

A historical and comparative review of 50 years of root data collection in Puerto Rico

Daniela Yaffar^{1,2}  | Richard J. Norby²

¹University of Tennessee, Knoxville, TN, USA

²Environmental Sciences Division, Oak Ridge National Laboratory, Climate Change Science Institute, Knoxville, TN, USA

Correspondence

Daniela Yaffar, University of Tennessee, Knoxville, TN, USA.

Email: danielayaffar@gmail.com

Funding information

U.S. Department of Energy

Associate Editor: Jennifer Powers

Handling Editor: Sabrina Russo

Abstract

Fine roots play an important role in plant nutrition, as well as in carbon, water, and nutrient cycling. Fine roots account for a third of terrestrial net primary production (NPP), and inclusion of their structure and function in global carbon models should improve predictions of ecosystem responses to climate change. However, studies focusing on underground plant components are much less frequent than those on aboveground structure. This is more marked in the tropics, where one-third of the planet's terrestrial NPP is produced. Some tropical forests have been more represented in the literature than others, as demonstrated in the collective studies in Puerto Rico. This Caribbean island's biodiversity, frequency of natural disturbances, ease of access to forests, and long-term plots have created an ideal place for the study of tropical ecological processes. This literature review emphasizes 50 years of root research and patterns revealed around Puerto Rico. The data in this review were compiled from scientific publications, conference reports, symposiums, and raw data shared by some researchers. Emergent patterns include the shallow distribution of fine roots, the great variation in root biomass among different forest types, little variation in root phosphorus concentrations, the slow recovery of root biomass after Hurricane Hugo, and the fact that most data on roots come from the wet tropical Luquillo Experimental Forest, causing other habitat types to be underrepresented. This review also shows the gaps in knowledge about fine roots in the island's ecosystems, which should be used to promote and guide future studies.

Abstract in Spanish is available with online material.

KEYWORDS

fine roots, hurricane, land-use history, luquillo experimental forest, rooting distribution, tropics

This manuscript has been authored by UT-Battelle, LLC, under Contract No. DE-AC05-00OR22725 with the U.S. Department of Energy. The US Government retains and the publisher, by accepting the article for publication, acknowledges that the US Government retains a non-exclusive, paid-up, irrevocable, worldwide license to publish or reproduce the published form of this manuscript, or allow others to do so, for US Government purposes. The Department of Energy will provide public access to these results of federally sponsored research in accordance with the DOE Public Access Plan (<http://energy.gov/downloads/doe-public-access-plan>).

1 | INTRODUCTION

Tree roots are an important carbon sink in plants representing approximately 26% of total plant biomass (Cairns, Brown, Helmer, & Baumgardner, 1997; Malhi, Doughty, & Galbraith, 2011). However, coarse and fine roots are the most poorly understood plant components in terrestrial ecology, which is especially true in the tropics (Comas & Eissenstat, 2009; Pregitzer, 2002). This is problematic because tropical forests are among the most productive ecosystems in the world (Malhi et al., 2011); thus, understanding global carbon cycling requires a thorough understanding of tropical forest components. From the little available data on tropical roots, the forests of Puerto Rico represent a disproportionately large amount relative to its land cover; however, many of these data are not readily available. Here, we assemble and summarize information on root systems from studies on tropical forests in Puerto Rico, including data from Spanish-language publications not previously published in English. We also discuss types of key research questions that could be addressed with these data.

Tree roots are categorized traditionally by their diameter. Roots bigger than 2 mm in diameter are called “coarse roots,” and roots smaller than 2 mm in diameter are often called “fine roots” (Vogt & Persson, 1991). Fine roots can be further divided into adsorptive and transport based on their function related to nutrient and water uptake (Iversen, 2014; McCormack et al., 2015; Pregitzer, 2002). Around 50% of soil respiration and 33% of net primary production (NPP) are attributed to fine roots (Hanson, Edwards, Garten,

& Andrews, 2000; Iversen et al., 2017; Jackson et al., 1996; Kong et al., 2014; McCormack, Adams, Smithwick, & Eissenstat, 2012; McCormack et al., 2015). Yet, despite their importance in plant survival, and global carbon and water cycling, fine roots are poorly represented in data bases and Earth System Models (ESM; Warren et al., 2015). One reason for this knowledge gap is the challenges associated with root sampling, which increase with higher plant diversity and poor infrastructure accessibility as is often the case when working in the tropics (Iversen et al., 2017; Lamanna et al., 2014; Siefert et al., 2015).

Tropical forests account for around a third of terrestrial NPP (Field, Behrenfeld, Randerson, & Falkowski, 1998), yet very little is known about fine-root traits (as defined by Violle et al., 2007) in the tropics compared to temperate forests (Freschet et al., 2017; Iversen et al., 2017). Tropical trees represent around 20% of the data in the Fine-Root Ecology Database (FRED) (Iversen et al., 2017), from which 4% is from Puerto Rico (Iversen et al., 2017). In this review, we will first discuss the source of root data in relation to the geography and land-use history of Puerto Rico. We then describe the sources of data from the published literature and present the results of analyses organized by the root trait categories of FRED (Iversen et al., 2017). We conclude with a discussion on root responses to environmental change and future research priorities.

PUERTO RICO AS A TROPICAL RESEARCH SITE.—Puerto Rico is a Caribbean archipelago located within the geographic zone of the tropics (Figure 1). Puerto Rico has a high diversity of ecosystems

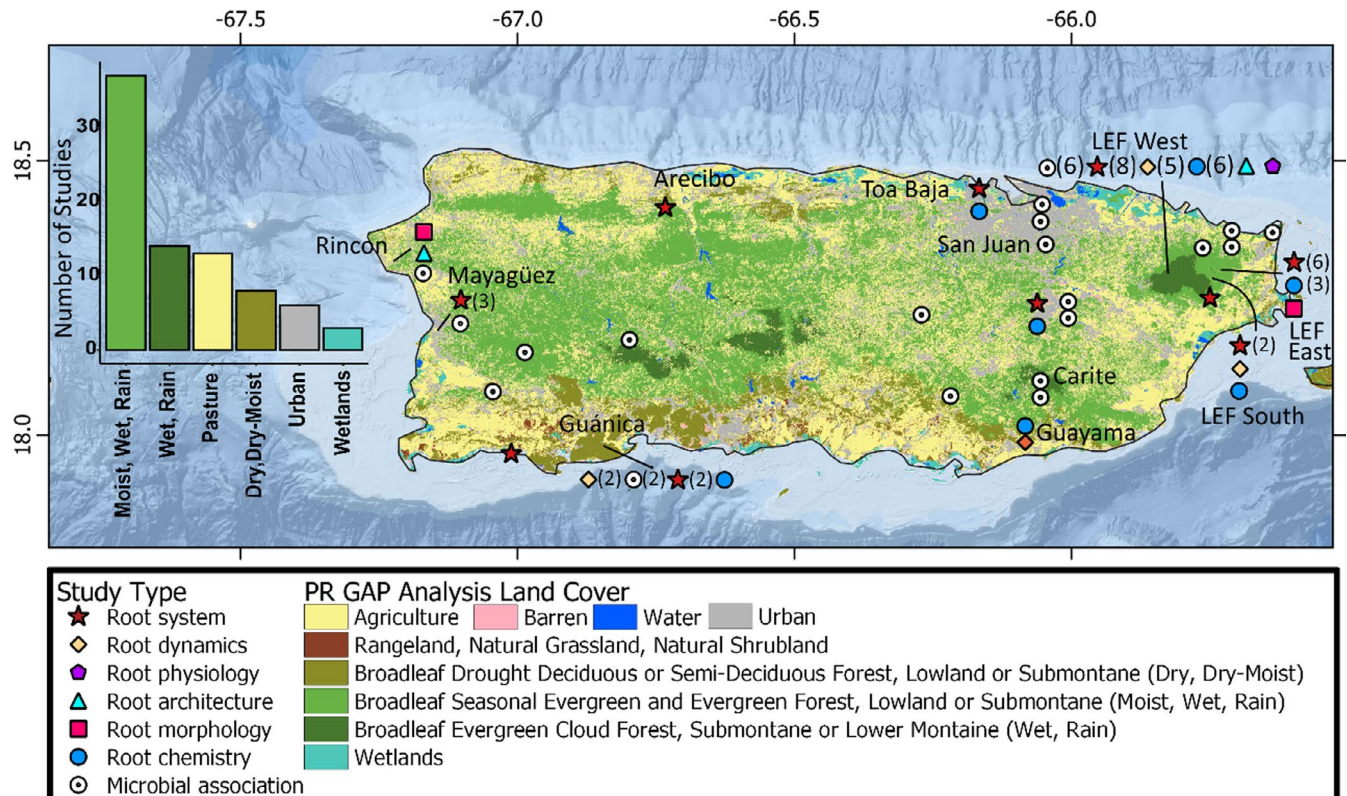


FIGURE 1 Map of the land cover of Puerto Rico from the USDA Gap Analysis Project (<https://www.treesearch.fs.fed.us/pubs/38430/>), showing where study sites were located. Symbols represent root traits according to FRED classification. The bar plot shows the number of studies per site

(Harris 2012), and 10 of the 12 world orders of soils. The mean annual precipitation, air temperature, and elevation range from 254 to 5,000 mm/year, 18–30°C, and from sea level to 1,338 m a.s.l., respectively (Frangi & Lugo, 1985; Miller & Lugo, 2009a; Murphy & Lugo, 1986a). According to the life zones of Holdridge, Puerto Rico's forests are considered "sub-tropical" (Ewel & Whitmore, 1973). However, according to the climate classification of Köppen-Geiger, Trewartha, and Walter's zonobiomes, these forests are "tropical."

Up until the 1940s, more than 90% of today's Puerto Rican forests were agricultural fields. Beginning in the 1960s, most of these lands were abandoned following a transition of the island's economy from agricultural to industrial (Edel, 1962; Miller & Lugo, 2009a), allowing the unmanaged reforestation of the island (Miller & Lugo, 2009b). Currently, more than 60% of Puerto Rico is covered by forests (Brandeis & Turner 2013).

Puerto Rico has a diverse fauna and flora that are greatly shaped by hurricane events on this island, which represent the greatest non-anthropogenic disturbance. The combination of the biological diversity, tropical climate, resilience to natural disturbances, and easy access to forest study areas makes Puerto Rico an ideal tropical island for scientific studies. This is especially true for the Luquillo Experimental Forest (LEF), which has been managed by the USDA Forest Service (Forestry Division) and their antecedents since 1898.

2 | DATA SOURCES AND ANALYSIS

We assembled source material using Google Scholar, Web of Science, and Scopus for English-language reports, and Google Scholar for studies in Spanish. We looked at all papers returned when searching for the key words: "root", "belowground", "plant", and "Puerto Rico" in English, and "raíz", "raíces", "planta", "Puerto Rico", "suelos" or "suelo", "árbol" or "árboles" in Spanish. Dr. Ariel Lugo, director of the International Institute of Tropical Forestry—Puerto Rico, provided raw data from Frangi and Lugo (1985), Murphy and Lugo (1986a), Cuevas, Brown, and Lugo (1991), and Lugo (1992). Molina Colón and Lugo (2006) and Teh, Silver, and Scatena (2009) also provided raw data for this review. Our data base contains 1,091 records from 46 studies, from which eight studies are in Spanish (Yaffar, Lugo, Cuevas, Silver, & Molina Colón, 2019).

To compare Puerto Rico's data with other tropical and global studies, we used data from FRED (Fine-Root Ecology Database Version 2, <https://root.ornl.gov>). To compare root biomass by depth in both dry and wet forests, we defined fine roots as all roots less than or equal to 2 mm in diameter. When a study involved experimental manipulations, we used only the control data for biomass and chemistry comparisons. We modeled root vertical distribution based on Gale and Grigal (1987) asymptotic equation $Y = 1 - \beta^d$, where d is depth, Y is the proportion of roots from the surface to depth d , and β is the numerical index of rooting

distribution (Jackson et al., 1996). High values of β represent deeper rooting. For this, we used cumulative fraction of biomass for all studies that classified root biomass by depth, including fine roots and mixed roots. We calculated the β for only the studies in which root biomass reached 70 cm or more, and we compared it with the β when using all the studies regardless of the maximum depth.

To compare root:shoot ratio, we used data that were collected using the destructive method (whole-tree sampling) and reported both belowground (fine + coarse roots) and aboveground biomass at the record level (trunk + branches + leaves) from species with at least three individuals. We calculated root:shoot ratio by dividing belowground biomass by aboveground biomass from each species. To compare Puerto Rico root:shoot ratio data with global meta-analyses from Cairns et al. (1997) and Mokany, Raison, and Prokushkin (2006), we used the same formula as their methods: root biomass = $\exp(-1.0850 + (0.9256 \times \ln(\text{shoot biomass})))$ and root biomass = $0.18 \times \text{shoot biomass}$, respectively.

All statistical analyses were performed in R studio (RStudio Team, 2016). We used logarithmic regressions to compare root biomass and root nutrient concentrations with depth. We performed simple linear regressions to compare root versus shoot biomass, soil versus root N and P, and fine-root biomass versus soil N. We used an ANOVA to compare root:shoot ratio among species, and N and P among species. We performed an ANCOVA to test the effect of tree bole diameter (>5 cm and <5 cm) and model source (i.e., meta-analyses) on the slope of our data regression. We ran multiple regressions between root biomass, depth, and mean annual precipitation from the book "Los Bosques de Puerto Rico" to find the best correlate of root biomass.

3 | THE STORY OF "ROOT DIGGING" IN PUERTO RICO

For scientific purposes, root descriptions from Puerto Rico have been documented since the 1940s. Most of these studies encompass qualitative descriptions of roots (LaRue, 1952; White & Childers, 1945). From 1962 on, the study of roots became more quantitative. In 1967, began a study on the structure and function of various ecological compartments in LEF, including roots. The book that resulted from this study (Odum & Pigeon, 1970), particularly chapters by Odum and Ovington & Olson, reported root biomass, nutrient concentrations, and morphology of 42 species in LEF. However, this work classified fine roots as <5 mm in diameter, making it difficult to compare with recent studies that focused on a narrower definition of fine roots (<2 mm).

Following these studies, others have reported root biomass and nutrient concentration as part of their measurements in Puerto Rico (Figure 1). Most studies were based in LEF, including the tabonuco forest (dominated by *Dacryodes excelsa*; Kangas, 1992; Bloomfield, Vogt, & Vogt, 1993; Cusack, Silver, Torn, & McDowell, 2011), the Sierra Palm forest (dominated by *Prestoea montana*; Frangi & Lugo,

1985), the Colorado forest (dominated by *Cyrilla racemiflora*; Cusack et al., 2011), and the elfin forest (dominated by *Tabebuia rigida*; Cordero, 1999). The most studied species from these forests that included belowground measurements were *D. excelsa*, *Cecropia schreberiana*, and *Manilkara bidentata*, from which only *C. schreberiana* is within the 10 species with greatest importance value on the island (Marcano Vega, 2019). The species with greatest importance value of Puerto Rico, *Spathodea campanulata* and *Guarea guidonea*, are underrepresented in these studies. The dry forest biome in general has less representation of root studies in Puerto Rico (Molina Colón & Lugo, 2006; Cusack, Chou, Yang, Harmon, & Silver, 2009; Murphy & Lugo, 1986a, 1986b). No whole-tree excavation was performed in forests outside of the LEF; thus, dry forest species (e.g., *Leucaena leucocephala*) are underrepresented for underground studies. Even fewer studies have measured roots in other ecosystems of the island (Parrotta, 1999; Viera Martínez et al., 2008; Marin-Spiotta, Silver, Swanston, & Ostertag, 2009; Ostertag, Marín-Spiotta, Silver, & Schulten, 2008; Lugo et al., 2011).

From all the studies considered here, 18% focused primarily on roots; the rest included roots as a secondary measurement. Following the FRED classification of fine-root traits (McCormack et al., 2017), 25 studies considered in this review measured root system traits, 13 measured chemical traits, nine studied root dynamics, six looked at microbial association, four measured root physiology, two measured root architecture and morphology, and none studied anatomical traits (Figure 1). Here, we summarize these studies, assigning them by the different root traits categories of FRED.

4 | ROOT SYSTEM

4.1 | Root biomass

Fine-root classification varied among the studies that measured fine-root biomass, making it difficult to synthesize across results. Ovington and Olson (1970) reported, using whole-tree removal method, an average biomass of 64.8 Mg/ha for coarse roots only (described as more than 5 mm in diameter), and Odum (1970a) reported 3.52 Mg/ha for small roots (described as <5 mm in diameter). Together, coarse and fine roots represent 25% of total tree biomass from these studies. Golley, Odum, and Wilson (1962) measured root biomass (fine + coarse) from a red mangrove (*Rhizophora mangle*) forest on the southern shores of Puerto Rico. Prop-root (adventitious aerial roots) biomass was taken by whole-tree removal; the total prop-root biomass was 14.37 Mg/ha. Fine roots (<5–10 mm in diameter) plus peat and coarse roots (>2 cm in diameter) were taken by cores and weighed 40 and 9.97 Mg/ha, respectively. Coarse root biomass is less than that reported by Ovington and Olson (1970) in the LEF, which may reflect differences in vegetation, root diameter classification, and the method of collection. Prop and coarse roots represent 46% of total tree biomass, which is more than in Ovington and Olson (1970). Although the diameter selected in this study for fine roots (5–10 mm) is greater than the rest of the studies presented

in this review, and the biomass included peat biomass, we can nevertheless conclude that mangroves present especially high fine-root biomass in Puerto Rico. Frangi and Lugo (1985) found that in a primary wet palm forest at LEF, total root biomass was 61.7 Mg/ha up to 95 cm deep, which represents 21.5% of total tree biomass, similar to what Ovington and Olson (1970) showed. Total root biomass was also obtained by using the coring method. Fine-root biomass (<1 mm) was 24.6 Mg/ha within 30 cm of depth and 27.2 Mg/ha at 95 cm of depth.

In the book “Los Bosques de Puerto Rico” (Lugo, 1983), seven studies reported root biomass by depth but not by species or diameter classification (Table S1). The variability in plant composition, precipitation, and soil type made root biomass distribution variable as well. We performed multiple regressions between root biomass, depth, and mean annual precipitation, but no pattern was found. The floodplain in Patillas (Alvarez, Quevedo, & Blay, 1983) has the highest root biomass in the book (35.5 Mg/ha), which could be related to the species composition (mangrove forest), high organic material accumulated in that horizon, and the anoxic conditions. This biomass is 15 Mg/ha less than the one reported by Golley et al. (1962), who included peat in the biomass calculations. The lowest root biomass was from a mature forest in Maricao with 6.27 Mg/ha in 30 cm of depth (Rivera, Toro, & Gómez, 1983) where the soils were very dry and poor in calcium (Whittaker, 1954).

In the 1990s, more studies began to consider fine roots following the “less than 2 mm in diameter” classification and using coring methods instead of total tree removal. Lugo (1992) reported 2.4 Mg/ha of fine-root biomass (<1 mm diameter) within 30 cm of depth in the tabonuco mature forest at LEF, which is around 10% of what was reported by Frangi and Lugo (1985). McGorddy and Silver (2000) found that fine-root biomass decreased in an elevation gradient at LEF (from 4.7 Mg/ha at 1,000 m.a.s.l to 1.5 Mg/ha at 180 m.a.s.l, in 10 cm of depth). For a secondary forest in LEF, Cuevas et al. (1991) and Lugo (1992) measured 3.6 Mg/ha of fine-root biomass (<2 mm diameter, to 30 cm depth) and 2.7 Mg/ha (<1 mm diameter, to 20 cm depth), respectively, which are slightly greater than the reported for a mature forest (2.4 Mg/ha; Lugo, 1992).

Fine-root biomass in a pine plantation in LEF was 0.7 Mg/ha (Cuevas et al., 1991) and 0.9 Mg/ha (Lugo, 1992). A mahogany (*Swietenia macrophylla*) plantation in LEF had an average fine-root biomass of 1.1 Mg/ha (Lugo, 1991), which is similar to the pine plantation and less than the secondary forest. Fine-root biomass (<1 mm) in this same study represents on average around 20% of total root biomass, and total root biomass did not exceed 20.6 Mg/ha (Lugo, 1992), which is a third of what Ovington and Olson (1970) reported.

In a dry mature forest, Murphy and Lugo (1986a) measured a total fine-root biomass (<1 mm diameter) of 1.5 Mg/ha up to a depth of 100 cm, and 1.25 Mg/ha up to 30 cm of depth, which is less than in the wet mature forest (Frangi & Lugo, 1985; Lugo, 1992). Total root biomass was also less than what Ovington and Olson (1970), and Frangi and Lugo (1985) reported for the wet mature forest 45 Mg/ha, but higher than the secondary forests and plantations (Lugo, 1992).

Molina Colón and Lugo (2006) reported a fine-root biomass (<2 mm diameter) of 5.39 Mg/ha at only 10 cm of depth in a dry mature forest, which is more than three times higher than Murphy and Lugo (1986a). The difference in fine-root biomass between Murphy and Lugo (1986a) and Molina Colón and Lugo (2006) might be explained by the root diameter size and the depth of collection.

Fine-root biomass from different land uses in the dry forest of Puerto Rico was also reported by Molina Colón and Lugo (2006). In the previous land-use types of former human settlements (houses), a baseball park, an agricultural field, and a charcoal production area, fine-root biomass was 0.2, 0.3, 0.28, and 0.47 Mg/ha of fine roots, respectively. These urban forests had less root biomass in the top 10 cm than any other site of the island.

4.2 | Vertical root distribution

Studies that have separated root data by different soil depth layers show a declining fine-root biomass with depth. This pattern is clear for both, wet and dry forests of Puerto Rico (Figure 2a,b). Data points taken by Molina Colón and Lugo (2006) and Murphy and Lugo (1986a) from the dry forest show less root biomass than in the rain forest.

The vertical root distribution of the dry forest of Puerto Rico is slightly deeper than the wet forest, based on the beta coefficient (Gale & Grigal, 1987; Jackson et al., 1996). However, Puerto Rico's rooting distribution is shallower than other tropical evergreen forests globally. On average, a tropical evergreen forest has a beta of 0.96–0.97 (Jackson et al., 1996; Schenk & Jackson, 2002), whereas beta in the wet tropical forest of Puerto Rico is 0.90 and 0.91 in the dry forest (Figure 3). A smaller beta value describes a greater proportion of roots closer to the soil surface. We obtained similar beta when we only used studies with depths greater than 70 cm (Frangi & Lugo, 1985; Lugo, 1992; Murphy & Lugo, 1986a). Although we need more studies that consider deeper sampling, we can conclude that more than 80% of root biomass in the island is in the first 20 cm of depth. Further, Odum (1970b) study showed that less than 1% of roots were found deeper than 80 cm at LEF.

4.3 | Root: shoot ratio

Some studies reported on belowground and aboveground biomass of common species by removing whole trees from seedlings to adult trees up to 35 cm in diameter (Cordero, 1999; Fetcher et al., 1996; Ovington & Olson, 1970; Parrotta, 1999; Stone, Plante, & Casper, 2013). Ovington and Olson (1970) studied total below- and aboveground biomass of 42 species in LEF. Fetcher et al. (1996) measured below- and aboveground biomass from two pioneer species (*Phytolacca rivinoides*, *C. schreberiana*) and two non-pioneer species (*P. riparia*, *M. bidentata*) in LEF under fertilization treatments. Cordero (1999) reported root biomass of *C. schreberiana* in the elfin forest of LEF from an experiment looking at wind exposure on plant form.

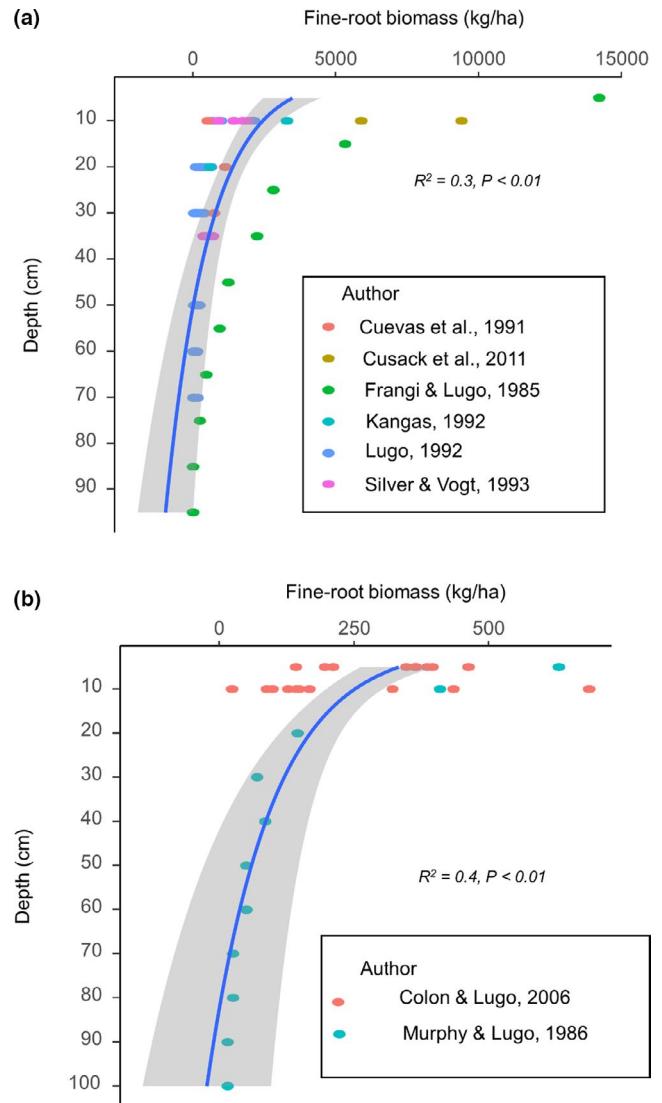


FIGURE 2 Logarithmic regression of root biomass in kg/ha by depth in (a) a wet forest and (b) a dry forest (studies are represented by authors, which are organized by colors)

Parrotta (1999) describes root biomass from *Casuarina equisetifolia*, *Eucalyptus robusta*, and *L. leucocephala* from experimental plantations at Toa Baja. Stone et al. (2013) measured above- and belowground biomass of *Tabebuia heterophylla* planted in a greenhouse with soil from LEF and different fertilization treatments. We used these data (with no treatment) to compare root:shoot ratio among species.

On average using all diameter roots, the root:shoot ratio from these studies is 0.45, ranging from 0.78 in *C. schreberiana* to 0.19 in *Ocotea leucoxylon*, but variation within species was large, and there was no statistically significant difference among species. Root:shoot ratio is greater in trees with bole diameter >5 cm ($p < .01$) compared to smaller trees (diameter <5 cm). However, we also found no differences among species within each size category. *C. borinquensis* and *C. schreberiana* have the highest root shoot ratio for the trees >5 cm in diameter, and *S. berteriana* has the lowest root shoot ratio in this size class. However, *S. berteriana* has the highest root:shoot ratio for trees <5 cm in diameter, and *O. leucoxylon* has the lowest

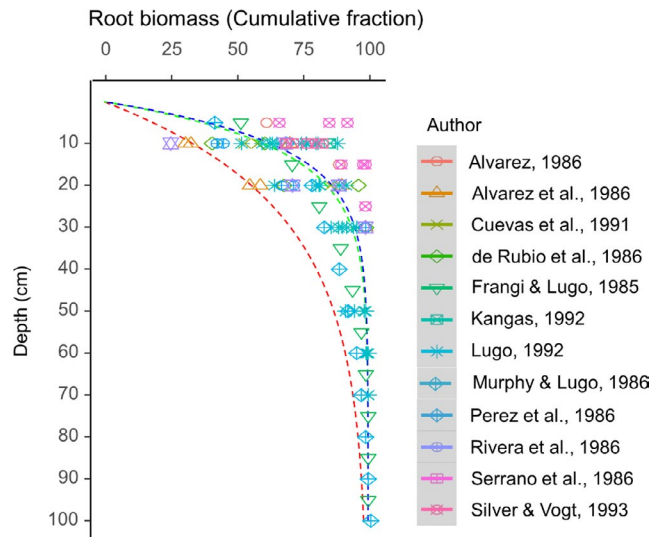


FIGURE 3 Comparison between the vertical rooting distribution of studies in Puerto Rico from wet forests (blue line), dry forests (green line), and the generalized beta distribution of the tropics (Jackson et al., 1996; red line)

ratio. Thus, we can conclude that tree diameter plays an important role in root:shoot ratio.

The root versus shoot biomass regression for trees of all diameters shows a significant difference ($p < .05$) of the slopes between our model and the models reported in two meta-analyses for tropical evergreen forests (Cairns et al., 1997; Mokany et al., 2006; Figure 4). Trees >5 cm diameter have greater root biomass than predicted in the two global meta-analyses (Cairns et al., 1997; Mokany et al., 2006), and trees <5 cm diameter have a shallower slope than that of the larger trees (Figure 4). These meta-analyses considered more samples from around the world and a wider range of tree size class. However, these studies also used root data from different methods of collection, such as soil cores for fine roots, whole-tree excavation (direct), and/or tree diameter (allometry: indirect), which could lead to the differences of total root biomass compared to using whole large tree excavation only (Waring & Powers, 2017).

5 | ROOT CHEMISTRY

A few studies measured root nitrogen (N) and phosphorus (P) concentrations in Puerto Rico, one of which (Pett-Ridge & Silver, 2002) did not consider tree roots and was thus dropped from the analysis. Some authors reported N and P from only fine roots (Cuevas et al., 1991; Lugo, 1992; Murphy & Lugo, 1986a; Parrotta, 1999; Scatena, Silver, Siccama, Johnson, & Sanchez, 1993), whereas others reported from a mixed sample of fine and coarse roots (Lugo et al., 2011; Ovington & Olson, 1970). Only Parrotta (1999), Lugo et al. (2011), and Ovington & Olson (1970) reported root nutrient concentration by species. The rest of the studies used coring methods, and root nutrient concentration was not species-specific

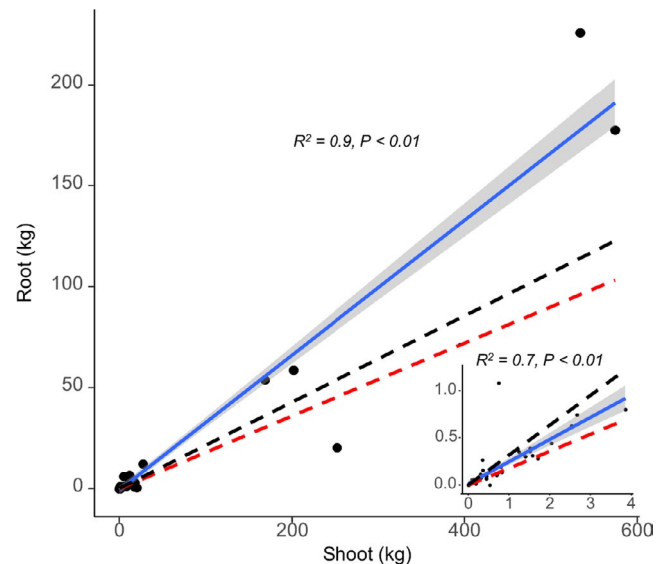


FIGURE 4 Linear correlation between root and shoot biomass from Puerto Rico data in blue, a worldwide meta-analysis (Cairns et al., 1997) in black, and another global meta-analysis only for forests (excluding shrublands, grasslands, Mokany et al., 2006) in red. The large graph shows all trees collected with various bole diameters, and the inset graph shows the correlation using only trees <5 cm bole diameter

(Table S2). We compared these data separately based on the method of collection. Nevertheless, considering that root nutrient concentration changes with root diameter (Iversen, Ledford, & Norby, 2008; Jia, Wang, Li, Zhang, & McLaughlin, 2011; Luse, 1970; Xia, Guo, & Pregitzer, 2010), soil nutrient availability (Gower, 1987; Li et al., 2015; Vogt et al., 1995), and whether the tree is an N-fixer (Valverde-Barrantes, Raich, & Russell, 2007), this comparison can suggest only broad patterns.

From the studies that used the coring methods, Cuevas et al. (1991) and Lugo (1992) reported very similar P (0.03%) and N (0.6%–0.8%) concentrations in fine roots (<2 mm) from a pine plantation and its adjacent secondary forest (Table S2). However, fine-root N and P concentrations were higher in the mahogany plantation (0.06% P, 1.0% N) and its adjacent secondary forest (0.06% P, 1.3% N; Lugo, 1992; Table S2). Scatena et al. (1993) showed similar P concentration (0.05%) but higher N concentration (1.57%) for fine roots (<5 mm in diameter) in a mature forest of Bisley, LEF (Table S2). Silver & Vogt (1993) found even higher fine-root N concentration (1.8%) in the same forest of Bisley, but still similar P concentration (0.05%; Table S2). In the dry forest, Murphy and Lugo (1986a) reported similar P and N concentrations to what was found for Bisley (0.06% and 1.4%, respectively; root diameter <1 mm; Table S2). Both fine-root N (Figure 5a) and fine-root P (Figure 5b) concentrations decrease exponentially with depth.

Fine roots reported in Puerto Rico have a similar range in root N concentration compared to other species from the tropics, ranging from 0.3% to 1.9% (Collins, Wright, & Wurzbarger, 2016; Gijsman, Alarcón, & Thomas, 1997). Gijsman et al. (1997) reported N

concentration in fine roots (<2 mm) from Panamá (1.25%), which is higher than the average for roots less than 2 mm in Puerto Rico (0.9% N). The lowest root N concentration is from the pine plantation and secondary forest of Guzmán, which skewed the total root N average. Puerto Rico has a slightly lower mean P concentration (0.04%) compared to other studies. A study in Barro Colorado, Panamá (Collins et al., 2016), and a study in Maui-Hawaii (Schuur, 2001) reported a P average for roots <2 mm in diameter of 0.06 and 0.05%, respectively. However, the average root P concentration in Puerto Rico is highly influenced by the low P concentration in the pine plantation. Further,

species composition plays an important role in fine-root nutrient concentrations, as well as root diameter, and soil nutrient availability as reported in other studies (Gordon & Jackson, 2000; Iversen et al., 2008; Jia et al., 2011; Li et al., 2015; Luse, 1970; Valverde-Barrantes et al., 2007; Xia et al., 2010).

Using available data for root nutrient concentration where species identity was known and tree diameters varied (Lugo et al., 2011; Ovington & Olson, 1970; Parrotta, 1999), we found that there is

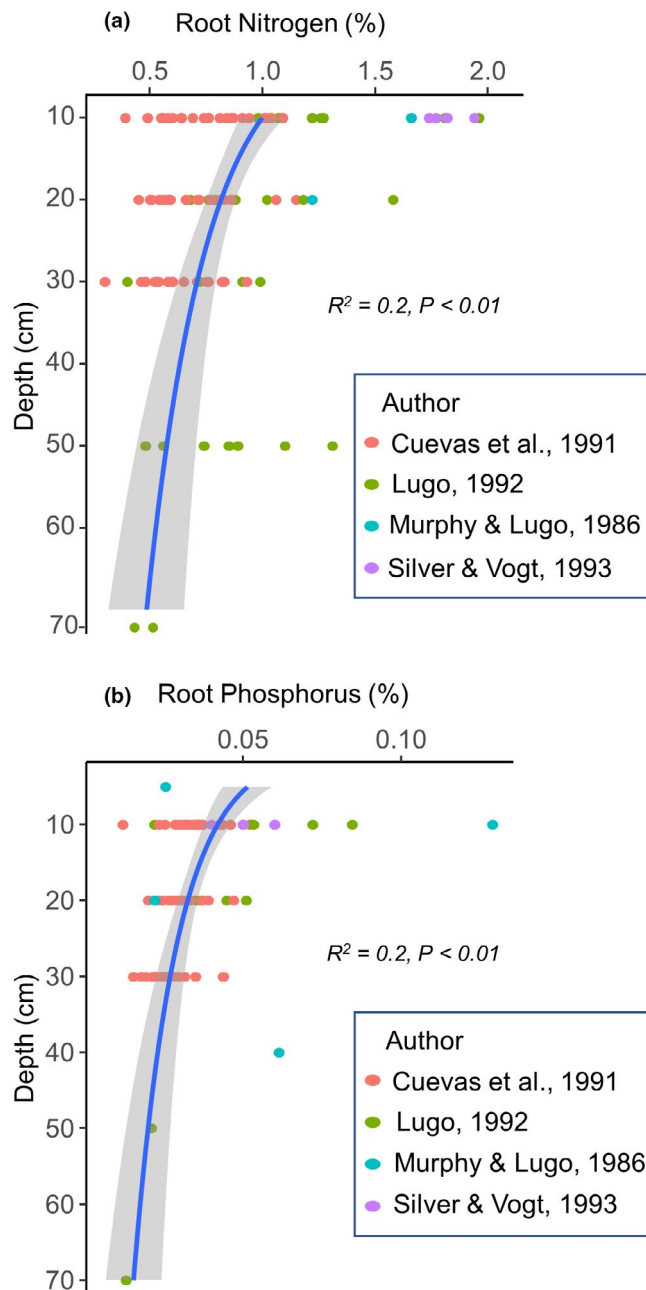


FIGURE 5 Logarithmic correlation between (a) fine-root nitrogen (%) and soil depth, and (b) fine-root phosphorus (%) and soil depth, using data from four studies in Puerto Rico that used the coring method

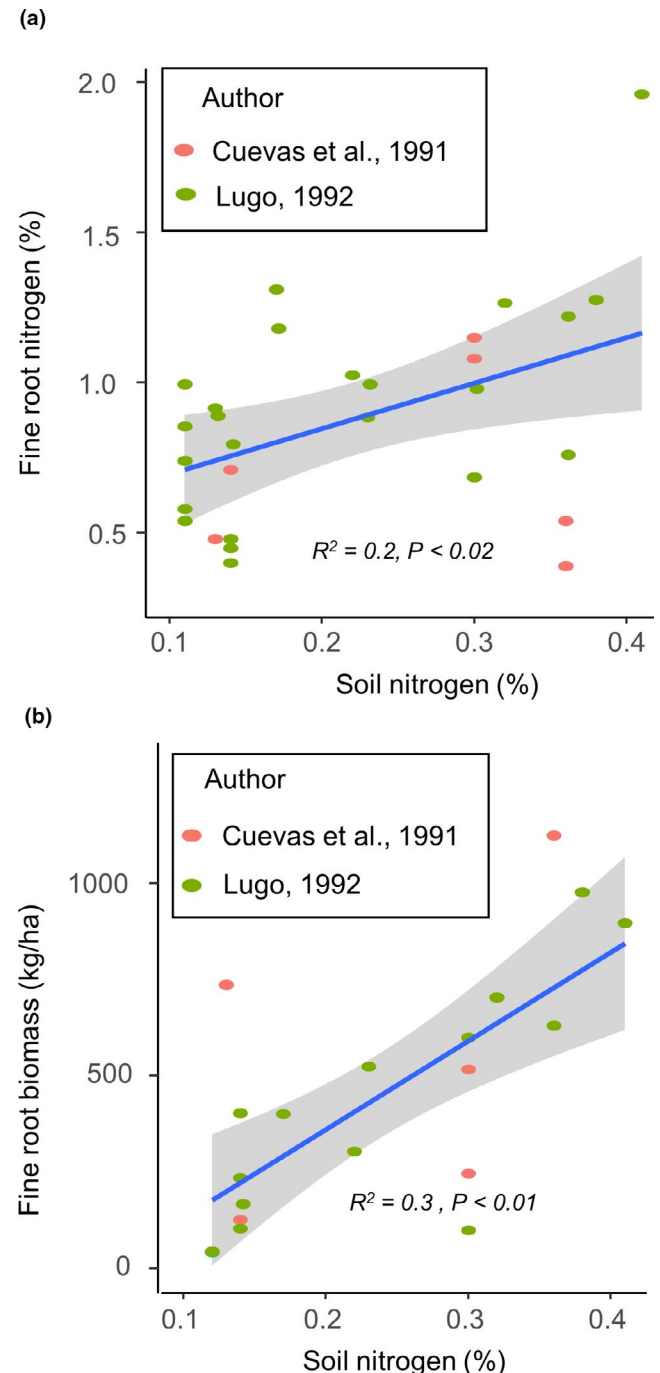


FIGURE 6 Linear correlation between (a) fine-root nitrogen (%) and soil nitrogen (%) and (b) linear correlation between fine-root biomass and soil nitrogen (%) from secondary forests, pine plantations, and mahogany plantations in LEF

a significant difference in N concentration ($p < .01$) among the 38 studied species (Figure S1), but no statistically significant difference in P concentration. The legumes *Ormosia rugii* and *Inga vera* had higher N (1.32% and 1.07%, respectively), and *L. leucocephala* had the lowest N concentration (0.13%) (Figure S2).

We correlated fine-root nutrient concentration with soil nutrient concentration using raw data from Lugo (1992) and Cuevas et al. (1991). There is a positive linear correlation between soil N and fine-root N (Figure 6a). The same pattern is shown for fine-root P and soil P, although there is an outlier that drives much of the regression (Figure S3). Fine-root biomass is also positively correlated with soil N (Figure 6b), but not with soil P.

6 | ROOT DYNAMICS

6.1 | Root production

Two studies analyzed root production among Puerto Rico's forests (Cuevas et al., 1991), and one measured root regrowth (Kangas, 1992). Cuevas et al. (1991) used ingrowth cores to measure root production (<2 mm in diameter) collected every 6 months in plantation plots and a paired secondary forest plot at LEF. They found that a secondary forest produced on average 8.54 Mg ha⁻¹ year⁻¹ of fine roots in the first 30 cm of soil depth, while that of a pine plantation was 1.15 Mg ha⁻¹ year⁻¹. The differences were explained by species richness, litterfall decomposition rate, and a combination of conditions that promote root production. Templer, Silver, Pett-Ridge, DeAngelis, and Firestone (2008) reported a root production (<2 mm in diameter) of 1.6 Mg/ha over 11 months in 10 cm of soil depth in a mature forest of LEF. If this production is maintained constant over a year, root production would be 1.74 Mg ha⁻¹ year⁻¹ which, despite the soil depth differences, is five times less than the one reported by Cuevas et al. (1991) for a secondary forest.

Kangas (1992) measured fine-root regrowth using pit excavation and re-excavation in 10 sites of a mature forest at LEF after 1 and 4 years. However, due to the long inter-collection intervals, only the

biomass accumulation was measured, not production. Kangas (1992) showed a root accumulation of 2.89 Mg ha⁻¹ year⁻¹ after a year and 4.77 Mg/ha after 3 years.

6.2 | Root decomposition

Six studies measured root decomposition in Puerto Rico, most of them in the wet forest of LEF and some in the dry forest (Table 1). Silver and Vogt (1993) used trench plots to measure fine-root decomposition in LEF (tabonuco forest). They found that 65% of fine-root biomass remained after a year (decay constant k of 0.4 per year), which resembles the global pattern of root decomposition for broadleaf trees (Silver & Miya, 2001; Table 1). In the same forest, Bloomfield et al. (1993) used litterbags to compare root and leaf decay. They found no difference in root decay between riparian and upper-slope sites, which means that moisture was not as important as substrate quality for decay rate. In this same study, they found that root decay was slower for roots than for leaves in *D. excelsa* and *P. montana*. Leaves had more Ca than roots, whereas Al and Fe were higher in roots than in leaves. Further, they found that root decay for *D. excelsa* had a slower rate than roots of *P. montana*. This was explained by the N found within its roots for microbial decomposition.

In southeastern Puerto Rico (Sierra de Cayey), Ostertag et al. (2008) measured root decomposition for a forest chronosequence. Root decomposition was fastest in the 60-year-old sites and slower in the 10- and 30-year-old sites (k constant: 0.76, 0.48, and 0.46 per year, respectively). The total final mass remaining ranged from 26% to 39% after 22 months. Similar patterns in decomposition with forest age were reported by Silver and Miya (2001); thus, older forests seem to have faster fine-root decomposition.

Cusack et al. (2009) analyzed root and leaf decomposition of *Andropogon gerardii*, *Drypetes glauca*, and *Pinus elliotti* from LIDET (Long-term Intersite Decomposition Experiment Team) data, which included Luquillo wet forest and Guánica dry forest, Puerto Rico. Fastest decomposition of root biomass was found in Luquillo compared to Guánica (k constant: 1.06 and 0.26 per year, respectively).

TABLE 1 Fine-root decomposition rate (k value) in Puerto Rico by site, author who reported, and forest species dominance

Site	Precipitation (mm)	Author	Species	k (per year)
LEF	4,000	Bloomfield et al. (1993)	<i>Prestoea montana</i>	0.6
LEF	4,000	Bloomfield et al. (1993)	<i>Dacryodes excelsa</i>	0.83
LEF	3,500	Silver and Vogt (1993)	Mix	0.4
LEF	3,363	Cusack et al. (2009)	Mix	1.06
Sierra de Cayey—10-year-old site	2,000	Ostertag et al. (2008)	Mix	0.48
Sierra de Cayey—30-year-old site	2,000	Ostertag et al. (2008)	Mix	0.46
Sierra de Cayey—60-year-old site	2,000	Ostertag et al. (2008)	Mix	0.76
Guánica—PR	508	Cusack et al. (2009)	Mix	0.26
Global	—	Silver and Miya (2001)	Mix	0.46

From the three species, *A. gerardi* had the fastest root decomposition, and *P. elliotti* had the slowest. Corroborating this, Harmon et al. (2009) reported, based on the same data base from LIDET, that *P. elliotti* had the largest root remaining of all the studied species (40.28%).

7 | ROOT PHYSIOLOGY

Templer et al. (2008) measured fine-root nitrogen uptake in a $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ addition experiment at LEF. They used ingrowth cores which were harvested sequentially up to 7 days. Fine roots took up 28% of the inorganic N during the first 24 hr, especially from $^{15}\text{NH}_4^+$ (~80%). Roots represented a significantly greater sink for N from $^{15}\text{NH}_4^+$ compared to microbial biomass, but not for $^{15}\text{NO}_3^-$.

Another physiological trait measured in Puerto Rico is root phosphatase activity. Luse (1970) found that when applying ^{32}P in the litter layer of a plot in LEF, fine roots from saplings had higher amounts of ^{32}P (20 times higher) than soils, and he attributed this to phosphatase activity and fungal diversity. Stone et al. (2013) used seedlings of *T. heterophylla* in a fertilization experiment and showed that, when adding P in the soil, phosphatase activity decreased significantly. Cabugao et al. (2017) corroborated this when they found a negative correlation of root phosphomonoesterase (PME) activity with P availability increase on adult trees up to 20 cm in diameter. However, Cabugao et al. (2017) also found that tree species play an important role in modulating root and bacterial PME activity even in the same P conditions. Both studies support the negative correlation pattern between phosphatase activity and soil P availability (Treseder & Vitousek, 2001).

8 | MICROBIAL ASSOCIATIONS

Root microbial associations have rarely been studied in Puerto Rico but have become more common in the past 5 years. The first time that root mycorrhizal colonization was mentioned in a Puerto Rico study was in 1950 by the Puerto Rican Forest Service (Briscoe, 1959), when *Pinus* species (*P. elliottii* and *P. caribaea*) were successfully established only after been inoculated with mycorrhizal fungi.

Due to Puerto Rico's large diversity in endemic orchids and their mycorrhizae specificity, fungal mycorrhizae and endophytes in these plants were also studied on the island. Bayman, Lebrón, Tremblay, and Lodge (1997) described fungal endophytes from seven species of orchid roots and leaves from Carite State Forest. They found that root endophytes *Xylaria* and *Rhizoctonia* were more commonly found in roots (29% and 45%, respectively). Further, the same authors found that the naturalized orchid *Oeceoclades maculata* is highly specific to the mycorrhizae fungi *Psathyrella* cf. *candolleana* during seed germination, but promiscuous as an adult (Bayman, Mosquera-Espinosa, Saladini-Aponte, Hurtado-Guevara, & Viera-Ruiz, 2016).

Bachelot, Uriarte, McGuire, Thompson, and Zimmerman (2017) and Bachelot et al. (2018) studied the diversity of mycorrhizal fungi in the wet forest of Puerto Rico. Bachelot et al. (2017) found that at the local scale, arbuscular mycorrhizal fungi (AMF) diversity in soil counteracted negative effects of leaf damage on seedling mortality. At the community scale, only rare tree species seedlings benefited from soil AMF diversity. Bachelot et al. (2018) showed that early-successional plant species are less dependent on the diversity of AMF than mid- and late-successional plant species, which contradicts other findings in tropical studies (Fischer et al., 1994; Kiers, Lovelock, Krueger, & Herre, 2000; Matsumoto et al., 2005).

The only study that has related the microbiota with root architecture and morphology is described in Irizarry and White (2017). They germinated wild cotton (*Gossypium hirsutum*) seeds that were inoculated with bacteria isolated from non-cultivated Malvaceae plants from various parts of Puerto Rico, including Rincón, Guayama, and LEF. They found that the bacteria *Bacillus amyloliquefaciens* enhanced primary and lateral root growth by three times in comparison with those without the bacteria. Further, roots from an inoculated seed had thinner roots and higher root branching ratio than with no inoculation.

9 | ROOT RESPONSE TO ENVIRONMENTAL CHANGES

Fine-root responses to environmental changes have not been well documented in the tropics compared to temperate forests (Cuevas & Medina, 1988; Fetcher et al., 1996; Silver & Vogt, 1993; Wright et al., 2011). However, since hurricanes are the major non-anthropogenic disturbance in Puerto Rico, a few studies measured root response to hurricanes. Soil fertilization and drought are other environmental changes that were less studied in the island. Human disturbance, specifically soil compaction, was also measured in Puerto Rico.

9.1 | Root adaptation to hurricanes

Root grafting is a common morphological root trait in hurricane prone areas (Basnet, Scatena, Likens, & Lugo, 1993; LaRue, 1952; Lugo & Scatena, 1995). LaRue (1952) found more tree genera exhibiting root grafting in Puerto Rico than in any temperate forests he studied. Lugo and Scatena (1995) suggested that tree unions may offer a more secure foundation when exposed to hurricane winds. For example, tabonuco (*D. excelsa*) trees on ridges tend to have more root grafting than on slopes and are known to be more successful in surviving and resprouting after hurricanes than trees without these unions (Lugo & Scatena, 1995). However, only bigger trees (>5 cm in diameter) present unions (Basnet et al., 1993). Further, root grafting also forms an organic bench which can

provide better conditions for root aeration and nutrient accumulation (Basnet et al., 1993).

9.2 | Root response to hurricanes

Studies showed a decrease in root biomass almost immediately after a hurricane disturbance (Parrotta & Lodge, 1991; Silver & Vogt, 1993). Root recovery rate varied depending on the hurricane intensity, precipitation during the recovery period, litter decomposition rate, and species-specific root traits such as root length (Beard et al., 2005; Lodge, Winter, González, & Clum, 2016; Parrotta & Lodge, 1991).

Silver and Vogt (1993) simulated a hurricane disturbance by removing all aboveground biomass. After 2 months from the removal, root biomass declined 40%. This same study measured root biomass after Hurricane Hugo, where root biomass declined for the next 8 months. Silver & Scatena (2009) continued measuring root biomass on the same sites and showed that it took more than 10 years to recover root biomass after Hurricane Hugo (Figure 7). Recovery was even slower for plots with aboveground removal. Root nutrient concentrations (P and K) decreased after biomass removal, and root P decreased even more after the hurricane.

Parrotta and Lodge (1991) measured fine-root (<3 mm) biomass before and after Hurricane Hugo at El Verde Field Station area (LEF). They showed that live fine-root biomass decreased from 4.23 Mg/ha to 0.02 Mg/ha 2 months following the hurricane. Fine-root biomass recovery was slow, reaching to 0.49 Mg/ha after 8 months (Parrotta & Lodge, 1991). This slow recovery was attributed to physical disturbance, moisture stress (low rainfall after Hugo), and changes in non-structural carbohydrates in coarse roots.

Beard et al. (2005) showed that root mortality increased immediately after Hurricane Hugo. They also noted that each species

had different decay rates and capacity to conserve nutrients. For example, tabonuco (*D. excelsa*) showed a faster decay rate compared to other common species, resulting in faster recovery time. Beard et al. (2005) concluded that the post-Hugo drought might have influenced the root recovery, causing high root mortality and emphasizing the importance of considering multiple disturbance responses. Ongoing investigations are measuring the effect of previous warming treatments in the TRACE experiment (Kimball et al., 2018) on root responses after Hurricanes Irma and Maria in 2017 (Yaffar 2020).

Lodge et al. (2016) correlated fine-root length with coarse woody debris from Hurricane Hugo and Hurricane Georges (Lodge et al., 2016). Root length was used to indicate nutrient hotspots. They found that root length was greater away from dead logs in the dry season and greater under logs during the wet season. Despite root length being significantly positively correlated with soil microbial C, the latter did not differ between dry and wet season, which is inconsistent with a competitive exclusion hypothesis. They hypothesized that soil P may have contributed to the rooting patterns, or the differences in the secondary compounds of the decaying logs might result in fine-root length differences. The Torres (1994) study suggested that aboveground adventitious roots from *Cyrtilla racemiflora* extract nutrients from dead wood from the same tree or nearby trees, allowing its recovery in LEF.

9.3 | Root response to soil chemical and physical changes

Fetcher et al. (1996) measured the response of tree seedlings, two pioneers (*C. schreberiana* and *P. rivinoides*) and two non-pioneers (*M. bidentata* and *riparia*), to fertilization in a landslide at LEF. Across all four species, there was more allocation to roots in the N + P treatment than in the N or P treatments alone. The pioneer species responded more to nutrient addition than the non-pioneer species. This was explained by the high potential growth and photosynthetic rates of pioneer species, as well as the mycorrhizal colonization.

Stone et al. (2013) found that seedlings of another early-successional native species, *T. heterophylla*, in LEF increased its root biomass only with P addition. Contrary to Fetcher et al. (1996), Stone et al. (2013) showed no changes in root biomass when increasing soil N + P. Additionally, they measured changes in five extracellular enzyme activities, which helped correlate soil P deficiency with root growth when P was added. Therefore, multiple species-specific root traits, such as enzymatic activity, root morphology, architecture, root hair density, and mycorrhizal colonization, should be taken into consideration in future studies to correlate with soil nutrient concentrations and better understand root uptake.

Soil compaction is another environmental factor, usually human-driven, that affects root growth. Tirado-Corbalá & Slater (2010) measured root biomass from seedlings of planted trees of Puerto Rico in different soil types and compaction levels.

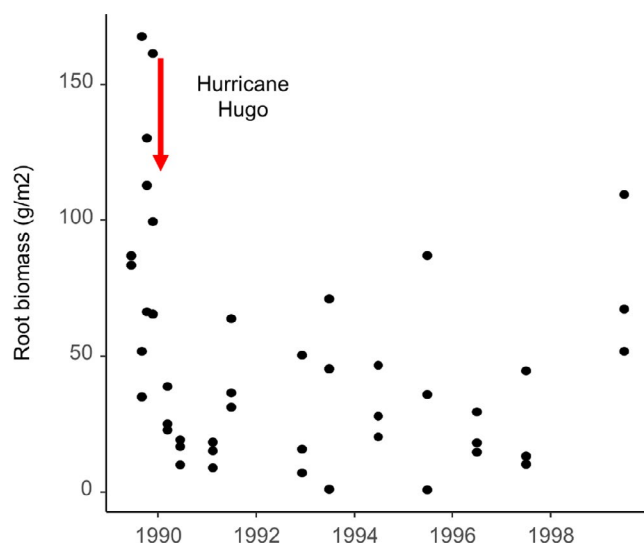


FIGURE 7 Ten years of root biomass from LEF, before and after hurricane Hugo, since 1990 to 1999

Compaction caused a significant decrease in root mass for *Tecoma stans* but not for *Tabebuia rosea* or *Callistemon citrinus*. The three tree species presented higher root mass grown in sandy clay loam soils compared to trees grown in clay soil. Future studies should measure soil texture and compaction in relationship to different root physiological traits to better understand root response to soil physical changes.

10 | CONCLUSIONS AND RESEARCH OPPORTUNITIES

The studies mentioned in this review gathered important pieces of information regarding root traits from different forest types in Puerto Rico over the past 50 years. Some of the conclusions we gathered from this collection are as follows: (a) Rooting depth distribution in the wet forest is shallower (above 20 cm) than presented in other tropical studies, yet only three studies considered rooting distribution further than 30 cm in depth. Thus, we suggest that more future studies confirm this pattern in the different forest types. The dry forest has slightly deeper distribution than the wet forest, but there are not enough data on vertical distribution of roots in the dry forest for a strong conclusion. (b) Total root biomass is greater in the wet forest than in the dry forest. (c) Fine-root biomass is much greater in the palm primary forest (wet forest-LEF), followed by the secondary wet forest (LEF), the dry mature forest (Guánica), a mahogany plantation, a pine plantation, and urban forests in the dry area of the island. (d) There is a positive correlation between fine-root biomass and soil N concentration in the secondary forest and plantation. (e) Root N and P concentrations are species-specific and vary with root diameter. (f) Root:shoot ratio varies depending the tree bole diameter (smaller trees have lower root:shoot ratio than larger trees), and it is higher in Puerto Rico (for trees >5 cm in diameter) compared to other tropical sites. (g) The diversity of mycorrhizal fungi is correlated with plant successional type, where early-successional plant species are less dependent on AMF diversity than mid- and late-successional plants. (h) Root grafting is an advantageous morphological trait in response to hurricane winds. (i) Root recovery after multiple disturbances (hurricane + drought) takes up to 10 years.

Studies including root data in Puerto Rico are very representative for the tropics, considering its land cover. However, there are many fine-root functional traits that have not been fully explored. There have only been two studies that have established long-term research to quantify the plasticity of root traits and their response to environmental changes. The nutritional advantage (if any) of root grafting has not been evaluated. Further, different root morphological, architectural, and chemical traits have not been directly correlated with the physiological traits. These are some of the understudied areas that could lead to future studies. Our synthesis can be used to enrich root data base representation of the tropics, as well as provide more conclusive evidence for important hypotheses in root ecology that will ultimately better inform Earth System Models.

ACKNOWLEDGMENTS

We are grateful to Ariel Lugo, Elvira Cuevas, Whendee Silver, Sandra Molina Colon, and the U.S. Forest Service International Institute of Tropical Forestry for providing raw data for this review paper, and to Ariel Lugo, Benjamin Branoff, and Colleen Iversen for reviewing this document and giving essential insights. This research was supported as part of the Next Generation Ecosystem Experiments-Tropics, funded by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research. Oak Ridge National Laboratory is managed by UT Battelle, LLC, for the U.S. Department of Energy under contract no. DE-AC05-00OR22725.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTIONS

DY developed the concept for the project, crated and analyzed the data, and wrote the paper. RJN assisted in data analysis and reviewed and edited the paper.

DATA AVAILABILITY STATEMENT

The data used in this review are openly available in the NGEE-Tropics data archive at <http://dx.doi.org/10.15486/ngt/1558773>.

ORCID

Daniela Yaffar  <https://orcid.org/0000-0002-8090-7096>

REFERENCES

- Alvarez, M., Quevedo, V., & Blay, J. S. (1983). Estructura de tres bosques de *Pterocarpus* en Puerto Rico. In A. E. Lugo (Ed.), *Los bosques de Puerto Rico* (pp 283–308). Rio Piedras Puerto Rico: Instituto de Dasonomía Tropical.
- Bachelot, B., Uriarte, M., McGuire, K. L., Thompson, J., & Zimmerman, J. (2017). Arbuscular mycorrhizal fungal diversity and natural enemies promote coexistence of tropical tree species. *Ecology*, 98, 712–720. <https://doi.org/10.1002/ecy.1683>
- Bachelot, B., Uriarte, M., Muscarella, R., Forero-Montaña, J., Thompson, J., McGuire, K., ... Clark, J. S. (2018). Associations among arbuscular mycorrhizal fungi and seedlings are predicted to change with tree successional status. *Ecology*, 99, 607–620. <https://doi.org/10.1002/ecy.2122>
- Basnet, K., Scatena, F. N., Likens, G. E., & Lugo, A. E. (1993). Ecological consequences of root grafting in Tabonuco (*Dacryodes excelsa*) trees in the Luquillo experimental forest, Puerto Rico. *Biotropica*, 25, 28–35. <https://doi.org/10.2307/2388976>
- Bayman, P., Lebrón, L. L., Tremblay, R. L., & Lodge, D. J. (1997). Variation in endophytic fungi from roots and leaves of *Lepanthes* (Orchidaceae). *New Phytologist*, 135, 143–149. <https://doi.org/10.1046/j.1469-8137.1997.00618.x>
- Bayman, P., Mosquera-Espinosa, A. T., Saladini-Aponte, C. M., Hurtado-Guevara, N. C., & Viera-Ruiz, N. L. (2016). Age-dependent mycorrhizal specificity in an invasive orchid, *Oeceoclades maculata*. *American Journal of Botany*, 103, 1880–1889.
- Beard, K. H., Vogt, K. A., Vogt, D. J., Scatena, F. N., Covich, A. P., Sigurdardottir, R., ... Crawl, T. A. (2005). Structural and

- functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs*, 75, 345–361. <https://doi.org/10.1890/04-1114>
- Bloomfield, J., Vogt, K. A., & Vogt, D. J. (1993). Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. *Plant and Soil*, 150, 233–245. <https://doi.org/10.1007/BF00013020>
- Brandeis, T. J., & Turner, J. A. (2013). *Puerto Rico's forests, 2009*. Resource Bulletin. SRS-RB-191. Asheville, NC. U.S. Department of Agriculture Forest Service, Southern Research Station. 85 p. <https://www.fs.usda.gov/treesearch/pubs/43624>
- Briscoe, C. (1959). *Early results of mycorrhizal inoculation of pine in Puerto Rico. Caribbean Forester July–December*, 73–77.
- Cabugao, K. G., Timm, C. M., Carrell, A. A., Childs, J., Lu, T.-Y.-S., Pelletier, D. A., ... Norby, R. J. (2017). Root and rhizosphere bacterial phosphatase activity varies with tree species and soil phosphorus availability in Puerto Rico tropical forest. *Frontiers in Plant Science*, 8, 1834. <https://doi.org/10.3389/fpls.2017.01834>
- Cairns, M. A., Brown, S., Helmer, E. H., & Baumgardner, G. A. (1997). Root biomass allocation in the world's upland forests. *Oecologia*, 111, 1–11. <https://doi.org/10.1007/s004420050201>
- Collins, C. G., Wright, S. J., & Wurzburger, N. (2016). Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees. *Oecologia*, 180, 1037–1047. <https://doi.org/10.1007/s00442-015-3410-7>
- Comas, L. H., & Eissenstat, D. M. (2009). Patterns in root trait variation among 25 co-existing North American forest species. *New Phytologist*, 182, 919–928. <https://doi.org/10.1111/j.1469-8137.2009.02799.x>
- Cordero, R. A. (1999). Ecophysiology of *Cecropia schreberiana* saplings in two wind regimes in an elfin cloud forest: Growth, gas exchange, architecture and stem biomechanics. *Tree Physiology*, 19, 153–163. <https://doi.org/10.1093/treephys/19.3.153>
- Cuevas, E., Brown, S., & Lugo, A. E. (1991). Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. *Plant and Soil*, 135, 257–268. <https://doi.org/10.1007/BF00010914>
- Cuevas, E., & Medina, E. (1988). Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability, and leaf litter decomposition. *Oecologia*, 76, 222–235. <https://doi.org/10.1007/BF00379956>
- Cusack, D. F., Chou, W. W., Yang, W. H., Harmon, M. E., & Silver, W. L. (2009). Controls on long-term root and leaf litter decomposition in neotropical forests. *Global Change Biology*, 15, 1339–1355. <https://doi.org/10.1111/j.1365-2486.2008.01781.x>
- Cusack, D. F., Silver, W. L., Torn, M. S., & McDowell, W. H. (2011). Effects of nitrogen additions on above- and belowground carbon dynamics in two tropical forests. *Biogeochemistry*, 104, 203–225. <https://doi.org/10.1007/s10533-010-9496-4>
- Edel, M. O. (1962). Land reform in Puerto Rico, 1940–1959: Part one. *Caribbean Studies*, 2, 26–60.
- Ewel, J. J., & Whitmore, J. L. (1973). *The ecological life zones of Puerto Rico and the U.S. Virgin Islands*. USDA Forest Service, Institute of Tropical Forestry, Research Paper ITF-018. <https://www.fs.usda.gov/treesearch/pubs/5551>
- Fetcher, N., Haines, B. L., Cordero, R. A., Lodge, D. J., Walker, L. R., Fernandez, D. S., & Lawrence, W. T. (1996). Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology*, 84, 331–341. <https://doi.org/10.2307/2261196>
- Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. (1998). Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*, 281, 237–240. <https://doi.org/10.1126/science.281.5374.237>
- Fischer, C. R., Janos, D. P., Perry, D. A., Linderman, R. G., Box, P. O., Gables, C., & Linderman, G. (1994). Mycorrhiza inoculum potentials in tropical secondary succession. *Biotropica*, 26, 369–377. <https://doi.org/10.2307/2389230>
- Frangi, J. L., & Lugo, A. E. (1985). Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs*, 55, 351–369. <https://doi.org/10.2307/1942582>
- Freschet, G. T., Valverde-Barrantes, O. J., Tucker, C. M., Craine, J. M., McCormack, M. L., Violle, C., ... Roumet, C. (2017). Climate, soil and plant functional types as drivers of global fine-root trait variation. *Journal of Ecology*, 105, 1182–1196. <https://doi.org/10.1111/1365-2745.12769>
- Gale, M. R., & Grigal, D. F. (1987). Vertical root distributions of northern tree species in relation to successional status. *Canadian Journal of Forest Research*, 17, 829–834. <https://doi.org/10.1139/x87-131>
- Gijsman, A. J., Alarcón, H. F., & Thomas, R. J. (1997). Root decomposition in tropical grasses and legumes, as affected by soil texture and season. *Soil Biology Biochemistry*, 29, 1443–1450. [https://doi.org/10.1016/S0038-0717\(97\)00039-4](https://doi.org/10.1016/S0038-0717(97)00039-4)
- Golley, F., Odum, H. T., & Wilson, R. F. (1962). The structure and metabolism of a Puerto Rican Red Mangrove forest in May. *Ecology*, 43, 9–19. <https://doi.org/10.2307/1932034>
- Gordon, W. S., & Jackson, R. B. (2000). Nutrient concentrations in fine roots. *Ecology*, 81, 275–280. [https://doi.org/10.1890/0012-9658\(2000\)081\[0275:NCIFR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0275:NCIFR]2.0.CO;2)
- Gower, S. T. (1987). Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: A hypothesis. *Biotropica*, 19, 171–175. <https://doi.org/10.2307/2388741>
- Hanson, P. J., Edwards, N. T., Garten, C. T., & Andrews, J. A. (2000). Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry*, 48, 115–146.
- Harmon, M. E., Silver, W. L., Fasth, B., Chen, H., Burke, I. C., Parton, W. J., ... Blum, L. (2009). Long-term patterns of mass loss during the decomposition of leaf and fine root litter: An intersite comparison. *Global Change Biology*, 15, 1320–1338. <https://doi.org/10.1111/j.1365-2486.2008.01837.x>
- Harris, N. L. (2012). General description of the research area. In N. L. Harris, A. E. Lugo, S. Brown, & T. Heatsill (Eds.), *Luquillo experimental forest: research history and opportunities* (p. 3). Washington, DC: Department of Agriculture.
- Irizarry, I., & White, J. F. (2017). Application of bacteria from non-cultivated plants to promote growth, alter root architecture and alleviate salt stress of cotton. *Journal of Applied Microbiology*, 122, 1110–1120. <https://doi.org/10.1111/jam.13414>
- Iversen, C. M. (2014). Using root form to improve our understanding of root function. *New Phytologist*, 203, 707–709. <https://doi.org/10.1111/nph.12902>
- Iversen, C. M., Ledford, J., & Norby, R. J. (2008). CO₂ enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. *New Phytologist*, 179, 837–847.
- Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., ... Violle, C. (2017). A global fine-root ecology database to address below-ground challenges in plant ecology. *New Phytologist*, 215, 15–26. <https://doi.org/10.1111/nph.14486>
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108, 389–411. <https://doi.org/10.1007/BF00333714>
- Jia, S., Wang, Z., Li, X., Zhang, X., & McLaughlin, N. B. (2011). Effect of nitrogen fertilizer, root branch order and temperature on respiration and tissue N concentration of fine roots in *Larix gmelinii* and *Fraxinus mandshurica*. *Tree Physiology*, 31, 718–726. <https://doi.org/10.1093/treephys/tp057>
- Kangas, P. (1992). Root regrowth in a subtropical wet forest in Puerto Rico. *Biotropica*, 24, 463–465. <https://doi.org/10.2307/2388619>
- Kiers, E. T., Lovelock, C. E., Krueger, E. L., & Herre, E. A. (2000). Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: Implications for

- tropical forest diversity. *Ecology Letters*, 3, 106–113. <https://doi.org/10.1046/j.1461-0248.2000.00126.x>
- Kimball, B. A., Alonso-Rodríguez, A. M., Cavaleri, M. A., Reed, S. C., González, G., & Wood, T. E. (2018). Infrared heater system for warming tropical forest understory plants and soils. *Ecology and Evolution*, 8, 1932–1944. <https://doi.org/10.1002/ece3.3780>
- Kong, D., Ma, C., Zhang, Q., Li, L., Chen, X., Zeng, H., & Guo, D. (2014). Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist*, 203, 863–872. <https://doi.org/10.1111/nph.12842>
- Lamanna, C. A., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Simova, I., ... Enquist, B. J. (2014). Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13745–13750. <https://doi.org/10.1073/pnas.1317722111>
- LaRue, C. D. (1952). Root-grafting in tropical trees. *Science*, 115(2985), 296. <https://doi.org/10.1126/science.115.2985.296>
- Li, W., Jin, C., Guan, D., Wang, Q., Wang, A., Yuan, F., & Wu, J. (2015). The effects of simulated nitrogen deposition on plant root traits: A meta-analysis. *Soil Biology & Biochemistry*, 82, 112–118. <https://doi.org/10.1016/j.soilbio.2015.01.001>
- Lodge, D. J., Winter, D., González, G., & Clum, N. (2016). Effects of hurricane-felled tree trunks on soil carbon, nitrogen, microbial biomass, and root length in a wet tropical forest. *Forests*, 7, 264. <https://doi.org/10.3390/f7110264>
- Lugo, A. E. (1983). *Los bosques de Puerto Rico* (p. 321). Rio Piedras: Instituto de Dasonomía Tropical.
- Lugo, A. E. (1992). Comparison of tropical tree plantations with secondary forests of similar age. *Ecological Monographs*, 62, 1–41. <https://doi.org/10.2307/2937169>
- Lugo, A. E., Abelleira, O. J., Collado, A., Viera, C. A., Santiago, C., Vélez, D. O., ... Vázquez, N. J. (2011). Allometry, biomass, and chemical content of Novel African Tulip Tree (*Spathodea campanulata*) Forests in Puerto Rico. *New Forests*, 42, 267–283. <https://doi.org/10.1007/s11056-011-9258-8>
- Lugo, A. E., & Scatena, F. N. (1995). Ecosystem-Level Properties of the Luquillo Experimental Forest with Emphasis on the Tabonuco Forest. In A. E. Lugo, & C. Lowe (Eds.), *Tropical forests: Management and ecology* (pp. 78–79). New York, NY: Springer-Verlag, New York Inc.
- Luse, R. (1970). The phosphorus cycle in a tropical rain forest. In H. T. Odum (Ed.), *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico* (pp. H161–H176). Springfield, VA: National Technical Information Service.
- Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society of London*, 366, 3225–3245. <https://doi.org/10.1098/rstb.2011.0062>
- Marcano Vega, H. (2019). *Los bosques de Puerto Rico, 2014. Boletín de Recursos SRS-224*. Asheville, NC: Departamento de Agricultura de los Estados Unidos Servicio Forestal, Estación de Investigación del Sur. 90 p. <https://www.fs.usda.gov/treesearch/pubs/58591>
- Marin-Spiotta, E., Silver, W. L., Swanston, C. W., & Ostertag, R. (2009). Soil organic matter dynamics during 80 years of reforestation of tropical pastures. *Global Change Biology*, 15, 1584–1597. <https://doi.org/10.1111/j.1365-2486.2008.01805.x>
- Matsumoto, L. S., Martines, A. M., Avanzi, M. A., Albino, U. B., Brasil, C. B., Saridakis, D. P., ... Andrade, G. (2005). Interactions among functional groups in the cycling of carbon, nitrogen and phosphorus in the rhizosphere of three successional species of tropical woody trees. *Applied Soil Ecology*, 28, 57–65. <https://doi.org/10.1016/j.apsoil.2004.06.008>
- McCormack, M. L., Adams, T. S., Smithwick, E. A. H., & Eissenstat, D. M. (2012). Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist*, 195, 823–831. <https://doi.org/10.1111/j.1469-8137.2012.04198.x>
- McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., ... Zadworny, M. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist*, 207, 505–518. <https://doi.org/10.1111/nph.13363>
- McCormack, M. L., Guo, D., Iversen, C. M., Chen, W., Eissenstat, D. M., Fernandez, C. W., ... Zanne, A. (2017). Building a better foundation: Improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist*, 215, 27–37. <https://doi.org/10.1111/nph.14459>
- McGorddy, M., & Silver, W. L. (2000). Variations in belowground carbon storage and soil CO₂ flux rates along a wet tropical climate gradient. *Biotropica*, 32, 6114–6624.
- Miller, G. L., & Lugo, A. E. (2009a). Overview of Puerto Rico. In G. L. Miller, & A. E. Lugo (Eds.), *Guide to the ecological systems of Puerto Rico* (pp. 1–26). USDA Forest Service, GTR-IITF-35.
- Miller, G. L., & Lugo, A. E. (2009b). Flora and Fauna of Puerto Rico and the Caribbean. In G. L. Miller, & A. E. Lugo (Eds.), *Guide to the ecological systems of Puerto Rico* (pp. 27–36). USDA Forest Service, GTR-IITF-35.
- Mokany, K., Raison, R. J., & Prokushkin, A. S. (2006). Critical analysis of root: Shoot ratios in terrestrial biomes. *Global Change Biology*, 12, 84–96. <https://doi.org/10.1111/j.1365-2486.2005.001043.x>
- Molina Colón, S., & Lugo, A. E. (2006). Recovery of a subtropical dry forest after abandonment of different land uses. *Biotropica*, 38, 354–364.
- Murphy, P. G., & Lugo, A. E. (1986a). Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica*, 18, 89. <https://doi.org/10.2307/2388750>
- Murphy, P. G., & Lugo, A. E. (1986b). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, 17, 67–88. <https://doi.org/10.1146/annurev.es.17.110186.000435>
- Odum, H. T. (1970a). Summary: An emerging view of the ecological system at El Verde. In H. T. Odum (Ed.), *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico* (pp. I191–I276). Springfield, VA: National Technical Information Service.
- Odum, H. T. (1970b). Rain forest structure and mineral-cycling homeostasis. In H. T. Odum (Ed.), *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico* (pp. I191–I276). Springfield, VA: National Technical Information Service.
- Odum, H. T., & Pigeon, R. F. (1970). *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Springfield, VA: National Technical Information Service.
- Ostertag, R., Marín-Spiotta, E., Silver, W. L., & Schulten, J. (2008). Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. *Ecosystems*, 11, 701–714. <https://doi.org/10.1007/s10021-008-9152-1>
- Ovington, J. D., & Olson, J. S. (1970). Biomass and chemical content of El Verde lower mountain rain forest plants. In H. T. Odum (Ed.), *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico* (pp. H53–77). Springfield, VA: National Technical Information Service.
- Parrotta, J. A. (1999). Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. *Forest Ecology and Management*, 124, 45–77. [https://doi.org/10.1016/S0378-1127\(99\)00049-3](https://doi.org/10.1016/S0378-1127(99)00049-3)
- Parrotta, J., & Lodge, D. (1991). Fine root dynamics in a subtropical wet forest following hurricane disturbance in Puerto Rico. *Biotropica*, 23, 343–347. <https://doi.org/10.2307/2388250>
- Pett-Ridge, J., & Silver, W. L. (2002). Survival, growth, and ecosystem dynamics of displaced bromeliads in a montane tropical forest. *Biotropica*, 34, 211–224.
- Pregitzer, K. S. (2002). Fine roots of trees - A new perspective. *New Phytologist*, 154, 267–270. https://doi.org/10.1046/j.1469-8137.2002.00413_1.x

- Rivera, Z. E., Toro, B. L., & Gómez, R. (1983). In A. E. Lugo (Ed.), *Los bosques de Puerto Rico* (pp. 283–308). Río Piedras Puerto Rico: Instituto de Dasonomía Tropical.
- RStudio Team (2016). *RStudio: Integrated development for R*. Boston, MA: RStudio Inc. <http://www.rstudio.com/>
- Scatena, F. N., Silver, W., Siccama, T., Johnson, A., & Sanchez, M. J. (1993). Biomass and nutrient content of the bisley experimental watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica*, 25, 15–27. <https://doi.org/10.2307/2388975>
- Schenk, H. J., & Jackson, R. B. (2002). The global biogeography of roots. *Ecological Monographs*, 72, 311–328. [https://doi.org/10.1890/0012-9615\(2002\)072\[0311:TGBOR\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2)
- Schuur, E. A. G. (2001). The effect of water on decomposition dynamics in mesic to wet Hawaiian montane forests. *Ecosystems*, 4, 259–273. <https://doi.org/10.1007/s10021-001-0008-1>
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18, 1406–1419. <https://doi.org/10.1111/ele.12508>
- Silver, W. L., & Miya, R. K. (2001). Global patterns in root decomposition: Comparisons of climate and litter quality effects. *Oecologia*, 129, 407–419. <https://doi.org/10.1007/s004420100740>
- Silver, W. L., & Vogt, K. A. (1993). Fine-root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *Journal of Ecology*, 81, 729–738. <https://doi.org/10.2307/2261670>
- Stone, M. M., Plante, A. F., & Casper, B. B. (2013). Plant and nutrient controls on microbial functional characteristics in a tropical Oxisol. *Plant and Soil*, 373, 893–905. <https://doi.org/10.1007/s11104-013-1840-8>
- Teh, Y. A., Silver, W. L., & Scatena, F. N. (2009). A decade of belowground reorganization following multiple disturbances in a subtropical wet forest. *Plant and Soil*, 323, 197–212. <https://doi.org/10.1007/s11104-009-9926-z>
- Templer, P. H., Silver, W. L., Pett-Ridge, J., DeAngelis, K. M., & Firestone, M. K. (2008). Plant and microbial controls on nitrogen retention and loss in a humid tropical forest. *Ecology*, 89, 3030–3040. <https://doi.org/10.1890/07-1631.1>
- Tirado-Corbalá, R., & Slater, B. K. (2010). Soil compaction effects on the establishment of three tropical tree species. *Arboriculture Urban Forestry*, 36, 164–170.
- Torres, J. A. (1994). Wood decomposition of *Cyrilla racemiflora* in a tropical montane forest. *Biotropica*, 26, 124–140. <https://doi.org/10.2307/2388803>
- Treseder, K. K., & Vitousek, P. M. (2001). Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology*, 82, 946–954. [https://doi.org/10.1890/0012-9658\(2001\)082\[0946:EOSNAO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0946:EOSNAO]2.0.CO;2)
- Valverde-Barrantes, O. J., Raich, J. W., & Russell, A. E. (2007). Fine-root mass, growth and nitrogen content for six tropical tree species. *Plant and Soil*, 290, 357–370. <https://doi.org/10.1007/s11104-006-9168-2>
- Viera Martínez, C., Abelleira Martínez, O., & Lugo, A. E. (2008). Estructura y química del suelo en un bosque de castilla elástica en el karso del norte de Puerto Rico: Resultados de una calicata. *Acta Científica*, 22, 29–35.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Vogt, K., & Persson, H. (1991). Measuring growth and development of roots. In J. P. Lassoie, & T. Hineley (Eds.), *Techniques and approaches in forest tree ecophysiology* (pp. 477–501). Boca Raton, FL: CRS Press Inc.
- Vogt, K. A., Vogt, D. J., Palmiotto, P. A., Boon, P., O'Hara, J., & Asbjornsen, H. (1995). Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant and Soil*, 187, 159–219. <https://doi.org/10.1007/BF00017088>
- Waring, B. G., & Powers, J. S. (2017). Overlooking what is underground: Root:Shoot ratios and coarse root allometric equations for tropical forests. *Forest Ecology and Management*, 385, 10–15. <https://doi.org/10.1016/j.foreco.2016.11.007>
- Warren, J. M., Hanson, P. J., Iversen, C. M., Kumar, J., Walker, A. P., & Wulfschleger, S. D. (2015). Root structural and functional dynamics in terrestrial biosphere models - evaluation and recommendations. *New Phytologist*, 205, 59–78. <https://doi.org/10.1111/nph.13034>
- White, D. G., & Childers, N. F. (1945). Bamboo for controlling soil erosion. *Journal of the American Society of Agronomy*, 37, 839–847.
- Whittaker, R. H. (1954). The ecology of serpentine soils. IV. The vegetational response to serpentine soils. *Ecology*, 35, 275–288.
- Wright, S. J., Yavitt, J. B., Wurzbarger, N., Turner, B. I., Tanner, E. V. J., Sayer, E. J., ... Corre, M. D. (2011). Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, 92, 1616–1625. <https://doi.org/10.1890/10-1558.1>
- Xia, M., Guo, D., & Pregitzer, K. S. (2010). Ephemeral root modules in *Fraxinus mandshurica*. *New Phytologist*, 188, 1065–1074. <https://doi.org/10.1111/j.1469-8137.2010.03423.x>
- Yaffar, D. (2020). *Root production Minirhizotron analysis from the TRACE_PR plot in Sabana, Puerto Rico*. NGEE Tropics Data Collection. <http://dx.doi.org/10.15486/ngt/1582598>. [dataset]
- Yaffar, D., Lugo, A. E., Cuevas, E., Silver, W. L., & Molina Colón, S. (2019). *Plant trait measurements raw data, 1962-2018, Island of Puerto Rico*. 1.0. NGEE Tropics Data Collection. <http://dx.doi.org/10.15486/ngt/1558773> [dataset]

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Yaffar D, Norby RJ. A historical and comparative review of 50 years of root data collection in Puerto Rico. *Biotropica*. 2020;52:563–576. <https://doi.org/10.1111/btp.12771>