




Fine-root exploitation strategies differ in tropical old growth and logged-over forests in Ghana

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ABSTRACT

Understanding the changes in root exploitation strategies during post-logging recovery is important for predicting forest productivity and carbon dynamics in tropical forests. We sampled fine (diameter < 2 mm) roots using the soil core method to quantify fine-root biomass and architectural and morphological traits to determine root exploitation strategies in an old growth forest and in a 54-yr-old logged-over forest influenced by similar parent material and climate. Seven root traits were considered: four associated with resource exploitation potential or an ‘extensive’ strategy (fine-root biomass, length, surface area, and volume), and three traits which reflect exploitation efficiency or an ‘intensive’ strategy (specific root area, specific root length, and root tissue density). We found that total fine-root biomass, length, surface area, volume, and fine-root tissue density were higher in the logged-over forest, whereas the old growth forest had higher total specific root length and specific root surface area than the logged-over forest. The results suggest different root exploitation strategies between the forests. Plants in the old growth forest invest root biomass more efficiently to maximize soil volume explored, whereas plants in the logged-over forest increase the spatial distribution of roots resulting in the expansion of the rhizosphere.

Key words: exploitation efficiency; exploitation potential; post-logging recovery; root architectural traits; root morphological traits; root tissue density; specific root length; tropical moist forest.

PLANT ROOTS ARE KEY COMPONENTS OF FOREST ECOSYSTEMS CONSTITUTING ABOUT 20–30 PERCENT OF THE TOTAL BIOMASS (Brunner & Godbold 2007). Roots provide anchorage and are critical for the exploitation of water and nutrients from soil to aboveground tissues (Fitter 2002). In addition, roots play major roles in the cycling and allocation of carbon (C) and nutrients in forest ecosystems (Hobbie *et al.* 2010, Prescott 2010). Between 22 and 75 percent of total forest productivity is allocated to roots and their symbionts (Malhi *et al.* 2011, McCormack *et al.* 2015). This significant flux of C to root systems and their symbionts may influence root biomass, architecture, and morphological patterns (Thaler & Pagès 1998, Bausch & Messier 1999), with associated effects on uptake of soil resources and belowground functioning (Bardgett *et al.* 2014). Plants employ a range of strategies to capture water and nutrient resources and to respond to changes in soil resources, mediated partly by root traits (*i.e.*, biomass, architecture, and morphology) (Ostonsen *et al.* 2007a, Hodge 2009, Paz *et al.* 2015).

Root traits associated with root quantity usually reflect exploitation potential, which relates to the total soil volume used

by plant roots (Berntson 1994, Löhmus *et al.* 2006) as represented by higher quantity and spatial distribution of length, surface area, volume, or biomass of roots in the soil (Löhmus *et al.* 2006, Xiang *et al.* 2013). Plants with a high exploitation potential exhibit an ‘extensive strategy’ (Löhmus *et al.* 2006). The use of this strategy results in expansion of the rhizosphere, which is filled by plant root systems. On the other hand, plants can optimize soil resource uptake by increasing efficiency of fine roots through the adaptation of their morphology such as specific root length (SRL; root length per unit dry mass), specific root area (SRA; root surface area per dry mass), or root tissue density (RTD; root dry mass per volume) (Fitter *et al.* 1991, Bausch & Messier 1999, Löhmus *et al.* 2006). Plants with high exploitation efficiency exhibit an ‘intensive strategy’ with a smaller investment to fine-root biomass (Löhmus *et al.* 2006). Plants that depend on the ‘intensive strategy’ capture soil resources by investing biomass more efficiently and increasing the volume of soil explored per unit biomass with the same C investment (Eissenstat 1991, Fitter *et al.* 1991).

Tropical forest structure and plant species composition change during post-logging recovery (Chazdon 2014, Cazzolla Gatti *et al.* 2015), which may also induce shifts in root dynamics (Leuschner *et al.* 2009, Barbhuiya *et al.* 2012). Most studies that

Received 13 February 2017; revision accepted 9 March 2018.

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have quantified root dynamics during tropical forest succession have focused on fine-root biomass (e.g., Hertel *et al.* 2007, Ibrahim *et al.* 2010, Barbhuiya *et al.* 2012, Gautam & Mandal 2012) and a few fine-root architectural and morphological traits (Hopkins *et al.* 1996, Leuschner *et al.* 2009, Hansson 2014). These studies have mainly reported higher fine-root biomass, but lower values for fine-root morphological traits (SRL and SRA) in old growth (unlogged) forests than in logged-over forests (Hopkins *et al.* 1996, Hertel *et al.* 2003, 2007, Leuschner *et al.* 2009). To determine whether changes in root biomass, architectural, and morphological traits during post-logging recovery reflect a potential shift in soil exploitation strategies of plants, it is necessary to not only compare root traits associated with resource use efficiency, as these studies did, but to also examine traits that depict the potential for resource exploitation. Understanding the changes in root exploitation strategies and the associated trade-offs during succession is important for predicting long-term C dynamics in tropical forests (Fischer *et al.* 2016). For example, it has been proposed that architectural root traits such as root length that are associated with exploitation potential can modify the soil physical environment and enhance soil C storage (Bardgett *et al.* 2014). Morphological traits, such as SRL and RTD, relate to physiological traits such as root respiration, which regulates CO₂ efflux from the soil (Makita *et al.* 2012). These architectural and morphological traits may change when tropical forests are recovering from disturbances (Leuschner *et al.* 2009, Hansson 2014).

In this study, we quantify fine-root biomass, architectural, and morphological traits in an old growth forest and a nearby 54-yr-old logged-over forest, which are influenced by similar parent material and climatic conditions. We considered seven root traits: four associated with resource exploitation potential (biomass, length, surface area, and volume), and three which reflect exploitation efficiency (specific root length, specific root area, and root tissue density). Our objective was to use the fine-root biomass and architectural and morphological traits of fine roots to determine the root exploitation strategies in the old growth and logged-over forests.

METHODS

STUDY SITE.—The study was conducted in the Bobiri Forest Reserve, situated in the Ejisu-Juaben District of the Ashanti Region, in southern Ghana. The Bobiri Forest Reserve (latitude 6°44'N and longitude 1°23'W) covers an area of 5504 ha and lies in the moist semi-deciduous forest zone (Hall & Swaine 1981). The Bobiri forest was demarcated in 1936 and reserved in a pristine, unexploited state in 1939 (Foggie 1947). The reserve lies on gently undulating terrain with a dominant slope of 6–7 percent and altitude between 183 m and 280 m above sea level (asl). The general slope is from northwest to southeast, and six streams flow in this direction to drain the reserve (Foggie 1947). The 10-yr mean monthly minimum and maximum temperatures range between 22.2°C and 31.2°C (Addo-Danso 2017). The mean temperature of the coolest month (August) ranges from 21.8°C to 27.4°C and for the hottest month (February) from 22.4°C to

33.8°C. The 10-yr annual rainfall ranges from 1210 to 1800 mm, with a dry season lasting from December to mid-March (Addo-Danso 2017). The relative humidity averages 55 percent in the afternoon and 85 percent at night.

The Bobiri forest has deeply weathered, well-drained soils with a clay-enriched illuvial subsoil developed on granite (Foggie 1947). The soil has been described as forest ochrosol type (Hall & Swaine 1981), which is the same as Acrisol for the FAO soil classification or Ultisol for the US soil classification system (Adjei-Gyapong & Asiamah 2000, IUSS Working Group WRB 2015). Soil texture varies from sandy loam to clay loam, passing into a gray leached sandy or silty soil in the periodically flooded river valleys, flats, and swamps (Foggie 1947, Adjei-Gyapong & Asiamah 2000). The structure of the forest is typical for a tropical moist forest type, with the upper canopy layer consisting of a mixture of deciduous and evergreen species in approximately equal proportions (Hall & Swaine 1981). Canopy height ranges from 30 to 50 m, with emergent trees up to 60 m tall.

STUDY FORESTS.—The Bobiri Forest Reserve has been compartmentalized and divided into four main blocks based on the designated use: research, butterfly sanctuary, protection old growth forest (strict nature forest), and production forest. Compartments were selected from the old growth forest and research forest for this study. The research forest (hereafter referred to as the 'logged-over' forest) covers an area of 64 ha and had been selectively logged 54 yr earlier (Forestry Department 1958, Djagbletey 2014), but no data exist on the species and volume of wood removed. No logging has been allowed after the first entry, but there is evidence of old tracks in the forest. Prior to logging, part of the forest was placed under the Tropical Shelterwood Silvicultural System in 1955, where lianas and overmature trees, as well as defective trees, were poisoned with sodium arsenite to allow desirable species to regenerate and grow (Forestry Department 1958). The strict nature forest is ca 23 ha and was described as an old growth forest because of certain structural and compositional attributes, including (1) multilayered canopy structure, (2) different gap sizes, (3) an understory composed of both shade-tolerant and shade-intolerant species, (4) large coarse woody debris in all decay stages on the forest floor, and (5) the presence of ferns (Wirth *et al.* 2009, Chazdon 2014, Djagbletey 2014, Addo-Danso 2017). No commercial logging has been allowed in the protection (old growth) forest, but the area may have been influenced by other human activities, which is common in most tropical mature forests (Chazdon 2014). The two study forests were separated by about 3 km, but they were similar in most factors related to energy budget, moisture, and soil fertility. Detailed descriptions of the two forests are provided in Table 1.

ROOT SAMPLING AND PROCESSING.—We sampled roots using the soil core method (Vogt *et al.* 1998). In April 2015 (*i.e.*, early rainfall season), soil samples were taken with a hand-driven soil auger (diameter 5.5-cm) to 30-cm depth in twelve plots (measuring 10 m × 10 m) randomly established across the study forests. Root samples were taken at three randomly located points within

TABLE 1. Site, soil characteristics, and structural characteristics of the two study forests in the Bobiri Forest Reserve in Ghana.

Parameter	Old growth forest	Logged-over forest
Coordinates	6.7°N 1.3'W	6.9°N 1.3'W
Elevation (a.s.l.)	268	276
Aspect	NW	NW
Soil type	Sandy loam	Sandy loam
Sand (%)	59.70 ± 1.85	58.30 ± 2.85
Silt (%)	17.60 ± 3.76	18.10 ± 1.60
Clay (%)	22.70 ± 2.70	23.60 ± 4.36
Bulk density (g/cm ³)	0.66 ± 0.09	0.42 ± 0.06
Organic matter (%)	6.94 ± 0.94	6.79 ± 1.02
Organic C (%)	4.02 ± 0.55	3.94 ± 0.59
Total N (%)	0.40 ± 0.06	0.39 ± 0.07
Available P (Bray) (mg/kg)	18.55 ± 1.76	15.26 ± 1.31
Available K (mg/kg)	120.52 ± 8.96	109.09 ± 8.70
C:N ratio	10.05 ± 0.85	10.10 ± 0.49
K:P ratio	6.50 ± 1.75	7.15 ± 0.37
pH (H ₂ O)	5.60 ± 0.06	5.90 ± 0.03
Base saturation (%)*	89.95 ± 1.74	98.93 ± 0.20
Mean dbh (dbh ≥ 10 cm)	21.50 ± 0.61	19.40 ± 0.43
Mean height (dbh ≥ 10 m)	17.80 ± 1.75	16.50 ± 0.19
Stand density (per ha)	475	755
Basal area (m ² /ha)*	23.07 ± 2.38	30.58 ± 2.38
APAR (%)	92.18 ± 3.07	94.90 ± 0.26

Initials refer to parameters as follows: APAR, absorbed photosynthetically active radiation; asl., above sea level; dbh, diameter at breast height; K, potassium; N, nitrogen; P, phosphorus. Data on stand structural attributes were collected in 2012 (Addo-Danso SD, unpubl. data) and were measured on trees ≥10 cm dbh in twenty-five 20 m × 20 m plots in each forest. Soil physical properties and chemistry were determined in samples collected in February (dry season) and July (wet season) of 2014 (Addo-Danso 2017). Soil was sampled to 30-cm depth in five randomly located positions in each forest.

Values are the mean and standard error (SE) of samples.

*Parameters that significantly differ between study forests ($P < 0.05$).

each plot. Roots were sampled to a 30-cm depth because studies in the tropics, including Ghana, have found that roots are highly concentrated in this layer (e.g., Lawson *et al.* 1970, Metcalfe *et al.* 2008). Hence, we assumed that the selected sampling depth would have a large portion of the total root mass in these forests. During soil sampling, when an obstacle such as a large structural root or stone obstructed the auger, it was relocated within an area of ca. 25 cm² until a suitable core was extracted.

Soil samples ($N = 216$) were kept separate for three depth intervals (0–10, 10–20, and 20–30 cm) and transferred into plastic bags for laboratory processing at the Forestry Research Institute of Ghana, ca 18 km from the study site. Samples were refrigerated at 4°C for 7 days before processing. Samples were soaked in plastic bowls and washed thoroughly using a 0.25-mm sieve to remove soil particles and debris. Collected roots were separated into fine (diameter < 2 mm) roots and into live

(biomass) and dead (necromass) based on visual inspection of morphological features such as color, tensile strength, and cortex and periderm characteristics (Vogt *et al.* 1998, Leuschner *et al.* 2009). Live roots are usually light in color (may not be white), not easily broken, turgid, and the cortex and periderm not easily separated. Dead roots are generally dark or brown, brittle, and shriveled with a non-turgid cortex, although this can be ambiguous when roots are not completely decomposed (Vogt *et al.* 1998). No attempt was made to separate roots into individual species or into trees and understory vegetation.

ROOT BIOMASS, ARCHITECTURE, AND MORPHOLOGY.—We considered seven traits: four associated with resource exploitation potential or ‘extensive strategy’ (fine-root biomass, length, surface area, and volume), and three that reflect exploitation efficiency or ‘intensive strategy’ (specific root area, specific root length, and root tissue density) (Fitter *et al.* 1991, Bauhus & Messier 1999, Löhmus *et al.* 2006, Xiang *et al.* 2013). Higher fine-root biomass, length, surface area, and volume indicate higher exploitation potential. Higher SRA and SRL show a greater dependence on ‘intensive strategy’ (Xiang *et al.* 2013). Composite live root samples were spread in a water-filled, transparent plastic tray and scanned using a high-resolution flatbed Epson Perfection v700 Photo/V750 Pro scanner, USA. Digital images were analyzed using WinRHIZO Basic 2013a software (Régent Instruments Inc., Québec, Canada) to estimate total root length, surface area, and volume. After scanning, root fresh weights were measured and then the roots were oven-dried at 60°C to determine their dry mass. Total fine-root biomass, length, surface area, and volume data were expressed per m² ground surface area. While root length, surface area, and volume were directly determined using the software, root traits, including specific root length (SRL), specific root area (SRA), and root tissue density (RTD), were calculated using the root dry mass and the estimated basic root traits from each core. Specific root length (m/g) in each core was calculated as root length divided by root dry mass, and specific root area (cm²/g) was obtained by dividing the root area by root dry mass (Ostonen *et al.* 2007b, Leuschner *et al.* 2009). Root tissue density (g/cm³) was calculated as root dry mass divided by the root volume (Eissenstat *et al.* 2015).

STATISTICAL ANALYSIS.—We tested fine-root biomass and architectural and morphological traits for normality using a Shapiro–Wilk test. Data were also tested for homogeneity of variance using Levene’s test of equality of error variances. Differences in fine-root traits between the old growth forest and the logged-over forest were tested by multivariate analysis of covariance (MANCOVA) with Bonferroni correction used to adjust for paired comparisons. Basal area was included in the models as a covariate to control for the potential confounding effect of aboveground biomass on root traits. Significant MANCOVA results were subsequently examined using univariate tests to determine which of the root traits contributed significantly to differences. In this analysis, the root trait data for three soil depths (0–10 cm, 10–20 cm, and 20–30 cm) were averaged for a given soil core.

Fine-root biomass and architectural and morphological traits at three soil depths were analyzed for each forest separately using MANCOVA with basal area as the covariate. For each MANCOVA, Wilks' lambda (λ) was used as the multivariate test of significance. All analyses were performed with IBM SPSS Statistics 20 (IBM Corporation, USA) and GraphPad Prism 7 (GraphPad Software, Inc., California, USA).

RESULTS

RELATIONSHIPS AMONG ROOT TRAITS.—Relationships among root traits differed somewhat between the old growth forest and the logged-over forest (Table 2). In the old growth forest, total fine-root biomass correlated positively with total fine-root length and volume, but not total surface area (Table 2). Total fine-root biomass and total RTD were positively correlated, but neither total SRA nor SRL were correlated with total fine-root biomass (Table 2). Total RTD correlated negatively with total SRA, but not total SRL. In the logged-over forest, total fine-root biomass correlated positively with total fine-root length, surface area, and volume. Total fine-root biomass correlated negatively with total SRA and SRL, but not total RTD (Table 2). Total RTD correlated negatively with total SRA and SRL (Table 2).

ROOT BIOMASS, ARCHITECTURAL, AND MORPHOLOGICAL TRAITS IN OLD GROWTH FOREST AND LOGGED-OVER FOREST.—The MANCOVA results revealed a significant effect of forest type on fine-root traits from 0 to 30 cm soil depth, Wilks' $\lambda = 0.521$, $F_{7,16} = 4.38$, $P = 0.011$, partial $\eta^2 = 0.48$. The univariate tests showed that there were significant differences in total fine-root biomass and

architectural traits between the two forests (Table 3). Total fine-root biomass was significantly higher in the logged-over forest than in the old growth forest (Tables 3 and 4). Total fine-root length, surface area, and volume were also significantly higher in the logged-over forest than in the old growth forest (Table 3). Total fine-root volume was 40 percent higher in the logged-over forest than in the old growth forest (Table 4). Although MANCOVA results suggested an overall effect of forest type on root traits, fine-root morphological traits did not differ between the two forests (Tables 3 and 4). For instance, fine-root morphological traits representing exploitation efficiency, including total SRA and SRL, were higher in the old growth forest than in the logged-over forest, but the difference was not significant. Total RTD was higher in the logged-over forest than in the old growth forest; however, the differences were not statistically significant.

ROOT BIOMASS AND ARCHITECTURAL AND MORPHOLOGICAL TRAIT DISTRIBUTION IN SOIL LAYERS.—The MANCOVA results showed significant effect of soil depth in the old growth forest (Wilks' $\lambda = 0.455$, $F_{14,52} = 2.801$, $P = 0.03$, partial $\eta^2 = 0.42$) and logged-over forest (Wilks' $\lambda = 0.288$, $F_{14,52} = 3.21$, $P = 0.01$, partial $\eta^2 = 0.46$). In both forests, total fine-root biomass and architectural traits representing resource exploitation potential (*i.e.*, total fine-root biomass, length, surface area, and volume) declined with soil depth (Tables 5 and 6; Fig. 1A–D). In the old growth forest, fine-root biomass was significantly higher in the upper 10 cm of soil, comprising 53 percent of the total fine-root biomass (Table 5 and Fig. 1A). Total fine-root surface area and volume were significantly higher in the 10 cm soil layer in the old growth forest (Table 5 and Fig. 1B–D). Total fine-root volume declined

TABLE 2. Coefficients of correlation (Pearson product-moment) among fine-root (diameter < 2 mm) biomass, architectural, and morphological traits in the old growth forest and the 54-yr-old logged-over forest.

	Biomass	Length	Surface area	Volume	SRA	SRL	RTD
<i>Old growth forest</i>							
Biomass	1						
Length	0.85***	1					
Surface area	-0.04	0.65*	1				
Volume	0.84***	0.92****	0.72**	1			
SRA	-0.49	-0.11	-0.16	-0.19	1		
SRL	-0.48	-0.1	-0.28	-0.31	0.92****	1	
RTD	0.60*	0.25	-0.03	0.13	-0.62*	-0.46	1
<i>Logged-over forest</i>							
Biomass	1						
Length	0.85***	1					
Surface area	0.88***	0.97****	1				
Volume	0.84***	0.88***	0.97****	1			
SRA	-0.83***	-0.54	-0.52	-0.43	1		
SRL	-0.80**	-0.47	-0.47	-0.41	0.98****	1	
RTD	0.55	0.27	0.22	0.11	-0.84***	-0.78**	1

RTD, root tissue density; SRA, specific root area; SRL, specific root length. Significant differences are denoted as: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

TABLE 3. Univariate results with fine-root (diameter <2 mm) biomass, architectural, and morphological traits from 0 to 30 cm soil depth as dependent variables and the old growth forest and the 54-yr-old logged-over forest as independent variables (Forest type $df = 1$; Error $df = 22$).

Fine-root trait	Sum of squares	F-value	P-value	Partial η^2
Biomass (g/m ³)	15.71	12.65	0.002	0.37
Length (m/m ²)	6443493.57	19.51	<0.0001	0.47
Surface area (m ² /m ²)	12.32	10.79	0.003	0.33
Volume (cm ³ /m ²)	247857.73	12.76	0.002	0.37
SRA (cm ² /g)	82815.70	1.89	0.18	0.08
SRL (m/g)	120.36	0.73	0.40	0.03
RTD (g/cm ³)	0.71	4.95	0.03	0.18

df, degrees of freedom; Partial η^2 , partial eta-squared; RTD, root tissue density; SRA, specific root area; SRL, specific root length.

Significant differences are Bonferroni-corrected as $P < 0.007$.

TABLE 4. Fine-root (diameter <2 mm) biomass, architectural, and morphological traits (mean \pm standard error) from 0 to 30 cm soil depth in the old growth forest and in the 54-yr-old logged-over forest.

Fine-root trait	Old growth forest	Logged-over forest
Biomass (g/m ²)	142.40 \pm 29.46	304.20 \pm 34.67
Length (m/m ²)	1066.00 \pm 102.80	2102.00 \pm 172.60
Surface area (m ² /m ²)	2.20 \pm 0.33	3.63 \pm 0.29
Volume (cm ³ /m ²)	299.20 \pm 41.00	502.40 \pm 39.45
SRA (cm ² /g)	769.70 \pm 54.01	652.20 \pm 51.95
SRL (m/g)	44.75 \pm 3.27	40.27 \pm 3.43
RTD (g/cm ³)	1.12 \pm 0.09	1.46 \pm 0.13

RTD, root tissue density; SRA, specific root area; SRL, specific root length.

from 420.80 cm³/m² in the 0–10 cm layer to 231.70 cm³/m² in the 20–30 cm soil layer (Fig. 1D). In the logged-over forest, total fine-root biomass was highly concentrated in the upper 10 cm of soil, comprising 43 percent of the total fine-root biomass (Fig. 1A). Total fine-root surface area declined with soil depth from 5.57 m²/m² in the uppermost soil layer to 2.55 m²/m² in the 20–30 cm layer. In the old growth forest, SRA and SRL tend to increase with soil depth, but the differences were not significant (Table 5 and Fig. 1E–F). On the other hand, SRL was significantly higher in the lower soil layers in the logged-over forest, ranging from 25.78 m/g in the 0–10 cm soil layer to 5.4 m/g in the 20–30 cm soil layer (Table 6 and Fig. 1F).

DISCUSSION

ROOT BIOMASS AND ARCHITECTURAL AND MORPHOLOGICAL TRAITS IN OLD GROWTH FOREST AND LOGGED-OVER FOREST.—The total fine-root biomass estimates (142.4–304.2 g/m²) were lower than estimates from other tropical moist forests in Ghana (280–1020 g/m², Greenland & Kowal 1960, Lawson *et al.* 1970) and other

TABLE 5. Univariate results with fine-root (diameter <2 mm) biomass, architectural, and morphological traits as dependent variables and soil depth as the independent variable for the old growth forest (Soil depth $df = 2$; Error $df = 32$).

Fine-root trait	Sum of squares	F-value	P-value	Partial η^2
Biomass (g/m ²)	62338.89	2.10	0.006	0.30
Length (m/m ²)	2468880.72	3.65	0.005	0.28
Surface area (m ² /m ²)	10.49	4.55	0.04	0.19
Volume (cm ³ /m ²)	267293.87	5.03	0.005	0.30
SRA (cm ² /g)	173286.96	0.80	0.46	0.05
SRL (m/g)	1274.71	1.67	0.20	0.10
RTD (g/cm ³)	1.01	2.40	0.11	0.13

df, degrees of freedom; Partial η^2 , partial eta-squared; RTD, root tissue density; SRA, specific root area; SRL, specific root length.

Significant differences are Bonferroni-corrected as $P < 0.007$.

TABLE 6. Univariate results with fine-root (diameter <2 mm) biomass, architectural, and morphological traits as dependent variables and soil depth as the independent variable for the 54-yr-old logged-over forest (Soil depth $df = 2$; Error $df = 32$).

Fine-root trait	Sum of squares	F-value	P-value	Partial η^2
Biomass (g/m ²)	872862.50	17.73	<0.0001	0.53
Length (m/m ²)	18199187.45	15.67	<0.0001	0.50
Surface area (m ² /m ²)	68.28	21.54	<0.0001	0.57
Volume (cm ³ /m ²)	1654117.95	25.57	<0.0001	0.62
SRA (cm ² /g)	826273.18	5.29	0.01	0.25
SRL (m/g)	4150.09	6.47	0.004	0.29
RTD (g/cm ³)	1.35	1.45	0.25	0.08

df, degrees of freedom; Partial η^2 , partial eta-squared; SRA, specific root area; SRL, specific root length; RTD, root tissue density.

Significant differences are Bonferroni-corrected as $P < 0.007$.

parts of Africa (170–2420 g/m², Ibrahima *et al.* 2010, Ifo *et al.* 2015). The total fine-root length for the two forests (1066–2102 m/m²) is at the lower end of values reported by studies that compared fine-root architectural traits in mature and logged forests in tropical forests (Table S1). Often, studies that have compared fine-root biomass and architectural and morphological traits in other tropical regions (Table S1) have revealed contrasting dominance of root traits in forests at different recovery stages. Contrary to our findings, comparative studies in the tropics have usually reported higher total fine-root biomass in old growth (unlogged) forests than in logged forests (Hopkins *et al.* 1996, Harteveld *et al.* 2007, Hertel *et al.* 2007, Leuschner *et al.* 2009, Ibrahima *et al.* 2010, Barbhuiya *et al.* 2012, Gautam & Mandal 2012). However, in broad-leaved evergreen subtropical forests in southeast China, Lin *et al.* (2015) reported higher total fine-root (diam. <2 mm) biomass in a 50-yr-old logged forest than in an old growth forest. In terms of fine-root morphological traits, Hansson (2014) reported higher fine-root (diam. <2 mm)

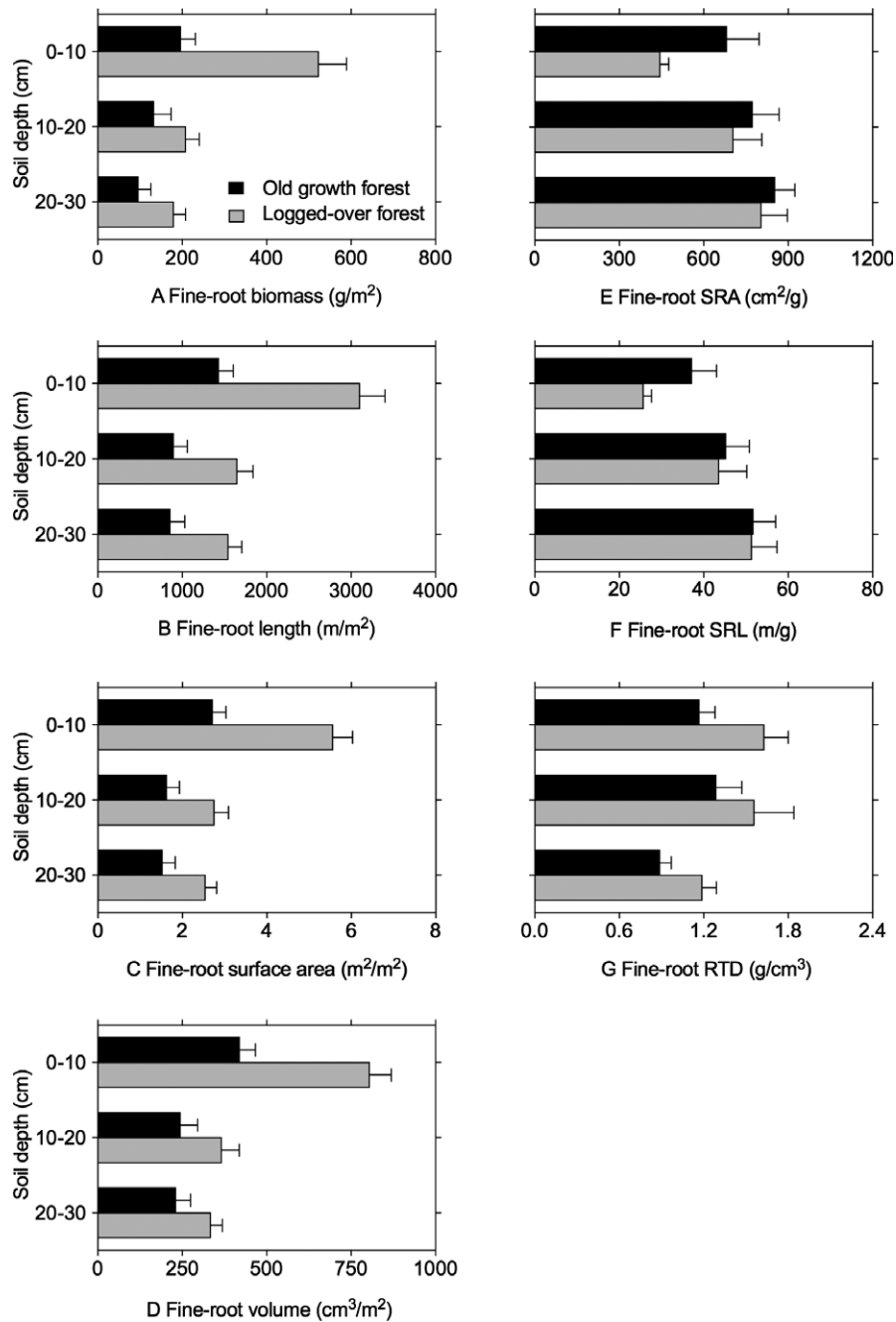


FIGURE 1. Vertical distribution of fine-root biomass, architectural and morphological traits (A–G) in different soil depths ($N = 36$). Data are mean \pm SE for old growth forest (black bars) and 54-year-old logged-over forest (grey bars). SE, standard error; SRA, specific root area; SRL, specific root length; RTD, root tissue density.

RTD in primary montane forests than sites affected by logging and other disturbances in Albertine Rift, Rwanda. Furthermore, Hopkins *et al.* (1996) reported higher total SRL in a selectively logged forest than an old growth forest on a metamorphic soil in North Queensland, Australia. These findings contradict the higher total RTD, but lower total SRL values we observed in the logged-over forest. These mixed results suggest dynamic responses of root traits to different site conditions during post-

disturbance recovery. Differences in sampling methodology, logging intensity, species composition, stand and soil characteristics, and the time elapsed between logging events and studies may also account for the conflicting results in the aforementioned studies (Espeleta & Clark 2007, Hertel *et al.* 2007, Chazdon 2014, Zangaro *et al.* 2008; 2012, Addo-Danso *et al.* 2016).

The differences in total fine-root biomass and architectural and morphological traits in the two forests may be partly

attributable to the species composition and soil factors. The two forests share some common plant species (Djagbletey 2014, Addo-Danso 2017), but certain shade-tolerant species such as *Berlinia confusa*, *Chrysophyllum beguei*, *Craterispermum caudatum*, and *Lecaniodiscus cupanioides* and others were only found in the canopy of the old growth forest (Addo-Danso 2017). Overall, the old growth forest contained 30 percent more shade-tolerant tree species ($\text{dbh} \geq 10$ cm) than the logged-over forest (Addo-Danso 2017). Moreover, stand-level tree wood density was significantly higher in the old growth forest than in the logged-over forest (Addo-Danso 2017). Shade-tolerant (usually late-successional) species with high wood density are slow growing and may have lower nutrient requirements and, therefore, allocate less C to traits such as root length and surface area leading to lower root biomass (Xiang *et al.* 2013). In addition, shade-tolerant species may increase nutrient uptake efficiency by producing roots with high SRL and SRA values (Xiang *et al.* 2013, Paz *et al.* 2015). On the other hand, shade-tolerant species may produce roots of low SRL and SRA as a conservative strategy to coexist with other species (Leuschner *et al.* 2009, Xiang *et al.* 2013, Reich 2014, Zangaro *et al.* 2014), which is inconsistent with our results. Shade-intolerant pioneer or light-demanding species usually have high root length, surface area, and biomass, which allow for the rapid exploitation of soil resources necessary to sustain the high growth rate of such species (Paz *et al.* 2015). Alternatively, shade-intolerant species may produce roots with high root length or surface area per dry mass investment as an adaptation to changes in soil resources after disturbance (Bauhus & Messier 1999, Leuschner *et al.* 2009). Soil properties also influence fine-root biomass and architectural and morphological traits (Braun *et al.* 2005, Metcalfe *et al.* 2008, Leuschner *et al.* 2009, Freschet *et al.* 2017). Although most of the soil physical and chemical properties were similar in the two forests, soil base saturation was higher in the logged-over forest than in the old growth forest (Table 1). Previous studies have reported a close association between soil base saturation and fine-root architectural and morphological traits (Leuschner *et al.* 2004, Braun *et al.* 2005). For example, Braun *et al.* (2005) reported that total fine-root length decreased with decreasing soil base saturation in young (6–20 yr) *Fagus sylvatica* stands in Switzerland. However, Leuschner *et al.* (2009) did not find any correlation between base saturation and total SRA in mature and logged forests in Indonesia.

ROOT BIOMASS AND ARCHITECTURAL AND MORPHOLOGICAL TRAIT DISTRIBUTION IN SOIL LAYERS.—Higher fine-root biomass in the upper soil is a common observation in all forest biomes (Finér *et al.* 2011), and it is thought to be important for nutrient conservation in tropical forests (Cavelier 1992). In agreement with the findings of this study, previous studies have reported that fine-root architectural and morphological root traits change with soil depth (*e.g.*, Hertel *et al.* 2003, Leuschner *et al.* 2009). For instance, Leuschner *et al.* (2009) reported a higher SRA in the 10–20 cm soil layer than in the top 0–10 cm soil layer in a mature forest in Sulawesi, Indonesia. The differences in some of the architectural and morphological traits among the soil depths may be related to

the changes in soil characteristics and resource availability in different soil layers (Ostonen *et al.* 2007a, Freschet *et al.* 2017). Soil organic matter and nutrient concentration decreased, while bulk density increased with soil depth in both forests (Addo-Danso SD, *unpublished data*). Indeed, increased soil bulk density may lead to roots with high SRA (Löhmus *et al.* 1989), reduced root surface area (Jamro *et al.* 2015), and reduced root length in plants (Kormanek *et al.* 2015). The high root length and surface area in the upper 0–10 cm would allow plants to capture the nutrients that are concentrated in that layer, which is particularly important in the tropics where leaching is high. In contrast, the higher SRA and SRL may be an adaptation to the higher soil bulk density in the deeper layers (Löhmus *et al.* 1989, Freschet *et al.* 2017).

ROOT EXPLOITATION STRATEGIES.—The old growth forest appears to produce fewer fine roots (on a forest area basis), as length of fine roots is lower, that have higher absorptive capacity (high total SRA, high total SRL, and low total RTD), whereas the logged-over forest produce more fine roots with greater biomass that are likely to live longer (low total SRA, low total SRL, and high RTD). These different root characteristics suggest an apparent difference in fine-root exploitation strategies in the study forests. Plants in the old growth forest have root traits that may be associated more with resource exploitation efficiency or an ‘intensive’ strategy, while plants in the logged-over forest may follow an ‘extensive’ strategy (Berntson 1994, Löhmus *et al.* 2006, Xiang *et al.* 2013). This is supported by the fact that fine-root biomass per stand basal area was higher in the logged-over forest (99.4 kg/m^2) than in the old growth forest (59.6 kg/m^2), indicating that the old growth forest is functionally more efficient because the same basal area unit in the aboveground is supported by less roots in the belowground. Plants in the old growth forest seem to optimize the capture of soil resources by investing root biomass more efficiently and increasing the volume of soil explored per unit biomass with the same C investment (Eissenstat 1991, Bauhus & Messier 1999). Plants with higher total SRL and total SRA, but lower total RTD, are likely to allocate more C to roots, which increases root proliferation, allowing the capture of more soil resources (Löhmus *et al.* 1989, Eissenstat *et al.* 2015). Indeed, a greater fraction of total net primary production was allocated to fine-root production in the old growth forest than in the logged-over forest (Addo-Danso 2017). On the other hand, plants in the logged-over forest may maximize soil resource uptake by increasing the spatial distribution of roots resulting in the expansion of the rhizosphere. These plants are expected to capture water and nutrients by producing roots that can last longer to conserve soil resources (Reich 2014). The old growth forest contains more shade-tolerant species (Addo-Danso 2017), and therefore, one would expect plants in this forest to exhibit greater conservative root traits (Leuschner *et al.* 2009, Xiang *et al.* 2013, Zangaro *et al.* 2014). This was not the case because studies have shown that old growth forests in Ghana seem to be increasing in proportion of shade-intolerant light-demanding species due to changing environmental conditions, including drought (*e.g.*, Fauset *et al.* 2012). The shift in floristic

species composition could be mirrored in biomass, architectural, and morphological traits of roots.

The contrasting exploitation strategies could alter the processes that affect nutrient cycling and soil C storage in these forest ecosystems (Bardgett *et al.* 2014). The old growth forest produced roots with low total biomass, low total RTD, and high total SRL, which could decompose more quickly (Hobbie *et al.* 2010) and potentially lead to high CO₂ losses (Bardgett *et al.* 2014). On the other hand, fast decomposition may quicken the chemical and microbial transformation of root litter into humus that may persist in the soil (Prescott 2010). The logged-over forest had roots that are likely to live long (low total SRA and SRL; high RTD) and decompose slowly (McCormack *et al.* 2012, Roumet *et al.* 2016), but have limited root growth and transport capacity (Eissenstat *et al.* 2015). The observed differences in root exploitation strategies in the two forests provide future opportunities to link root architectural and morphological traits in tropical forests to processes such as root production, turnover, and decomposition.

CONCLUSIONS

We found differences in total fine-root biomass and some architectural and morphological traits between the old growth and logged-over forests, suggesting that plants in these forests employ divergent fine-root strategies to exploit soil resources. Plants in the old growth forest have root traits that are associated more with increased resource exploitation efficiency or an ‘intensive’ strategy, while plants in the logged-over forest may follow an ‘extensive’ strategy. The different strategies could partly reflect differences in plant species composition and soil factors. We suggest that root systems in these species-diverse tropical forests are modified in response to changing conditions during forest recovery from logging.

ACKNOWLEDGMENTS

This work was supported by the Natural Environment Research Council (NERC) of UK, a University of British Columbia Doctoral Fellowship, a Peter Rennie Memorial Award, Mary and David Macaree Fellowship (Faculty of Forestry, University of British Columbia), and the International Foundation for Science, Stockholm, Sweden, through a grant to Shalom D. Addo-Danso. Writing was supported by a NSERC grant to Cindy E. Prescott. The authors are grateful to the field and laboratory assistants, especially Emmanuel Amponsah Manu, Jonathan Dabo, Afriyie Agyekum, Forzia Ibrahim, Rita Oppong, Martin Lathbridge, Felix Mensah, Ntim Kofi, Bismark Aboagye, and James Boadu. We also thank Mrs. Stella Britwum Acquah for assistance with statistical analysis.

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.c710g76> (Addo-Danso *et al.* 2018).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Fine-root architectural and morphological traits compared in old growth forests and logged/secondary regrowth forests in the tropics.*

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