Cordeiro and others 2020). Additionally, across tropical forests in the Americas, Africa, and Asia, fine root biomass to 30 cm depth ranges from 0.85 Mg C/ha in a wet Malaysian rainforest to 24.29 Mg C/ha in a wet eastern Amazonian forest (Huaraca Huasco and others 2021). Therefore, this study's root biomass values were in the lower range of the broader range observed globally, which extended to much wetter sites and did not go as deep.

Root Morphological, Chemical, and Symbiotic Traits Across Tropical Forests

Our study expanded the available data for tropical forest deep root morphological and chemical traits. Across all sites, plots and depths, SRL ranged from 0.09 to 14.7 cm/mg, SRA from 0.04 to 3.12 cm^2/mg, fine root diameter from 0.28 to 1.44 mm, and RTD from 0.02 to 1.62 g/cm^3. Compared to a global large-scale assessment of 59 tropical forest sites to 30 cm depth, where SRL ranges from 0.74 to 7.93 cm/mg, SRA from 0.079 to 0.879 cm^2/mg, root diameter from 0.2 to 1.8 mm, and RTD from 0.13 to 0.68 g/cm^3, our findings extend the known ranges for SRL, SRA and RTD, but not for root diameter (Addo-Danso and others 2020).

The root chemistry values reported here were similar to other tropical forests. Across all sites, plots and depths, fine roots had a range of 32.81–52.41% C and 0.41–2.05% N in our Panama study. Previous tropical studies to 30 cm depth or from lateral roots at the species level have reported ranges of %C from 20.53 to 63.77 (Hogan and others 2021; Lugli and others 2021), and ranges of %N from 0.4 to 3.95 (Yaffar and Norby, 2020; Hogan and others 2021; Lugli and others 2021), so, the present study is within these ranges. In addition, AMF colonization rates across all sites, plots and at 0–10 and 10–20 cm depths ranged from 0 to 84.44% which is similar to the range of 10.17–80.95% reported in a low-fertility site in the Amazon to 10 cm (Lugli and others 2020), showing that there is great variation in AMF colonization even within similar environmental conditions.

Coordination and Tradeoffs in Tropical Fine Root Characteristics

Tradeoffs in fine root characteristics as suggested by our PCA axis loadings of opposite sign/direction, followed some global patterns (McCormack and Iversen 2019; Bergmann and others 2020), such as a tradeoff between high SRL versus larger fine root diameter, which we observed on PC1. This tradeoff has been suggested to indicate that plants either use an ''outsourcing'' resource acquisition strategy (thicker roots hosting AMF), versus a ''do it yourself'' strategy (longer, thinner, high SRL roots) (Bergmann and others 2020). However, our study only showed a weak and not significant relationship between diameter and AMF colonization, and a weak tradeoff between AMF colonization and SRL. Thus, the SRL-diameter tradeoff might be less related to plant resource acquisition strategy, and could result more from the mathematical relationship between the two metrics (Ostonen and others 2007). While a species-scale study with > 100,000 observations across major vegetated biomes (but with the tropics poorly represented) showed a positive relationship between AMF colonization and root diameter (McCormack and Iversen 2019), a community-scale study in Central Amazonia showed no relationship (Lugli and others 2020). Thus, it cannot be assumed that a tradeoff between SRL versus diameter is necessarily indicative of different resource acquisition strategies at a community-level.

Our data also did not support a posited tradeoff between high RTD as a ''slow'' resource return on investment root strategy, versus high root %N as a ''fast'' turnover root strategy (McCormack and Iversen 2019; Bergmann and others 2020). In some Northern ecosystems, root %N might be indicative of general nutrient scarcity, but our sites have relatively N-rich soils, so this measurement is less meaningful.

We suggest that investigation into plant strategies for soil resource acquisition go beyond these types of simple tradeoff approaches, incorporating broader representation of root structure and function (Cusack and others 2021b; Dallstream and others 2023; Cusack and others 2024).

Relationships of Fine root Characteristics with Soil C Stocks

The positive relationship we observed between root biomass stocks and soil C stocks follows broader-scale patterns across 50 forest plots on the Isthmus of Panama (Cusack and others 2018a; Cusack and Turner 2020), and support the hypothesis that roots provide the primary inputs of new C to mineral soils (Rasse and others 2005). The more novel finding here was that fine root SRL is negatively correlated to soil C stocks and extractable DOC, with SRL adding predictive power in these analyses beyond live root biomass stocks alone. Thus, soil profiles characterized by longer, thinner roots had smaller soil C stocks, whereas soil profiles with larger root biomass stocks had larger soil C stocks. This finding was opposite to our prediction, that higher SRL would promote aggregate formation and C protection from decomposition. There was a negative correlation between SRL and live root biomass across our sites and soil depths, but this relationship was not particularly strong ($R^2 = 0.37$), and the stepwise model building activity identified SRL as the most significant predictor of soil C stocks after live root biomass and soil depth. For extractable DOC, SRL was the single strongest predictor. Here, SRL was also negatively correlated with RTD, indicating that the longer, thinner roots are also likely more labile and easily decomposed. A temperate tree study found that high SRL was correlated to shorter root lifespans (McCormack and others 2012), which could represent a more consistent input of labile C into soils, possibly promoting priming effects and faster overall decomposition of soil C (Fontaine and others 2004; Nottingham and others 2009), primarily in the rhizosphere (Cheng and others 2014). Beyond root biomass, our results and other studies across the literature (Poirier and others 2018) call for further exploration of root morphology and other traits as drivers of soil C storage in tropical forests tropical forests.

Conclusion

This study illustrates emergent properties of root characteristics with depth across four distinct tropical forests. At the same time, the study identifies important differences in some root properties among forests, likely related to soil fertility and moisture. These results support the idea that some root characteristics change consistently with depth in tropical forests, which could provide insight to tropical forest ecosystem strategies. For example, reduced root biomass with depth was accompanied by declines in root tissue density, AMF colonization, and greater SRL, all of which suggest that fewer, less biomass-intensive roots at depth might be used for short-term resource exploration, such as during short dry seasons. The main differences among sites occurred in the soil surface. For example, higher SRL, RTD, and smaller diameter in the driest forest, indicate unique adaptations in this site, potentially to the longer, stronger dry season and lower overall rainfall compared to other sites. These findings could be used to improve representation of dynamic root systems in ecosystem models. A key question for future research is the extent to which tropical forests will be able to adapt root characteristics to rapid changes in climate and resource availability.

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