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Tradeoffs and Synergies in Tropical Forest Root Traits and Dynamics for Nutrient and Water Acquisition: Field and Modeling Advances

Daniela Francis Cusack[1,2]*, Shalom D. Addo-Danso[3], Elizabeth A. Agee[4], Kelly M. Andersen[5], Marie Arnaud[6,7], Sarah A. Batterman[2,8,9], Francis Q. Brearley[10], Mark I. Ciochina[11], Amanda L. Cordeiro[1], Caroline Dallstream[12], Milton H. Diaz-Toribio[13], Lee H. Dietterich[1], Joshua B. Fisher[14,15], Katrin Fleischer[16], Claire Fortunel[17], Lucia Fuchslueger[18], Nathaly R. Guerrero-Ramírez[19], Martyna M. Kotowska[20], Laynara Figueiredo Lugli[21], César Marín[22,23], Lindsay A. McCulloch[24], Jean-Luc Maeght[17], Dan Metcalfe[25], Richard J. Norby[26], Rafael S. Oliveira[27], Jennifer S. Powers[28,29], Tatiana Reichert[30], Stuart W. Smith[5], Chris M. Smith-Martin[31], Fiona M. Soper[12], Laura Toro[28,29], Maria N. Umaña[32], Oscar Valverde-Barrantes[33], Monique Weemstra[32], Leland K. Werden[34], Michelle Wong[8], Cynthia L. Wright[4], Stuart Joseph Wright[2] and Daniela Yaffar[4,26]

[1] Department of Ecosystem Science and Sustainability, Warner College of Natural Resources, Colorado State University, Fort Collins, CO, United States, [2] Smithsonian Tropical Research Institute, Balboa, Panama, [3] CSIR-Forestry Research Institute of Ghana, KNUST, Kumasi, Ghana, [4] Environmental Sciences Division, Climate Change Sciences Institute, Oak Ridge National Laboratory, Oak Ridge, TN, United States, [5] Asian School of the Environment, Nanyang Technological University, Singapore, Singapore, [6] IFREMER, Laboratoire Environnement et Ressources des Pertuis Charentais (LER-PC), La Tremblade, France, [7] School of Geography, Earth, and Environmental Sciences, University of Birmingham, Birmingham, United Kingdom, [8] Cary Institute of Ecosystem Studies, Millbrook, NY, United States, [9] School of Geography, University of Leeds, Leeds, United Kingdom, [10] Department of Natural Sciences, Manchester Metropolitan University, Manchester, United Kingdom, [11] Department of Geography, UCLA, Los Angeles, CA, United States, [12] Department of Biology, Bieler School of Environment, McGill University, Montreal, QC, Canada, [13] Jardín Botánico Francisco Javier Clavijero, Instituto de Ecología, Xalapa, Mexico, [14] Schmid College of Science and Technology, Chapman University, Orange, CA, United States, [15] Joint Institute for Regional Earth System Science and Engineering, University of California, Los Angeles, Los Angeles, CA, United States, [16] Department Biogeochemical Signals, Max-Planck-Institute for Biogeochemistry, Jena, Germany, [17] AMAP (botAnique et Modélisation de l'Architecture des Plantes et des Végétations), Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France, [18] Centre of Microbiology and Environmental Systems Science, University of Vienna, Vienna, Austria, [19] Biodiversity, Macroecology, and Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany, [20] Plant Ecology and Ecosystems Research, Albrecht von Haller Institute for Plant Sciences, University of Göttingen, Göttingen, Germany, [21] Coordination of Environmental Dynamics, National Institute of Amazonian Research, Manaus, Brazil, [22] Center of Applied Ecology and Sustainability, Pontificia Universidad Católica de Chile, Santiago, Chile, [23] Institute of Botany, The Czech Academy of Sciences, Průhonice, Czechia, [24] Department of Ecology and Evolutionary Biology, Brown University, Providence, RI, United States, [25] Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden, [26] Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Knoxville, TN, United States, [27] Department of Plant Biology, Institute of Biology, University of Campinas – UNICAMP, Campinas, Brazil, [28] Department of Plant and Microbial Biology, University of Minnesota, St. Paul, MN, United States, [29] Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN, United States, [30] School of Life Sciences Weihenstephan, Technical University of Munich, Freising, Germany, [31] Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, United States, [32] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, United States, [33] Department of Biological Sciences, Institute of Environment, International Center of Tropical Biodiversity, Florida International University, Miami, FL, United States, [34] Lyon Arboretum, University of Hawaii at Mânoa, Honolulu, HI, United States

Vegetation processes are fundamentally limited by nutrient and water availability, the uptake of which is mediated by plant roots in terrestrial ecosystems. While tropical forests play a central role in global water, carbon, and nutrient cycling, we know very little about tradeoffs and synergies in root traits that respond to resource scarcity.

Tropical trees face a unique set of resource limitations, with rock-derived nutrients and moisture seasonality governing many ecosystem functions, and nutrient versus water availability often separated spatially and temporally. Root traits that characterize biomass, depth distributions, production and phenology, morphology, physiology, chemistry, and symbiotic relationships can be predictive of plants' capacities to access and acquire nutrients and water, with links to aboveground processes like transpiration, wood productivity, and leaf phenology. In this review, we identify an emerging trend in the literature that tropical fine root biomass and production in surface soils are greatest in infertile or sufficiently moist soils. We also identify interesting paradoxes in tropical forest root responses to changing resources that merit further exploration. For example, specific root length, which typically increases under resource scarcity to expand the volume of soil explored, instead can increase with greater base cation availability, both across natural tropical forest gradients and in fertilization experiments. Also, nutrient additions, rather than reducing mycorrhizal colonization of fine roots as might be expected, increased colonization rates under scenarios of water scarcity in some forests. Efforts to include fine root traits and functions in vegetation models have grown more sophisticated over time, yet there is a disconnect between the emphasis in models characterizing nutrient and water uptake rates and carbon costs versus the emphasis in field experiments on measuring root biomass, production, and morphology in response to changes in resource availability. Closer integration of field and modeling efforts could connect mechanistic investigation of fine-root dynamics to ecosystem-scale understanding of nutrient and water cycling, allowing us to better predict tropical forest-climate feedbacks.

INTRODUCTION: TROPICAL ROOT ACQUISITION OF NUTRIENTS AND WATER

Tropical forests play a dominant role in regulating global water, nutrient, and carbon (C) cycles (Field et al., 1998; Jobbagy and Jackson, 2000; Cleveland et al., 2011), and fine root biomass, production, and uptake activity mediate all of these biogeochemical cycles. Fine roots in tropical forests are responsible for acquisition of water and nutrients under very different climatic and edaphic conditions compared to temperate forests, where most of our knowledge on root traits and function originates. First, seasonality in tropical forests is typically dictated by changes in rainfall rather than temperature. Second, deep, clay-rich, strongly weathered soils scarce in rock-derived nutrients are dominant in >50% of tropical forests (Holzman, 2008), unlike most temperate forests. Thus, surface soil water availability is often scarce in tropical forests for parts of the year and must be sourced from deeper soil (Davidson et al., 2011), while available nutrients accumulate in the seasonally dry surface soils (Cornejo et al., 1994), creating temporal and spatial separation between water and nutrient availability. Tropical forests rely on fine root adaptations to overcome these resource scarcities to support some of the greatest annual primary productivity rates on Earth (Field et al., 1998). Vegetation models

increasingly include the complexity and functionality of water, nitrogen (N), and phosphorus (P) availability in order to predict responses of tropical forests to global change (Fleischer et al., 2019). Nonetheless, in vegetation models, tradeoffs and synergies in root traits for water uptake and nutrient acquisition in tropical forests are largely unknown, or continue to be derived from models based on temperate forest observations. A better understanding of how commonly measured tropical root traits relate to nutrient and water uptake and plant function in tropical forests could help us improve predictive models of forest-climate feedbacks for tropical biomes.

One of the largest challenges facing tropical forests is chronic atmospheric drying and increased severity and frequency of episodic drought as a result of climate change. These drying trends have already been documented in some tropical regions (Aleixo et al., 2019; Powers et al., 2020) and are predicted to be the primary manifestations of climate change for the majority of tropical regions (Kharin et al., 2007; Feng et al., 2013; Magrin et al., 2014; Duffy et al., 2015; Chadwick et al., 2016; Barkhordarian et al., 2019), with likely catastrophic effects for tropical forest persistence and function in some areas (Brodribb et al., 2020). Extreme droughts are predicted to shift tropical plant community assemblages and select for drought tolerant plant functional types, suppress net primary production (NPP), increase plant mortality, and reduce ecosystem C storage

(Nepstad et al., 2002, 2007; da-Costa et al., 2010; Doughty et al., 2015; Cusack et al., 2016; Feldpausch et al., 2016; Aguirre-Gutierrez et al., 2019). For example, in areas of the Amazon, dry-adapted species are increasing in abundance (Esquivel-Muelbert et al., 2019). However, the high diversity of plant hydraulic strategies, as well as niche partitioning belowground could help mitigate the negative effects of drought on net water and nutrient uptake at the ecosystem level, as shown in some Amazon forests (Chitra-Tarak et al., 2018; Brum et al., 2019; Janssen et al., 2020; Oliveira et al., 2021). Belowground niche partitioning among plant functional types and taxonomic units is still poorly characterized in most tropical forests, and should be investigated through soil profiles vertically, laterally, and temporally. Understanding the mechanisms and capacity for tropical forests to overcome increasingly scarce resources through diverse root acquisition strategies will help us better predict broad-scale responses of tropical forests to expected climate change.

Nutrient and water acquisition occur primarily through fine roots (roots < 2 mm diameter), particularly by absorptive roots, which are the most distal orders of fine root systems (typically first- to third-order roots) (McCormack et al., 2015). The production, turnover, and physiological activity of fine roots therefore mediate nutrient, water, and carbon exchanges among soils, plants, and the atmosphere (Bardgett et al., 2014). To overcome resource scarcity, plants can dynamically allocate assimilated C to biomass growth above- or belowground, including C allocation to microbial symbionts that assist with resource acquisition (Davidson, 1969; Thornley, 1972; Bloom et al., 1985). For example, when water or nutrients are relatively more limiting to growth than aboveground resources (e.g., light), plants can increase the relative allocation of C to root biomass, increasing root:shoot ratios (Brouwer, 1963; Shipley and Meziane, 2002; Roa-Fuentes et al., 2021). Under these conditions, plants tend to express fine root morphological, physiological, and phenological traits that maximize resource acquisition (Violle et al., 2007).

Many fine root traits assist with multiple functions, such that a single trait can contribute to water and nutrient acquisition (Comas et al., 2013; Freschet et al., 2021). For example, specific root length (SRL, or length per mass), fine root biomass depth distribution, root elongation rate, root branching density, and mycorrhizal colonization intensity are all traits that can adjust to multiple resource scarcities (Kong et al., 2014). Other root traits are associated more specifically with acquisition of only one resource, like root nodulation to host symbiotic N-fixing microbes for N acquisition, root phosphatase production for P acquisition, or hydraulic conductance and cortical thickness for water acquisition (Lambers et al., 2008). Thus, root physiology and symbiotic associations can be more targeted at the acquisition of a particular resource. For fine root traits that are associated with the acquisition of multiple resources, the responses to water versus nutrient scarcity can differ, which might lead to tradeoffs among traits expressed, and spatial and temporal offsets in resource availability versus plant growth. For example, root biomass depth distributions and productivity through the soil profile, which are traits of overall root architecture and phenology, could be concentrated in surface soils for nutrient acquisition, or could shift to deeper soil for water acquisition (at the expense of nutrient acquisition) during dry periods.

Key uncertainties exist surrounding model representations of tropical plant biomass allocation belowground, root depth distributions, and responses to water and nutrient limitation (Fisher et al., 2012; Smithwick et al., 2014; Warren et al., 2015; Fleischer et al., 2019). While recent progress has been made to improve water, nutrient, and C cycling in vegetation and nutrient uptake models (Zhu et al., 2019; Fisher and Koven, 2020), realistic representations of drying and drought effects on belowground C allocation and water sourcing in diverse tropical forests are challenging (Ciais et al., 2013; Todd-Brown et al., 2014; Tang and Riley, 2021). Trait-based modeling, which relies on plant parameters measured in the field, is increasingly being explored as an alternative to empirical parameters to constrain model uncertainty and improve projections (Xu and Trugman, 2021). Since different resource acquisition strategies exist, which presumably have varying costs and benefits for plants, parameterization and representation of tropical forest nutrient and water uptake require empirical, process-based understanding from field research (Zhu et al., 2019; Allen et al., 2020). A recent surge in field experiments and observations of tropical root responses to changing soil resource conditions could help address these modeling needs.

Here, we synthesize the available data on tropical forest root traits linked to nutrient and water acquisition, assess variation across resource gradients, and based on these patterns, make inferences about how fine root traits might respond to predicted changes in resource availability. We first give sections "Methods" and "Background", and then explore "Fine Root Traits Linked to Nutrient and Water Acquisition in Tropical Forests." Within this section we review commonly measured fine root traits and dynamics that are linked to water and nutrient acquisition (**Figure 1**), including: (1) fine root biomass stocks and depth distributions; (2) fine root dynamics, including patterns in production, mortality, turnover, and phenology; (3) fine root morphological traits; (4) fine root physiological traits; (5) fine root symbiotic associations (i.e., "symbiotic traits"), including mycorrhizas and N-fixing microbes. We then assess "Representation of Root Nutrient and Water Acquisition in Terrestrial Vegetation Models," assessing advances to improve the parameterization and representation of fine root dynamics for nutrient and water acquisition, particularly for tropical forests. Finally, we suggest section "Frontiers in Tropical Root Acquisition Research" for research and data-model integration to improve our understanding of how tropical forest fine roots mediate and respond to changes in resource availability.

METHODS

Online search engines, including Web of Science and Scopus, were initially explored in October 2020 using a combination of 118 keywords, yielding 390 results, which were then screened by the authors for relevance (**Appendix 1a** for
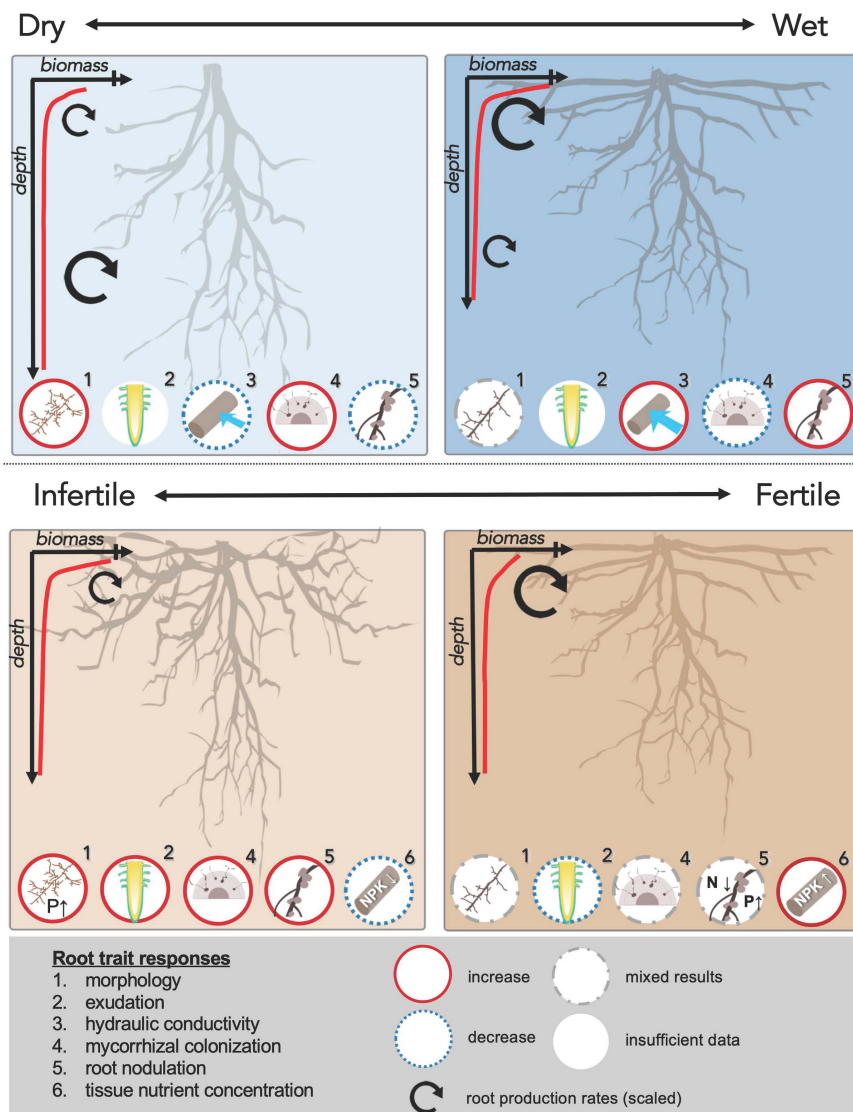
FIGURE 1 | Fine root trait responses to variation in moisture and nutrient availability are shown for tropical forests, following empirical studies in the text. Differences in overall root architecture are shown in each panel, with representative fine root biomass depth distribution curves. Relative differences in fine root production rates are shown as different sized curved arrows for surface soils and subsoils. For example, on the dry-to-wet gradient, wetter sites have shallower root architecture with more surface root biomass, and faster root turnover at the surface but slower root turnover at depth relative to drier sites. Insets show responses of 6 additional fine root traits to the resource conditions, including: (1) root morphology – specific root length per mass (SRL) and/or average diameter; (2) root organic acid and phosphatase enzyme exudates; (3) hydraulic conductance; (4) mycorrhizal colonization rates; (5) root nodulation for N fixing symbionts; (6) fine root tissue content of N, P and K. In the lower panels, circles with N or P and arrows show how increased availability of that nutrient increases or decreases that fine root trait (e.g. increased P increases root SRL in the lower left panel). Missing numbers in some panels are from traits with no relevant data for the gradient shown (e.g., #3 - hydraulic traits - are not shown on the soil fertility gradient). Colored lines around the inset circles indicate: solid line = increase, small dashed line = decrease, mid-dashed line = mixed effects across studies, no line = no data.

initial keywords, **Appendix 2a** for initial results and screening). These initial results formed the basis of the review. Subsequent literature searches were completed in May 2021, in which we repeated the initial search and then optimized the initial keyword searches by text-mining and keyword co-occurrence networks using the R package "LitSearchR" resulting in a final search that used 118 alternative keywords (**Appendix 1b**; Grames et al., 2019). These final keywords were generated based on titles, abstracts, and keywords from papers identified in the initial search. These final keywords were adjusted for Boolean operator strings of search engines, structured to include terms related to root traits and nutrient and water cycling in tropical forest ecosystems and exclude agricultural terms. The revised searches in English, Spanish and Portuguese using Web of Science and Scopus found 2,500 potentially relevant articles (**Appendix 2b**). This set of articles was further screened by

requiring that the title or abstract contained the root trait terms emphasized in this study (e.g., see headings of root trait sections below), and that soil nutrients/fertility or water/moisture was also included, and that the article focused on tropical forests. This further screening resulted in 70 potentially relevant articles not already included in the review to that point (**Appendix 2c**). These additional articles were then assessed by the authors for inclusion in the final manuscript. Nearly all empirical field and modeling studies report results for bulk, community-scale root traits, unless noted in the text that results are at the species-level.

BACKGROUND: RESOURCE VARIATION ACROSS TROPICAL FORESTS

Variation in Water Availability Across Tropical Forests

Ecosystem moisture conditions vary considerably among tropical forests, setting different baselines for plant adaptations to water scarcity and acquisition strategies (Worden et al., 2021). Tropical forests are often differentiated by spatial variation in mean annual precipitation (MAP) and temporal variation in rainfall seasonality. Moist and wet forests span a range of 2,000 to >8,000 mm/year MAP (Holdridge et al., 1971), with many of these forests having an extended dry season of up to 3 months (FAO, 2012). By contrast, dry forests are distinguished by lower MAP of 500–2,000 mm/y, and one or more longer dry seasons (Murphy and Lugo, 1986). Mangrove forests are dispersed across tropical and subtropical coastlines, encompassing a broad range of MAP and seasonality, and are best delimited by the 20°C winter isotherm of sea-surface temperature (Tomlinson, 1986; Duke et al., 1998; Simard et al., 2019). Evapotranspiration in the tropics is often incorrectly considered a constant, but in fact varies widely and is particularly sensitive to net radiation and cloud cover (Fisher et al., 2009). Thus, there is wide variation of climate seasonality and ecosystem water fluxes within forests of any given MAP (Schwartz et al., 2020).

During dry seasons in tropical forests, surface soil moisture can decline dramatically, although the magnitude of the decline varies substantially depending on background rainfall and soil properties (e.g., clay content), as seen across 15 seasonal forests in Panama along rainfall and soil gradients (Cusack et al., 2019). While plants within communities have adapted to seasonal drying, severe episodic drought is defined as outside the normal range of conditions, and has been identified as a period when the relative extractable soil water is less than the 10% quantile of all average dry season months (Janssen et al., 2020). These droughts can manifest as an extension of the dry season, and/or as chronic reductions in rainfall throughout all or part of the wet season (e.g., due to ENSO events) (Ropelewski and Halpert, 1987), and can reduce deep soil water and lower water tables (Broedel et al., 2017). At the other end of the soil moisture spectrum, some tropical forests in valleys are characterized by seasonal flooding and prolonged anaerobic conditions (Esteban et al., 2021). Most data from tropical forests are from upland sites, but we include available studies from mangroves and flooded forests for completeness.

Variation in Nutrient Availability Across Tropical Forests

More than 50% of tropical forests occur on the two most strongly weathered soil orders in USDA soil taxonomy: Ultisols and Oxisols (Holzman, 2008). In these soils, available P and base cations tend to be scarce due to long-term weathering, leaching, and erosion losses of primary minerals (Walker and Syers, 1976; Crews et al., 1995). Thus, P and base cations tend to be cycled quickly and conservatively, with availability of these nutrients driven by decomposition of organic matter (Vitousek and Sanford, 1986). The remaining tropical forests grow on a wide range of soil types that are less weathered and more fertile in P and bases (e.g., Alfisols, Mollisols), but where N is typically more scarce (Sayer and Banin, 2016; Fujii et al., 2018). Variation among soil types and soil orders in tropical forests can occur at landscape- and regional-scales, such as within the lowland forests of Panama and the Amazon basin, both of which include a broad range of soil orders and corresponding nutrient availabilities (Turner and Engelbrecht, 2011; Cusack et al., 2018; Quesada et al., 2020). Thus, tropical forests across geologically diverse landscapes can encompass a broad range of soil orders and nutrient conditions, as observed in >250-fold variation in soil available P and base cations across lowland Panamanian forests (Turner and Engelbrecht, 2011; Cusack et al., 2018), and the Amazon Basin (Quesada et al., 2020). Vertical distributions of nutrients through the soil profile can also vary, with sharp P and base cation depletion at depth in strongly weathered soils, and more even depth distributions of nutrients in fertile soils (Cusack and Turner, 2020). Among tropical mangrove soils, which are typically marine alluvium, there is substantial variation in texture, nutrient content, and organic matter (Hossain and Nuruddin, 2016). This variation in nutrient availability gives rise to large-scale variation in which nutrients limit or co-limit tropical forest NPP and belowground C allocation among sites, as observed across natural soil gradients in the Amazon Basin, Borneo, Costa Rica, French Guiana, Puerto Rico, Panama, and Peru (Medina and Cuevas, 1989; Beinroth et al., 1996; Higgins et al., 2011; Quesada et al., 2012; Russo et al., 2012, 2013; Fisher et al., 2013, 2020; Hofhansl et al., 2020; Soong et al., 2020), and in nutrient fertilization studies across 48 tropical forest sites (Wright, 2019).

There is also temporal variation in nutrient availability in tropical forests, commonly resulting from patterns in litterfall biomass related to rainfall seasonality. With greater litterfall biomass during dry seasons, nutrients tend to accumulate at the soil surface, and then decline rapidly with the onset of the rainy season as plant and microbial uptake and leaching accelerate (Herrera et al., 1978; Yavitt and Wright, 1996; James et al., 2003; Kunert et al., 2010; Cusack et al., 2019). Tropical mangroves and forests on floodplains also have temporal variation in nutrient availability regulated by inputs from flooding (Koschorreck and Darwich, 2003; Chacón et al., 2008) and upstream nutrient discharges (e.g., from upstream farmland and sewage) (Sanders et al., 2014; Reis et al., 2017; Alongi, 2018).

Spatial and temporal trends in N availability in tropical forests are shifting with rapidly increasing atmospheric N deposition from human activity (Schwede et al., 2018). The external inputs of biologically available N to tropical forests have the capacity to change nutrient availability, decomposer activity, and root biomass (Matson et al., 1999; Cusack et al., 2011, 2015; Hietz et al., 2011; Liu et al., 2011). Together, variation in MAP, rainfall seasonality, and nutrient availability set different resource baselines upon which climate change and other global change factors like N deposition are occurring.

FINE ROOT TRAITS LINKED TO NUTRIENT AND WATER ACQUISITION IN TROPICAL FORESTS

Next, we review patterns of tropical forest fine root trait variation across nutrient and moisture availability gradients, which reflect long-term adaptations of plant communities. We also discuss tropical root trait responses to drying and fertilization experiments, which more likely reflect plasticity (i.e., ability to respond to changing conditions) within plant communities. Overall, tropical root traits tend to vary with changing moisture and soil fertility (**Table 1** and **Figure 1**).

Root Biomass Variation and Depth Distributions
Root Biomass: Nutrient Responses
Fine root biomass at the community scale has been by far the most readily available root data across tropical forest root studies (Vogt et al., 1996), particularly for surface soils (e.g., 0–10 cm), as evidenced in the global Fine-Root Ecology Database (FRED) (Iversen et al., 2017, 2021). Thus, patterns of fine root biomass with changes in resource availability are some of the most robust data for drawing insights into tropical forest water and nutrient acquisition strategies, particularly in deeper soils where other root trait data are very scarce. In general, greater P and base cation availability along soil fertility gradients correlate negatively with fine root biomass stocks in surface soils (∼0–30 cm), with this pattern occurring in dry, wet, and mangrove tropical forests (Gower, 1987; Maycock and Congdon, 2000; Ostertag, 2001; Espeleta and Clark, 2007; Castaneda-Moya et al., 2011; Powers and Perez-Aviles, 2013; Cormier et al., 2015; Simard et al., 2019; Huasco et al., 2021). This widespread pattern suggests reduced community-scale belowground biomass allocation when P or base cations are plentiful in tropical forests (Bloom et al., 1985), and can also result from faster turnover rates of fine roots in more fertile soils (Nadelhoffer et al., 1985; Aragao et al., 2009). This inverse relationship also holds for deeper fine-root biomass stocks at 1–2 m depths, as seen for fine roots versus P and base cations across lowland tropical forest soil fertility gradients in Queensland, Costa Rica, and Panama (Cavelier, 1992; Maycock and Congdon, 2000; Espeleta and Clark, 2007; Cusack et al., 2018). There are exceptions to this pattern, particularly in sites where other environmental drivers are stronger drivers of root biomass, such as salinity or hydroperiod in some mangrove

forests (Adame et al., 2014, 2017). Other soil factors like texture have also been related to fine root stock variation across tropical forest gradients (Huasco et al., 2021). Still, the inverse relationship is prevalent enough across tropical forests to suggest that soil P and base cations are a dominant driver of fine root biomass stocks.

Fertilization experiments in tropical forests provide more mixed support for the inverse relationship between nutrient availability and C allocation to fine roots, possibly because not all fertilization experiments successfully alleviate nutrient limitation. A full factorial nutrient fertilization experiment with N, P, potassium (K) and micronutrients in a lowland Panamanian forest found that K additions significantly suppressed root biomass stocks in surface soils, suggesting an alleviation of K limitation (Wurzburger and Wright, 2015). The results from this fertilization experiment in Panama were corroborated by biogeographic patterns of increased root biomass stocks with declining soil K across natural soil gradients in the same region (Cusack et al., 2018). In a factorial N and P fertilization experiment in old-growth and secondary forests in Borneo, fine-root biomass also decreased in response to P fertilization in both old-growth and secondary forests (Yokoyama et al., 2017). However, there are also some mixed results. For example, some studies on infertile soils in montane Puerto Rican forests found positive effects of N or N + P additions on fine root biomass (Fetcher et al., 1996; Yaffar and Norby, 2020), while another montane Puerto Rican study found that N fertilization decreased surface fine root biomass stocks for two forest types (Cusack et al., 2011). Also, a meta-analysis of tropical forest fertilization experiments did not find an overall effect of fertilization with N, P and/or base cations on fine root biomass across 48 sites, likely reflecting site-scale variation in nutrient availability, and also possibly because other aspects of plant C allocation belowground were not considered (e.g., root turnover, organic exudates and root respiration) (Wright, 2019). Thus, assessment of fertilization effects on fine root biomass should consider baseline nutrient availability within a site, whether there is sufficient water availability for uptake of added nutrients, and the effects of fertilization on other root traits. Across these fertilization studies, it seems likely that experiments that added a limiting nutrient effectively reduced root biomass stocks, whereas fertilization experiments that added a non-limiting nutrient (relative to local conditions) did not alter root biomass stocks.

Root biomass depth distributions through the soil profile also often correspond to soil nutrient availability. In infertile soils, which have relatively larger root biomass stocks (see above), the majority of the fine root biomass is often concentrated in the surface soils (0–20 cm), whereas more fertile soils can have more even depth distributions of fine root biomass. This pattern was observed across 43 Panamanian forests where extractable K was the best predictor of root depth distributions (Cusack and Turner, 2020). Similarly, studies in rainforests of Borneo, Costa Rica, Jamaica, and Colombia have found that forest stands on acidic and infertile soils poor in P, K, and/or calcium (Ca) have relatively more fine root biomass concentrated in surface soils compared with more fertile and neutral pH soils (Berish, 1982; Gower, 1987; Espeleta and Clark, 2007;

TABLE 1 | Summary of how the different root traits respond to resource variation (blue = water, green = nutrients) based on empirical studies in tropical forests (cited in the text), and summary of the roles of different root traits in vegetation and nutrient uptake models.

Fine root trait	Wet conditions and wet forests	Dry periods, dry forests, and extreme drought effects	Experimental drying or irrigation	Infertile soil	Fertile soil	Nutrient fertilization	Model parameter	Model process	Related model output
Fine root biomass									
Belowground C allocation				Increases (weak support, inferred from total root biomass changes)	Decreases (weak support, inferred from total root biomass changes)		C allocation to roots is a fixed parameter of NPP in some models (e.g., CABLE, CASA-CNP), or can be based on functional allometric relationships between biomass components, or based on resource limitations	C allocation to roots can be modeled: (1) dynamically, (2) based on allometric relationships (e.g., leaf:root ratios, LPJ-GUESS), or (3) as resource-dependent, wherein low water and nutrient availability lead to increased root allocation	
Root biomass (surface soil < 30 cm depth in most studies)	Greater in surface soil of wetter vs. drier sites (strong support)	Less in surface soil (strong support); also can increase in deeper soil if deep moisture present (some support)	Mixed: Declines with drying, but often no response	More (strong support)	Less (strong support)	Mixed: sometimes declines dependent on relative scarcity of other nutrients and water			Root biomass is modeled as a function of root C allocation and turnover
Root biomass depth distribution (usually measured to 1 m depth)	Fine roots concentrated in shallow soil (weak evidence, little response to rainfall)	More evenly distributed, with more deep roots and deeper maximum rooting depth (medium evidence, sometimes no trend in biomass distribution with rainfall)	Generally no changes observed	Fine roots concentrated in shallow soil with sharp decrease with depth	Distributed evenly with depth	Dependent on moisture scarcity	Rooting depth can be fixed per plant functional type (PFT) or biome in some models, with exponential decay or beta-parameter distribution of roots (e.g., QUINCY). Size-dependent rooting depth is considered in some demographic models (e.g., ED2). Fine tuning this distribution to resource availability in soil could be an area for model improvement	Root biomass depth distribution is modeled dynamically in some models as function resource availability in soil layers (representing horizons or depth increments), and maximum rooting depth	

(Continued)

TABLE 1 | (Continued)

Fine root trait	Wet conditions and wet forests	Dry periods, dry forests, and extreme drought effects	Experimental drying or irrigation	Infertile soil	Fertile soil	Nutrient fertilization	Model parameter	Model process	Related model output
Maximum rooting depth	Shallower maximum rooting depth (strong support)	Deeper maximum rooting depth (strong support)	No change with irrigation				Commonly a fixed parameter in models		
Fine root dynamics									
Fine root production rate	More root production in surface soils, deeper soils less responsive	Less root production	Mixed: decline with drying in seasonal sites, no changes with irrigation during wet season, or drying in an aseasonal site	Slower root production, except in extreme nutrient scarcity sometimes faster	Faster	Mixed: increase with fertilization, unless other more important drivers	Represented as belowground C allocation (described above)	Fine root production is resource-dependent in many models, so that water and nutrient availability control dynamic root allocation	
Fine root mortality rate	Faster mortality rate	Slower mortality rate					Root mortality generally follows overall plant mortality, and is not tied to a soil mechanism	Phenology (difference in timing of production versus mortality) is an area for further development in models	
Fine root turnover time				Longer, except in extreme nutrient scarcity sometimes shorter	Shorter		Turnover is assumed a fixed parameter of fine root C stock, and is in equilibrium with production		

(Continued)

TABLE 1 | (Continued)

Fine root trait	Wet conditions and wet forests	Dry periods, dry forests, and extreme drought effects	Experimental drying or irrigation	Infertile soil	Fertile soil	Nutrient fertilization	Model parameter	Model process	Related model output
Fine root morphology (community-scale)									
Specific root length (SRL)	Decrease within a given root order (strong evidence)	Increase within a given root order (strong evidence)	Increase with drying within a given root order	Mixed: increase in P-poor soils, decrease in base-poor soils within a given root order	Mixed: decrease in P-rich soils, increase in base-rich soils within a given root order	Mixed: increase with 10 year of NPK in Panama; but no change with 1 year of NPK in Brazil within a given root order	Most models do not consider SRL, with some exceptions where SRL or root length are fixed parameters (CASA-CNP, ORCHIDEE, FATES-Hydro). This could be a trait to incorporate in more models	Used to scale hydraulic conductivity to conductance, and to convert fine root biomass to absorptive length or area for nutrient/water uptake rate calculations	
Specific root area (SRA)	Decrease within a given root order	Increase within a given root order	Increase within a given root order			No change with 1 year of NPK in Brazil within a given root order			Used to convert fine root mass to absorptive length or area for nutrient/water uptake rate calculations
Root tissue density (RTD)	No effect at pantropical scale	No effect at pantropical scale		Increase within a given root order	Decline within a given root order	Decline with 10 years of NPK fertilization In Panama			
Fine root diameter	Conserved taxonomically within a given root order	Conserved taxonomically within a given root order	Conserved taxonomically within a given root order	Conserved taxonomically within a given root order	Conserved taxonomically within a given root order	Increase with 1 year of P and cation fertilization in Brazil			

(Continued)

TABLE 1 | (Continued)

Fine root trait	Wet conditions and wet forests	Dry periods, dry forests, and extreme drought effects	Experimental drying or irrigation	Infertile soil	Fertile soil	Nutrient fertilization	Model parameter	Model process	Related model output
Fine Root Nutrient Content / Stoichiometry						Increased P content with 1 year of P fertilization In Brazil	Plant stoichiometry is generally a fixed parameter for different tissues		
Fine root physiology									
Nutrient uptake rates				Rapid P uptake in the litter layer with tracer ^{32}P addition			Nutrient uptake rates are heavily tuned, primarily by parameter calibration. How to parameterize is still a question. Uptake rates are determined by the type of nutrient uptake scheme, with major types of scheme including: (1) Plant demand (2) Equilibrium Chemistry Approximation (ECA) (3) Michaelis-Menten (MM) kinetics (4) Cost-optimization	In the 4 schemes: (1) Plant demand-based, where N/P uptake is a function of plant demand and N/P availability (e.g., CAVLE, JULES-CN) – demand-based is further modeled as a function of root biomass and root uptake capacity (ORCHIDEE-CNP. GDAY) (2) ECA, considering plant competition with microorganisms and mineral surfaces (CLM-ECA) (3) MM kinetics (e.g., FUN, O-CN) (4) The cost-optimization approaches, which use available plant C to "pay" for nutrient uptake C-costs (FUN)	N and P content in plant components

(Continued)

TABLE 1 | (Continued)

Fine root trait	Wet conditions and wet forests	Dry periods, dry forests, and extreme drought effects	Experimental drying or irrigation	Infertile soil	Fertile soil	Nutrient fertilization	Model parameter	Model process	Related model output
Water uptake rates							Water uptake rates are a function between physical gradients and root system hydraulic conductance with more detailed representation found in plant hydrodynamic schemes (e.g., FATES-Hydro, CLM- PHS, ED2-Hydro)	Water uptake rate is a process that depends on external atmospheric demand (potential transpiration)	Transpiration
Organic acid exudation rates				Increase	Decrease		Nutrient cost-optimization models specify exudate rates as C expenditure per unit nutrient uptake, based on field measurements (e.g., FUN)	Sometimes included as a process in soil carbon cycle models (e.g., CORPSE). Nutrient uptake models transfer plant C to soil, in part as exudates, in exchange for nutrients (e.g., FUN)	Soil C and soil respiration

(Continued)

TABLE 1 | (Continued)

Fine root trait	Wet conditions and wet forests	Dry periods, dry forests, and extreme drought effects	Experimental drying or irrigation	Infertile soil	Fertile soil	Nutrient fertilization	Model parameter	Model process	Related model output
Root enzyme production				Increase	Decrease	P fertilization decreases phosphatase enzyme activity, N fertilization increases phosphatase enzyme activities	Phosphatase can be set as a parameter which interacts with soil biogeochemistry to increase available P for uptake (e.g., ELM)	Enzyme production is most often represented indirectly as biochemical mineralization, and can respond to plant or soil nutrient status or temperature (e.g., CABLE, ORCHIDEE-CNP). Vegetation models typically do not include a C cost explicitly for root enzyme production, or they are implicitly encompassed into bulk plant carbon export to soil for nutrient uptake (e.g., nutrient cost-optimization models, FUN)	
Hydraulic conductivity	Greater for light demanding tree species, lower for shade tolerant	Decline, root death, hydraulic failure					Hydraulic conductivity from soil to root is often a tunable parameter		
Fine root symbioses									
AMF - colonization rates, hyphal length, and effect on plant growth		AMF colonization withstands dry periods, increases plant tolerance to drying	Mixed: increased plant growth during drought compared to non-AMF plants	Mixed	Mixed	Mixed: decreased and increased colonization rates with P fertilization (possibly related to water scarcity), decrease with N and cation fertilization		Rarely represented in vegetation models, but sometimes included with no C cost associated, as with AMF distributions specified per plant functional type (e.g., FUN, Coup-CNP)	

(Continued)

TABLE 1 | (Continued)

Fine root trait	Wet conditions and wet forests	Dry periods, dry forests, and extreme drought effects	Experimental drying or irrigation	Infertile soil	Fertile soil	Nutrient fertilization	Model parameter	Model process	Related model output
ECM - colonization rates, hyphal length, and effect on plant growth		ECM withstand dry periods, increases plant tolerance to drying		Mixed	Mixed	Mixed		Rarely represented in vegetation models, but sometimes included with no C cost associated, as with AMF distributions specified per plant functional type (e.g., FUN, Coup-CNP)	
N fixation rates, nodule biomass		N fixation activity declines	N fixation activity declines with drying	N fixation activity increases in low N, decreases in low P	N fixation activity increases in high P	N fertilization decreases N fixation; P fertilization increases N fixation	N-fixing plants are often included as a distinct functional types	Usually represented in vegetation models, where N fixation rates are often estimated empirically as a function of climate or based on NPP. Rates are often constrained by temperature, and can respond dynamically to N availability or be down-regulated by P limitation. N fixation is only sometimes associated with fixed C cost (e.g., FUN, Coup-CNP)	Plant net N uptake from biological N fixation (FUN)

Boxes with no text indicate no known data and highlight areas of research that are needed. Areas with particularly strong support (multiple studies from different sites agree), or weak support (some evidence but requires further research) in the literature are indicated.

Jimenez et al., 2009; Brearley, 2013; Kochsiek et al., 2013). This concentration of root biomass in surface soils likely promotes rapid uptake of nutrients at the soil surface, as observed with ^{32}P additions in an Amazon forest (Stark and Jordan, 1978). Still, a substantial proportion of root biomass can occur at depth even in infertile soils. More than 40% of fine-root biomass and productivity occurred deeper than 30 cm in a P-deficient site in the Brazilian Amazon (Cordeiro et al., 2020), which could be related to water acquisition in these nutrient-poor subsoils.

Root Biomass: Water Responses

In contrast to nutrient availability, soil moisture has been positively correlated with fine root biomass stocks in humid tropical forests. For example, fine root biomass stocks declined during dry periods in Brazilian forests (Metcalfe et al., 2008), and surface root biomass decreased during the dry season in a Brazilian eucalyptus plantation (Jourdan et al., 2008), and during the dry season in a Panamanian forest (Cavelier et al., 1999). In a 7-year Costa Rican study, root growth increased with monthly and annual increases in soil moisture, while the magnitude of the response varied across soil fertility gradients (Espeleta and Clark, 2007). Similarly, surface root biomass was positively correlated with the soil water content of the preceding 30 days in Malaysian forests with little rainfall seasonality (Green et al., 2005). Thus, there is relatively strong evidence that surface root biomass tends to decline during dry periods in tropical forests, which could be accompanied by allocation of root biomass deeper in the soil profile with greater moisture availability.

In contrast to temporal seasonality, there is less indication of variation in root biomass stocks across rainfall gradients. Across a gradient representing a near doubling of rainfall in seasonal lowland forests in Panama from 1,750 to 3,300 mm MAP, there was no relationship between MAP and root biomass stocks to 1 m depth (Cusack et al., 2018), or root depth distributions (Cusack and Turner, 2020), both of which were instead related to soil nutrients (see above). However, in three sites along a drier rainfall gradient in Ghana from 1,200 to 2,050 mm MAP there was a significant increase in root biomass stocks to 30 cm depth with increased rainfall (Ibrahim et al., 2020), which the authors suggest could be related to more acidic soils, larger trees, and reduced fire occurrence in the wetter forest.

Tropical forest rainfall manipulations have shown that fine root biomass sometimes responds to relatively extreme changes in moisture. A 60–80% experimental reduction in rainfall in Indonesia led to a decline in live fine root biomass to 120 cm depth, with the largest decline from 20 to 40 cm depth, and ∼3-fold increase in dead root biomass to 40 cm depth (Moser et al., 2014). In contrast, fine root biomass to 20 cm depth did not change with a 50% reduction in rainfall in southern China, but fine root biomass increased by 20% when rainfall frequency increased (Deng et al., 2018). In a lowland Panamanian forest, 5 years of irrigation during the dry season did not change fine root biomass to 30 cm depth (Yavitt and Wright, 2001). Thus, moisture manipulations

in tropical forests sometimes lead to root biomass responses that mimic natural seasonal patterns, but not in all cases. At sites where irrigation did not lead to increased root biomass, root phenology might respond to other climatic cues besides (or in addition to) increased moisture, such as day length. Or, a different resource, like soil nutrients, might limit root biomass responses to increased moisture. In sites where drying did not lead to declines in root biomass, plant communities might have strong root drought tolerance, or root biomass might not change if roots are dormant but do not turn over during dry periods.

Root biomass depth distributions are important in relation to water acquisition during dry seasons and episodic droughts, with deeper roots likely being able to access deep soil water when surface soils are dry. According to a seminal study on global root distributions (Jackson et al., 1996), ∼ 70% of root biomass in tropical deciduous and evergreen forests occurs in the top 30 cm of soil, but this varies according to moisture regime. For example, a dry forest of Puerto Rico had relatively more deep root biomass compared with wetter Puerto Rican forests (Yaffar and Norby, 2020), although rainfall was not a predictor of root biomass depth distributions over a doubling of rainfall in Panama forests, and instead nutrients predicted depth distributions (Cusack and Turner, 2020). Even though a relatively small proportion of root biomass is typically distributed below 30 cm, even in drier tropical forests, deep roots can be disproportionately important for accessing deep soil water during dry periods in tropical forests (Wagner et al., 2011).

Maximum rooting depth is therefore an important aspect of root depth distributions when considering water acquisition. For example, fine roots in highly seasonal evergreen forests in the eastern Amazon reach depths of up to 18 m, and during the dry season, these trees commonly rely on water obtained from soil depths greater than 8 m (Nepstad et al., 1994). Similarly, a study of 62 tree seedling species in the Amazon found deeper root distributions in drier versus wetter forests (Markesteijn and Poorter, 2009). Isotopic δ^{18}O data from xylem water on Barro Colorado Island (BCI) in Panama indicated that a subset of canopy trees accessed groundwater during the dry season (Meinzer et al., 1999; Andrade et al., 2005). In addition to supplying water directly to plant xylem, deep roots can also redistribute water to recharge surface soils during the dry season in a process termed "hydraulic lift," which has been observed in seasonal Amazonian forests (Oliveira et al., 2005; Markewitz et al., 2010). A synthesis for tropical ecosystems showed that evergreen trees tend to be more deep-rooted in drier forests, but this relationship was not observed for tropical deciduous trees (Oliveira et al., 2021). This same synthesis and another global synthesis found that water table depth is a key factor determining maximum rooting depth within tropical ecosystems (Fan et al., 2017; Oliveira et al., 2021).

Moisture manipulations have generally had no effect on tropical forest root depth distributions and maximum rooting depths. In common garden irrigation experiments in seasonal Panamanian forests, watering for 4 years did not affect the

maximum rooting depth of lianas or trees (Smith-Martin et al., 2019), nor did another dry season irrigation experiment with seedlings in Panama (Yavitt and Wright, 2001). Deep roots are important for withstanding drought and experimental drying, however. For example, a 30% throughfall reduction for 3 years in a strongly seasonal Amazon forest in Tapajos (6-month dry season), did not alter evapotranspiration rates, which a hydraulic uptake model attributed to increased water acquisition from 750 to 1,150 cm depths (Markewitz et al., 2010). Then, in years four and five of this experiment, water was no longer accessed from the deep soil, indicating water depletion that coincided with tree mortality in the drought treatment (Nepstad et al., 2007). Thus, while root depth distributions and maximum rooting depth may not be very plastic root traits, these are important characteristics to withstand drought in tropical forests.

While deep-rooted trees are associated with greater water uptake during dry periods in tropical forests, this is not the only plant strategy for surviving drought. Deep-rooted plants have access to relatively stable deep soil water sources and maintain higher transpiration rates during dry periods, but they also tend to be less resistant to embolism, and have been termed "drought avoiders." This type of drought avoidance can support evergreen trees through dry periods, as observed in seasonal Amazonian forests (Nepstad et al., 1994; Jackson et al., 1995; Davidson et al., 2011). This is in contrast to "drought tolerant" species that have been observed across moisture gradients in the Amazon, which maintain shallow root depth distributions during dry periods, have reduced water uptake, and can also maintain canopy foliage during dry periods (Barros et al., 2019). Forests with long dry seasons in the Amazon have been shown to include a mixture of species with these different strategies (Brum et al., 2019). In tropical dry forests, drought deciduousness, another type of drought avoidance, tends to be the dominant ecological strategy (Oliveira et al., 2021).

Although the majority of our information about tropical roots comes from biomass data, there are some limitations to consider. First, many studies, especially on mature trees, measure changes in absolute fine root biomass rather than root mass fraction (i.e., fine root dry mass per total plant dry mass) along resource gradients. To detect increased plant biomass allocation belowground to roots, studies that measure changes in root biomass should account for aboveground changes in plant biomass, although this is difficult for community-scale studies. Also, root biomass production is only one component of plant belowground C allocation, with root respiration and root organic acid exudates potentially comprising a large proportion of plant belowground C flux (Gill and Jackson, 2000; Phillips et al., 2008). Finally, the relationship between resource acquisition and root biomass is indirect, since root biomass data does not directly indicate water or nutrient uptake activity. These problems create a disconnect between field data and vegetation model approaches, which typically parameterize and represent C allocation belowground dynamically, based on allometric relationships (e.g., leaf:root ratios), or dependent on resources (De Kauwe et al., 2014; Trugman et al., 2019). Plant C allocation belowground is also the main determinant of root biomass and root production in many vegetation models. Thus, field studies

should accompany fine root biomass measurements with whole-plant measures when possible, and with more functional root traits, as described below.

Fine Root Dynamics: Production, Turnover Rates, and Phenology

The timespan from fine root production to mortality is termed the turnover rate, and the timing of root flushing to mortality is termed phenology. Globally, fine root production tends to increase with MAT and MAP, and fine root turnover is greatest in tropical forests compared with temperate and boreal forests (Finer et al., 2011). Below, we consider fine root production and turnover rates from different tropical forest studies, and where possible, also the timing of root flushing and mortality relative to shifts in resource availability and seasonality.

Production and Turnover: Nutrient Responses

Many tropical soils are characterized as nutrient-poor (typically poor in P and base cations), and these soils tend to have larger stocks of fine root biomass, slower fine root production rates, and longer root turnover times compared to more fertile tropical soils. For example, faster fine root production rates have been observed in Hawaiian sites with greater P availability across soil gradients (Ostertag, 2001), and also in higher fertility sites across Central Amazonian soil gradients (Aragao et al., 2009). There was a positive relationship of fine root productivity and turnover rate with greater total soil N and K levels in a wet Colombian forest, as well as greater productivity in more fertile surface soils versus less fertile deeper soils (Quinto et al., 2016). Greater root production rates were also observed in more fertile landward mangroves relative to infertile seaward sites in China (Zhang et al., 2021). However, a contrasting pattern has been observed with extreme nutrient scarcity, with faster root turnover rates in extremely P-scarce ecosystems, possibly because P resorption from roots is efficient (relative to N resorption), so turnover allowed for expanded soil exploration by roots with minimal P losses (Laliberte et al., 2015). Similarly, an extremely infertile sandy soil in the Colombian Amazon had greater root productivity rates in surface soils compared with a more fertile loamy soil (Jimenez et al., 2009). Thus, natural soil fertility gradients indicate that a more conservative strategy of slower production and longer turnover times are typical on infertile sites, although extremely infertile sites can have increased productivity and mortality rates to facilitate exploration of greater soil volumes.

Plot-scale nutrient addition experiments had mixed effects on root productivity. Fine root production rates increased after 10 years of K fertilization in a Panamanian forest (Yavitt et al., 2011), and with N fertilization in Brazilian plantations (Jourdan et al., 2008). Similarly, P addition increased fine root productivity by 23% after 1 year in the Central Amazon (Lugli et al., 2021). In tropical mangroves, P addition also significantly increased fine and coarse root production in sites with infrequent tidal inundation and high salinity (McKee et al., 2007; Adame et al., 2014). In contrast, P addition had no effect on root production in a mangrove frequently inundated with water with low salinity (Adame et al., 2017). Thus, fertilization experiments can yield

similar results as observed across natural soil fertility gradients, depending on other modulating environmental factors.

Production and Turnover: Water Responses

Root dynamics in tropical forests tend to respond strongly to seasonal moisture cycles, with more root production in surface soils being typical during the wet season (Luizao et al., 2007; Rodtassana and Tanner, 2018; Singha et al., 2020). For example, fine root production was greatest during wet periods in an Amazonian rainforest (0–90 cm depth), and this relationship was strongest in surface soils. Fine root mortality was also greater during rainy periods for the top 0–30 cm of soil, while mortality in deeper layers decreased slightly with increased precipitation (Cordeiro et al., 2020). Similarly, there was less production of surface roots (0–15 cm) during the dry season in a Panamanian forest, followed by root flushing upon re-wetting (Yavitt and Wright, 2001). In dry forests in Thailand, mature rubber trees had the greatest root growth 3 months into the rainy season in the top 2 m of the soil, while root growth below this depth did not respond to increased rainfall (Maeght et al., 2015). Even in wetter tropical forests, moisture commonly limits plant growth and dry periods can quickly suppress root production and activity (Clark et al., 2010; Vasconcelos et al., 2012). Thus, tropical forest tree species seem well-adapted to natural moisture shifts, with increased production and mortality during wetter periods, particularly in surface soils.

Experimental manipulation of soil moisture via precipitation diversion has had more mixed effects on root dynamics. For example, increased moisture inputs via dry season irrigation did not affect root growth in a Panamanian forest (Yavitt and Wright, 2001). Fine root production to 20 cm depth also did not change in response to 2 years of experimental drought in Indonesia (Moser et al., 2014). In contrast, fine root mass, length, and production at 0–30 cm soil depth decreased with 2–4 years of experimental drought in a sandy Oxisol in the Brazilian Amazon (Metcalfe et al., 2008). These contrasting results could be related to different baseline conditions in Indonesian versus Brazilian sites, which had 1,894 mm MAP versus 2,500 mm MAP, no dry season versus a 6-month dry season, and pre-montane versus lowland forests, respectively. In particular, the Brazilian forest is adapted to a long natural dry season, which may have increased the responsiveness of roots to experimental drought. Understanding the plasticity of root systems at different sites in response to drought, either via avoidance (e.g., shifting root production deeper for water uptake), or via tolerance (e.g., dormancy through dry periods), will be crucial for predicting spatial variation in forest responses to climatic drying.
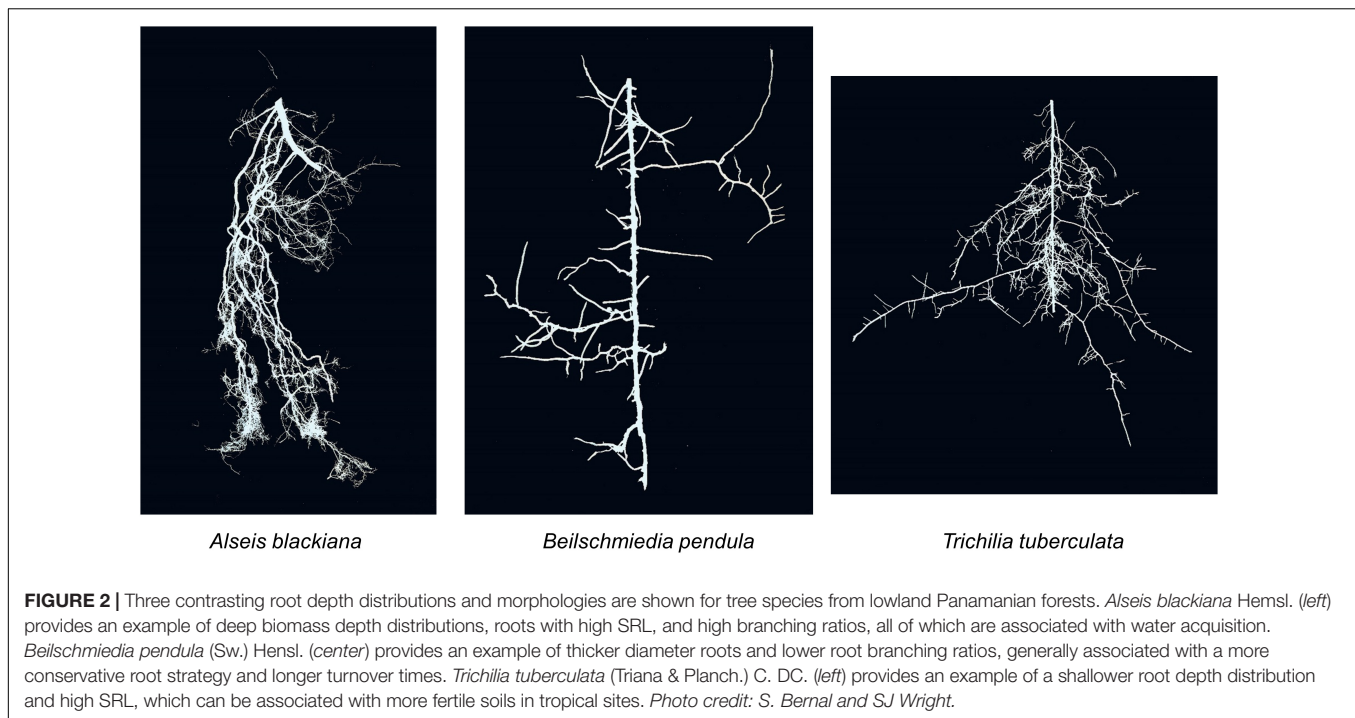
Overall, root phenology appears to respond to the spatial and temporal variations in nutrient availability and seasonality in a particular site, whereas experimental manipulations have had only mixed success at changing fine root production and turnover rates. Thus, environmental cues in addition to moisture likely influence the timing of root production and turnover in many forests. The degree of plasticity in root phenology, both at species and community scales, will be a crucial trait for tropical forests to withstand more intense drought periods. From the limited data, community-scale plasticity in root phenology seems to be far more restricted than might be assumed from patterns across gradients and seasons.

Morphological Root Traits

Fine root morphological traits have been linked to nutrient and water acquisition. For example, plants can explore a larger volume of soil for a given biomass investment with roots that have greater SRL (length per mass), greater specific root area (SRA, area per mass), reduced root tissue density (RTD, mass per volume), greater root branching (e.g., how many first order roots per second order root), and increased root hair density (Eissenstat and Yanai, 1997; Hodge, 2004; Metcalfe et al., 2008). These more acquisitive root traits often present together, as illustrated by some Panamanian tree species (**Figure 2**), and these traits may vary over soil depth. Root hairs can be especially important in plants with minimal mycorrhizal associations, exploring soil volumes that would not be explored by hairless roots (Bates and Lynch, 2001; Abrahao et al., 2019). Higher SRL, or longer and thinner fine roots, can increase overall absorptive capacity, but this morphology has also been associated with greater respiration costs, faster turnover times, decreased mycorrhizal association, and increased susceptibility to pathogen and herbivore attack (Maherali, 2014; Laliberte et al., 2015; McCormack et al., 2015; Weemstra et al., 2019). Root tissue density is associated with longer turnover times and a negative relationship to nutrient uptake capacity (Eissenstat, 1992; Comas and Eissenstat, 2004), such that low density roots are associated with greater resource acquisition. Cluster roots - clusters of closely spaced short lateral rootlets characteristic of plants in the Proteaceae growing in extremely nutrient-poor habitats - can respond to microsites of resource availability and often produce large amounts of organic acid exudates and phosphatase enzymes (Skene, 2001; Costa et al., 2016).

While some fine root morphological traits are generally considered to be responsive to changes in resource availability, other morphological traits, like average root diameter per root order, can be taxonomically conserved (McCormack and Iversen, 2019). The distribution of fine root diameters for tropical forests globally is flatter and evenly distributed from 0.1 to 1 mm, compared to a greater abundance of very fine roots <0.5 mm in other biomes (Ma et al., 2018). Thicker diameter has been associated with longer root turnover times, may have improved resource transport within roots, and have been associated with greater arbuscular mycorrhizal fungi (AMF) colonization rates, as observed in a Brazilian forest (Lugli et al., 2020), suggesting that these roots are more dependent on symbiotic relationships for resource acquisition (Hodge, 2004; Liu et al., 2015; McCormack et al., 2015). There appear to be phylogenetic constraints on the extent to which root morphological traits can respond to changing resources, according studies in subtropical China and French Guiana (Kong et al., 2014; Sun et al., 2020; Valverde-Barrantes et al., 2020). Understanding the plasticity of morphological traits, within and among tropical species, is a crucial step for predicting how tropical forest communities will withstand climatic drying and changes in nutrient availability.

FIGURE 2 | Three contrasting root depth distributions and morphologies are shown for tree species from lowland Panamanian forests. *Alseis blackiana* Hemsl. (*left*) provides an example of deep biomass depth distributions, roots with high SRL, and high branching ratios, all of which are associated with water acquisition. *Beilschmiedia pendula* (Sw.) Hensl. (*center*) provides an example of thicker diameter roots and lower root branching ratios, generally associated with a more conservative root strategy and longer turnover times. *Trichilia tuberculata* (Triana & Planch.) C. DC. (*left*) provides an example of a shallower root depth distribution and high SRL, which can be associated with more fertile soils in tropical sites. *Photo credit: S. Bernal and SJ Wright.*

The relative tradeoffs represented by these different root morphologies have been described as a multi-dimensional spectrum of plant belowground strategies (Bergmann et al., 2020). In this conceptualization, one axis encompasses the classic tradeoff between fast growth, resource acquisition (indicated by root %N), and rapid turnover (i.e., "grow fast die young") at one end of the spectrum, versus slow growth, resource conservation (indicated by dense roots), and longer lifespan at the other end (Reich, 2014). A second axis encompasses a spectrum of resource exploration strategies, with thicker diameter roots that have greater mycorrhizal colonization at one end of the spectrum, versus more long, thin roots with high SRL and less mycorrhizal colonization at the other end.
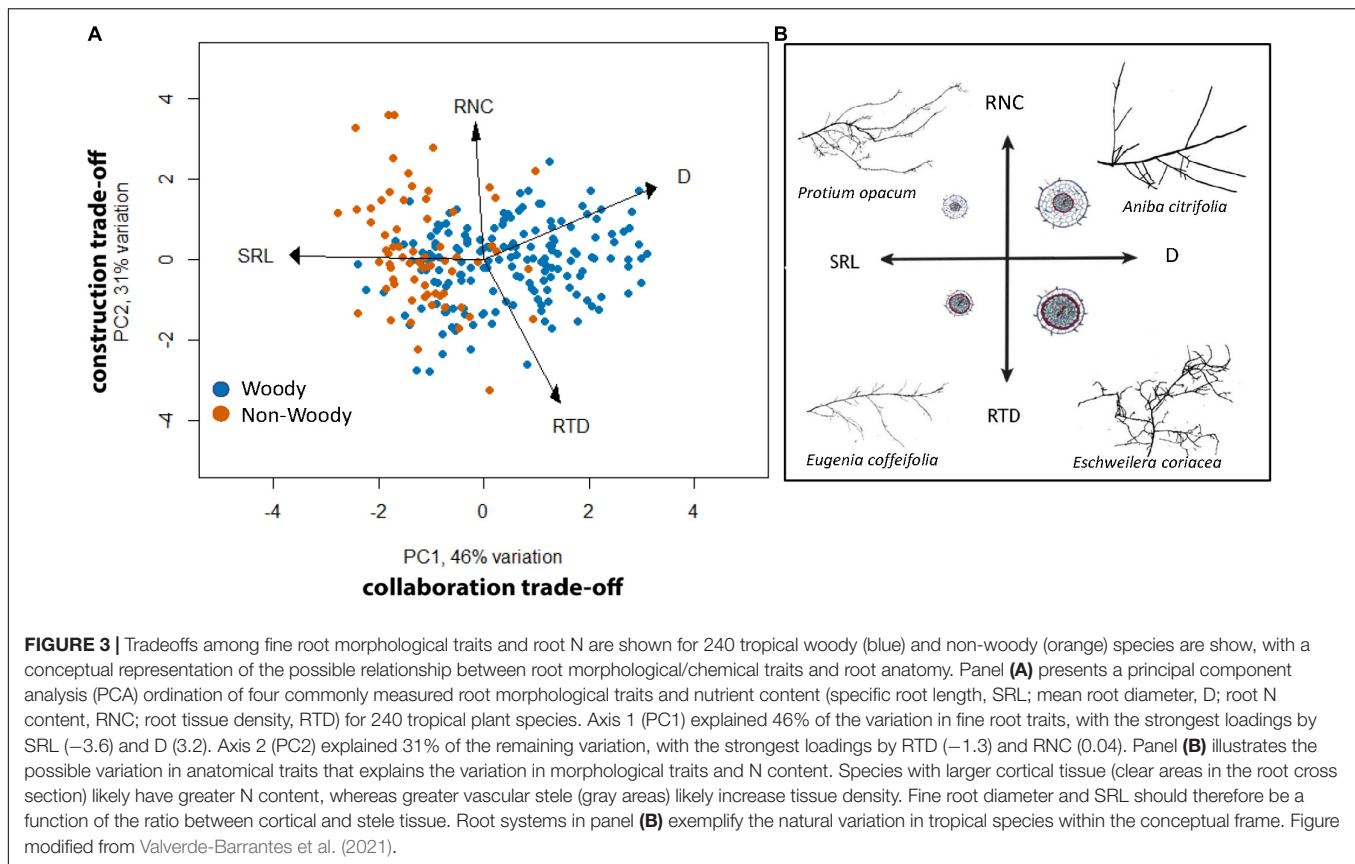
At the biome scale, tropical forests have, on average, root systems with thicker diameter roots, lower SRL, lower N content, and higher RTD than those reported for temperate, boreal or arid ecosystems (Freschet et al., 2017). Following the multidimensional root spectrum hypothesis (Bergmann et al., 2020), these trends suggest that there is an overall selection in tropical areas for long-living root systems that depend largely on mycorrhizal associations for nutrient acquisition. A recent study of variation in fine roots of tropical trees showed that species in dominant tropical families (Moraceae, Fabaceae, and Sapotaceae) have relatively thick diameter, unbranched root systems, which are usually associated with basal angiosperm groups (Valverde-Barrantes et al., 2020). Thicker diameter fine roots in this study were also associated with a set of root anatomical traits, including thick cortical tissue, high cortex:stele ratio, and low root tip abundance, which may also be indicative of increased root

colonization by AMF for resource scavenging. This type of study linking anatomical traits with more commonly measured morphological traits are rare in the tropics, and are very useful for corroborating the function of fine root morphologies.

We assessed a subset of 240 tropical plant species (**Appendix 3**) included in a broader study of root trait syndromes (Valverde-Barrantes et al., 2021), to show that among tropical plants, the strongest fine root morphological tradeoff is between SRL and diameter, which create an axis along which woody and non-woody tropical species separate (**Figure 3**), with a second axis separating along RTD and root N content. These axes separating fine root morphological traits and nutrient content could be explained by different root architectural anatomies, and in particular differences in cortical versus vascular root tissues (**Figure 3**). Globally, tropical forest fine woody root N content tends to span a broader range, from ~0.005 to 0.04% N, compared with other biomes where woody roots tend to have narrower ranges (e.g., ~0.012 to 0.03% N in temperate forests) (Ma et al., 2018).

Morphological Traits: Nutrient Responses

The relationships between fine root morphology, particularly SRL, and nutrient availability in different tropical forest studies are mixed. A pan-tropical review recently indicated that SRL was strongly positively related to base saturation, somewhat contradictory to the expectation that SRL increases when nutrients are scarce (Addo-Danso et al., 2020). This same study found that SRL was weakly negatively correlated with inorganic soil P across global tropical forest regions, similar to local-scale gradient studies in Borneo and Brazil where SRL also decreases

FIGURE 3 | Tradeoffs among fine root morphological traits and root N are shown for 240 tropical woody (blue) and non-woody (orange) species are show, with a conceptual representation of the possible relationship between root morphological/chemical traits and root anatomy. Panel **(A)** presents a principal component analysis (PCA) ordination of four commonly measured root morphological traits and nutrient content (specific root length, SRL; mean root diameter, D; root N content, RNC; root tissue density, RTD) for 240 tropical plant species. Axis 1 (PC1) explained 46% of the variation in fine root traits, with the strongest loadings by SRL (−3.6) and D (3.2). Axis 2 (PC2) explained 31% of the remaining variation, with the strongest loadings by RTD (−1.3) and RNC (0.04). Panel **(B)** illustrates the possible variation in anatomical traits that explains the variation in morphological traits and N content. Species with larger cortical tissue (clear areas in the root cross section) likely have greater N content, whereas greater vascular stele (gray areas) likely increase tissue density. Fine root diameter and SRL should therefore be a function of the ratio between cortical and stele tissue. Root systems in panel **(B)** exemplify the natural variation in tropical species within the conceptual frame. Figure modified from Valverde-Barrantes et al. (2021).

in sites with greater inorganic P (Metcalfe et al., 2008; Zangaro et al., 2008; Kochsiek et al., 2013). Greater root branching, which can also increase root surface area, was observed in response to P scarcity in Puerto Rico (Yaffar et al., 2021). Thus, root SRL appears to respond differently to P versus base cation availability at landscape and larger biogeographic scales, and the functional link between SRL and the uptake of different nutrients requires more investigation.

Fertilization experiments provide some insight into how a community can respond to changes in *in situ* nutrient availability. In lowland seasonal forests in Panama, community-scale RTD declined with 10+ years of N, K, and NPK fertilization, and fine root SRL increased up to 50% with addition of K, NP and NPK (Wurzburger and Wright, 2015), indicating that long-term fertilization led to plants with longer, thinner, and less dense roots, typically associated with greater soil exploration, rapid nutrient uptake, and faster turnover. In contrast, 1 year of N, P, and base cation fertilization in the Central Amazon did not alter RTD, SRL, or SRA in newly produced roots from in-growth cores, and only fine root diameter increased with the addition of P and cations separately (Lugli et al., 2021), although it was unclear in this study whether the same species were being observed, or if there was a shift in which species were represented in the cores. Together, these data suggest that most morphological root traits can adapt to changes in nutrient availability, but the change can be gradual in response to fertilization (i.e., more than 1 year). Clearly, more

data from tropical fertilization experiments over longer time periods are needed for a better assessment of the plasticity of morphological root traits.

Morphological Traits: Water Responses

Tree species and community-scale fine root morphological traits tend to assemble in predictable ways in relation to soil moisture (Holdaway et al., 2011). Plants adapted to dry conditions often have smaller diameter fine roots and greater SRL relative to wetter sites, increasing the volume of soil explored and decreasing the apoplastic barrier for water entering the xylem (Comas et al., 2013). However, data for root morphology across tropical rainfall gradients are lacking. An experimental drought in seasonal Amazonian forests increased SRA and SRL at the same time that overall root biomass decreased, indicating reduced biomass with longer, thinner roots in drier soils (Metcalfe et al., 2008). Thus, SRL can increase in response to greater moisture, and appears to be a relatively plastic trait in response to drought, although more research on the biogeographic patterns and plasticity of SRL with changes in moisture is needed.

Physiological Root Traits: Nutrient Uptake, Root Enzyme Activities, and Exudation Rates

In general, fine root physiological traits are less studied compared with morphological traits in tropical forests, constituting a key knowledge gap in tropical ecology.

Physiological traits directly measure root function, whereas the biomass and morphological traits discussed above are generally surrogates for root physiological functions (Freschet et al., 2021). Fine root nutrient and water uptake rates are physiological traits, as are root exudation rates of nutrient-acquiring enzymes and organic acids, and hydraulic conductance.

There is very little data for nutrient uptake rates in tropical forests aside from uptake of N, which as discussed above is often relatively abundant in tropical soils. As might be expected given the relative abundance of N in tropical forests, the few published N uptake rates for tropical forests indicate much slower uptake compared with other biomes (e.g., 1.6 μgN/g-root/h in tropical forests, versus 17.7 in temperate forests μgN/g-root/h) (Ma et al., 2018). Nutrient uptake rates can be measured directly using a solution-depletion method in the field on in-tact roots (Lucash et al., 2007). Plant nutrient uptake rates can also be directly measured by tracing isotopically labeled nutrients and/or water, using the rare stable isotopes ^{15}N, ^{2}H, and ^{17}O, and the much more logistically challenging radio-isotope ^{32}P (Herrera et al., 1978; Templer et al., 2008).

Fine root exudation of organic acids and nutrient-acquiring enzymes, like phosphatases, increase nutrient availability in the rhizosphere. First, organic acid exudates solubilize inorganic nutrients in general, leading to greater availability (Costa et al., 2016). Second, root extracellular enzymes released into soils hydrolyze ester bonds in organic matter and release inorganic nutrients. Organic acid exudation has been measured primarily in temperate forests and tropical savannas on individual, intact roots immersed in water solutions (Phillips et al., 2008; Abrahao et al., 2014, 2019; Teodoro et al., 2019). Root extracellular enzyme activities are often measured on cut roots in the lab using standard hydrolytic enzyme substrates (Steidinger et al., 2015; Yokoyama et al., 2017), although many more studies have measured bulk soil enzyme activities as an integrated measure of root plus microbial enzyme activities.

For water acquisition, root hydraulic conductance has been used as a direct measure of water uptake capacity. Fine root hydraulic conductance is linked to a plants' capacity to withstand drought (Comas et al., 2013), and can also aid in passive uptake of nutrients dissolved in soil water (McMurtrie and Nasholm, 2018). The hydraulic efficiency of water uptake can be measured as root hydraulic conductivity, a property of root tissue, or as root hydraulic conductance, a rate (Hunt et al., 1991; Schuldt et al., 2013). Root hydraulic conductivity is comprises radial and axial components, with radial conductivity indicating water flow from soil-to-root, and axial conductivity indicating water flow within root xylem. Root radial hydraulic conductivity is orders of magnitude lower than axial conductivity, and is often the rate limiting step for water acquisition. Radial hydraulic conductivity commonly varies greatly in magnitude both intra- and

interspecifically for tropical trees (Tyree et al., 1998; Shimizu et al., 2005).

In general, these physiological traits are targeted at either nutrient or water acquisition, but overlaps and indirect effects among them deserve more investigation.

Physiological Traits: Nutrient Responses

Direct measures of nutrient uptake rates are very rare for tropical forests, and most have focused on plant nutrient preferences, rather than comparing nutrient uptake rates across soil fertility gradients. For example, trees in a montane Puerto Rican forest showed preference for ammonium (NH_4^+) over nitrate (NO_3^-) in a study using ^{15}N isotopic tracers (Templer et al., 2008). A sapling study in a montane forest in Ecuador showed that four species preferred NO_3^- over NH_4^+, but the two species with the highest growth rates preferred NH_4^+ (Wittich et al., 2015). In Panama, ^{15}N isotopic tracer additions showed no overall preference among palm and woody tree species for NO_3^-, NH_4^+, or glycine (Andersen and Turner, 2013; Andersen et al., 2017), and there was a similar lack of preference among N chemical forms for nine Bornean tree species (Russo et al., 2013). These studies indicate that plant species within the same site vary in N preference, or show no N preference. Addition of trace amounts of ^{32}P in an infertile Amazon forest showed rapid and almost complete uptake of added P in the litter layer of soil (Herrera et al., 1978; Stark and Jordan, 1978), showing conservative cycling of P. An important next step in this line of research will be to compare uptake rates among N, P and base cations within and among tree species, and across sites with different soil fertility. This type of study would indicate the capacity for fine roots to adjust uptake rates in response to changing resources.

Rates of root organic acid exudation generally increase when soil nutrients are scarce (Costa et al., 2016). For example, root exudation rates in Malaysian forests were greater in P-poor soils and used a greater proportion of plant NPP, and exudation rates were lower in a P-rich soil (Aoki et al., 2012). In this study, organic acid exudation rates were positively correlated with fine root surface area, indicating a link between morphology and physiology. Similarly, 18 tree species in a subtropical forest in China had fine root organic exudation rates that were positively associated with other traits indicative of nutrient acquisition (e.g., root N concentration), and exudate rates were negatively associated with root traits indicative of more conservative fine root strategies (e.g., RTD) (Sun et al., 2020). Thus, fine root morphology and nutrient content, which are relatively easy to measure, might be good indicators of root exudation activity, which is much more difficult to quantify extensively.

Fine root phosphatase activities are generally inversely related to soil P availability in tropical forests. Across lowland Panamanian forests, fine root phosphatase activity rates were higher in P-scarce soils and lower in P-rich soils, but there was also high interspecific variation in fine root phosphatase activity in the P-scarce soils, suggesting a range of strategies to tolerate P scarcity (Guilbeault-Mayers et al., 2020). A study in Puerto Rico showed that fine root phosphatase activity was negatively associated with soil extractable inorganic P (Cabugao et al., 2021). Fine root phosphatase activity decreased with

P fertilization in a Central Amazonian forest (Lugli et al., 2021), and in old-growth and secondary forests in SE Asia (Yokoyama et al., 2017). Increased phosphatase enzyme activity has also been associated with greater SRL (Cabugao et al., 2021) and fine root P content (Lugli et al., 2021), but the relationship with SRL was observed only at the community level and not at the species level in Puerto Rico (Yaffar et al., 2021). Nevertheless, these results suggest that occurrence of plants with longer, thinner roots (high SRL) can increase resource acquisition in nutrient-poor soils, in this case via enzyme production.

While direct studies of root phosphatase activities in tropical forests are still relatively scarce, a broader set of research using bulk soils indicates that N availability might also influence root phosphatase activities. A global meta-analysis found that P addition suppressed phosphatase activity, but N fertilization increased root phosphatase activity, possibly because of the high N requirement for enzyme production (Marklein and Houlton, 2012). The meta-analysis had very few tropical studies, but similar increases in soil phosphatase enzymes with N fertilization in an upper elevation Puerto Rican forest confirm the trend (Cusack et al., 2010). Also, fertilization in Hawaiian forests showed that P addition reduced root phosphatase enzyme activities in a forest on strongly-weathered, P-scarce soils, while N fertilization increased root phosphatase production (Treseder and Vitousek, 2001; Fujii et al., 2018). More studies of interacting nutrient effects on a broader suite of root enzyme activities are needed.

Physiological Traits: Water Responses

Dry soils with large soil water potential gradients can lead to embolisms in the root xylem vessels, decreasing hydraulic conductance from the soil into the plant. Within the rhizosphere, root dehydration can lead to mechanical failure of cortical cells followed by the shrinkage of roots, promoting a disconnection from soils (Carminati et al., 2009; Cuneo et al., 2016). The capacity for roots to dynamically adjust their water uptake surface area via length growth and mucilage excretions in response to desiccation can minimize the risk of embolism (Carminati and Vetterlein, 2013). Unlike the robust structural and physiological protection plants have against stem hydraulic failure, root mortality, and turnover are common during drought, which can be less costly to plants than investing C in root hydraulic infrastructure.

There are limited field measurements of hydraulic conductance responses to changing moisture availability in tropical regions. In Paleotropical forests, light-demanding, pioneer tree species had more dynamic change in root hydraulic conductance in response to soil water gradients compared with slower growing, late successional species (Shimizu et al., 2005). In Neotropical forests, roots of shade-tolerant species had lower overall hydraulic conductance and were less susceptible to mechanical or hydraulic damage with drying (Tyree et al., 1998). It is unclear whether greater plasticity in root hydraulic conductance of light-demanding species, or the lower but more robust hydraulic conductance of shade-tolerant species, would be more advantageous in drought conditions.

Symbiotic Traits

Mycorrhizal fungal associations are the primary symbiotic root trait related to both nutrient and water uptake. Arbuscular mycorrhizal fungi (AMF) are dominant globally, comprising >72% of associations with plants (Smith and Read, 2008; Brundrett and Tedersoo, 2018). Ectomycorrhizal (ECM) fungal associations are more common in temperate ecosystems (Tedersoo et al., 2010, 2012), but ECM fungi also associate with between 6% (Neotropics) and 19% (Paleotropics) of tropical tree species (Brundrett, 2009; Fukami et al., 2017). There is evidence that 283 plant species from 18 tropical plant families can form ECM associations (Corrales et al., 2018), with ECM fungi commonly dominating in localized areas, comprising up to 75% of tree species symbioses in some tropical forest communities (Lu and Hedin, 2019). Mycorrhizal fungal associations are most commonly measured as the intensity of intraradical colonization, which can be measured for AMF using root staining and microscopic assessment (McGonigle et al., 1990). However, other fungal traits have been proposed to better capture the functional nature of the symbiosis, including: hyphal length, fusions and lifespan, speed of root colonization, formation of vesicles and auxiliary cells, and spore production (van der Heijden and Scheublin, 2007). Molecular techniques to identify specific fungal groups are also increasing in use (McGuire et al., 2012), but the relationship between these molecular studies and nutrient or water uptake rates are limited.

Root nodulation is another symbiotic root trait for hosting N-fixing bacteria, predominantly in leguminous trees (Fabaceae). Generally, this symbiosis can supply substantial quantities of N to plants, and this plant functional type is abundant in many tropical forests (Menge et al., 2017). Plants that establish N-fixing symbioses can also have systematically higher root phosphatase activity than other species, although this differs across species (Nasto et al., 2014, 2017, 2019; Batterman et al., 2018; Soper et al., 2019), and it is unclear whether it results from the high requirement for N in phosphatase production (Houlton et al., 2008) or the alleviation of N limitation by fixation (Batterman et al., 2013a, 2018). Some field and experimental evidence suggests that N fixation can also be associated with improved water use efficiency and tolerance of drought (Adams et al., 2016; McCulloch et al., 2021). Root traits associated with N fixation include nodulation rates, with uptake rates measured using isotopically labeled $^{15}N_2$ or acetylene reduction (Barron et al., 2009; Batterman et al., 2018). One common method to infer the contribution of N fixation to nutrient uptake is by measuring fine root N content. Many plants associate with both mycorrhizal fungi and symbiotic N-fixing bacteria simultaneously (Brearley et al., 2016), and the direct interactions between these two resource-acquiring symbionts require further study in the tropics.

Symbiotic Traits: Nutrient Responses

The major benefit of the association between plants and AMF is the translocation of inorganic P to the host plant, particularly in infertile soils (Smith and Read, 2008). Root-associated AMF

also acquire and translocate other micro- and macronutrients, as observed for some Brazilian trees (Siqueira et al., 1998; Zangaro et al., 2003). Tissue N:P stoichiometry of AMF hyphae has been used in other biomes to assess P versus N uptake by this symbiont, and to indicate fungal growth strategies, such as acquisitive, facilitative, and growth-investing fungi, versus conservative, competitive, and C immobilizing fungi (Powell and Rillig, 2018), and fungal mycelia have more flexible C:N:P stoichiometry than most plant tissues (Camenzind et al., 2021).

The dominant paradigm is that plants invest in mycorrhizal symbioses when nutrients are scarce, and reduce these associations when nutrients are plentiful, which has been observed across many nutrient addition studies globally (Wallenda and Kottke, 1998; Treseder, 2004). Accordingly, P fertilization consistently reduced mycorrhizal colonization rates in Hawaiian forests with P-poor soils (Treseder and Vitousek, 2001). Addition of P and N+P in the Peruvian Amazon decreased fungal hyphal respiration rates, suggesting reduced AMF activity (Fisher et al., 2013). Similarly, a negative relationship between AMF colonization and P availability has been observed in Brazilian savannas (Oliveira et al., 2015). However, an inverse relationship between soil fertility and AMF colonization is not consistently observed across tropical forests. A biogeographic study across Brazil, Costa Rica, Panama, and Peru found that AMF hyphal length was not related to soil nutrient concentrations (Powers et al., 2005). A nutrient fertilization experiment in dry Costa Rican forests also found no effect on AMF colonization (Waring et al., 2019). At mid-elevations in Ecuador, AMF colonization rates increased with added P, and AMF biomass increased with added P and N + P, decreasing only with N fertilization (Camenzind et al., 2016). Similarly, in Panama, added N decreased AMF while added P increased AMF (Wurzburger and Wright, 2015; Sheldrake et al., 2018). Also, cation fertilization, but not P fertilization, increased fine root AMF colonization after 1 year of nutrient manipulation in the Central Amazon (Lugli et al., 2021). These mixed responses of AMF to increased nutrient availability presents something of a paradox. One explanation is that plants invest more in AMF symbioses when one scarce nutrient becomes available but other nutrients are still limiting to plant growth, or water is scarce, or a short term response to increased nutrients. It could also be because many studies examine bulked root samples of a whole community response, which can miss species-specific responses. Also, AMF symbiosis is one of several strategies for plants to acquire P, as suggested by a study of five Puerto Rican canopy tree species where there appeared to be a tradeoff among AMF colonization, root phosphatase enzyme activity, or branching density (Yaffar et al., 2021).

While AMF primarily acquire inorganic nutrients, ECM fungi can acquire nutrients in both organic and inorganic forms (Liu et al., 2018), but remain an understudied symbiont in tropical forests. The abundance of ECM did not vary along a natural P gradient in French Guiana (Soong et al., 2020). A long-term N fertilization experiment in a montane Panamanian forest showed decreased ECM abundance in *Oreomunnea mexicana* roots and a change in the overall ECM genetic composition (Corrales et al., 2017). In contrast, pot experiments with Dipterocarpaceae seedlings, *Shorea macroptera* (Turner et al., 1993) and *Drybalanops lanceolata* (Irino et al., 2004) had increased ECM colonization with NPK fertilization. Another study showed no overall effect of P addition on ECM colonization in two Dipterocarp species, but there were contrasting effects of P on individual ECM taxa (Brearley et al., 2007). Thus, ECM responses to changes in nutrient availability are mixed, similar to AMF responses, and the functional response of mycorrhizae to changes in multiple nutrient and water availability requires more attention.

There is a substantial body of literature suggesting that investment in symbiotic N fixation is regulated by both N and P availability in tropical forests. Experiments demonstrate that tropical N-fixing trees generally utilize a facultative fixation strategy in response to soil N scarcity (Menge et al., 2009), as seen following disturbance and during periods of high net biomass accumulation in forests of Panama, Costa Rica, Congo, and Trinidad (Barron et al., 2011; Batterman et al., 2013a; Sullivan et al., 2014; Bauters et al., 2016; Brookshire et al., 2019; Taylor et al., 2019). This facultative response is characterized by downregulation of root nodule biomass and N fixation rates in response to added N, and upregulation of N fixation rates in response to addition of scarce rock-derived nutrients like P and molybdenum, as observed for canopy trees and seedlings in Panama (Barron et al., 2009; Batterman et al., 2013b; Trierweiler et al., 2018). In a Costa Rican dry forest there were large increases in nodule abundance in response to P fertilization (Waring et al., 2019). In Panamanian forests plant phylogeny is the strongest determinant of N fixation rates, but root nodulation and N fixation rates also increased in tree fall gaps, where soil nutrient availability is greater than in surrounding undisturbed forest (Wurzburger and Hedin, 2016). Across nutrient gradients in Panamanian forests, root nodule biomass was inversely related to soil mineral N availability (Barron et al., 2011), but in a wet Costa Rican forest, N fixation rates have been more strongly related to light availability (Taylor and Menge, 2018; McCulloch and Porder, 2021).

Symbiotic Traits: Water Responses

Both ECM and AMF fungi can access soil meso- and micropores with their hyphae that fine roots with relatively larger diameters cannot access (Allen, 2007). Also, ECM can increase plant water access because fungal hyphae can tolerate lower water potentials and continue to absorb moisture when root hairs cannot (Theodorou, 1978). These advantages might enhance plant drought tolerance, extend the plant growing seasons by several weeks into dry periods (Allen and Allen, 1986; Auge, 2001), and reduce root mortality rates during dry periods (Allen, 2011). Not many studies have assessed how mycorrhizal fungi influence plant species responses to drought in tropical forests. A drying experiment conducted on one species in French Guiana showed that AMF colonized seedlings had larger biomass compared to non-colonized seedlings under water stress (Bereau et al., 2005). However, an experiment conducted in a dry forest in Mexico found no benefits for plants inoculated with AMF under water stress compared to non-inoculated plants (Gavito et al.,

2008). The role of AMF and ECM in water acquisition across environmental gradients and with sporadic drought requires further investigation in tropical forests.

The link between N fixation and water acquisition is unclear. On the one hand, nodulation and N fixation rates are sensitive to soil moisture (Serraj et al., 1999). Experimental evidence indicates drought negatively affects root nodule N fixation in Neotropical tropical tree seedlings (McCulloch et al., 2021). Seasonal variability in root nodule N fixation activity has also been observed in tropical dry forests, with reduced activity during dry periods (Gei and Powers, 2013). On the other hand, trees with N fixation symbioses are much more abundant in dry than wet tropical forests (Gei et al., 2018; Steidinger et al., 2019), suggesting that the trait conveys a benefit in water use or acquisition. Indeed, Adams et al. (2016) found trees with N fixation symbioses have higher water use efficiency than non-fixing trees. Thus, while symbiotic N fixation itself can be constrained by water (**Table 1**), it also appears to benefit trees in water-stressed conditions. Direct links between root nodule N fixation activity and water acquisition require further study.

Overall, the functional role of root symbionts for nutrient and water uptake remains poorly characterized for tropical forests. In particular, the interacting or tradeoff effects of symbioses on water versus nutrient acquisition require further study. Measuring these functional roles in the field, and integrating these processes into ecosystem models are crucial next steps for predicting how tropical forests will respond to global change.

REPRESENTATION OF ROOT NUTRIENT AND WATER ACQUISITION IN TERRESTRIAL VEGETATION MODELS

Process-based models of the terrestrial biosphere project ecosystem responses to changing environmental drivers. The ability of vegetation models to meet plant demands for water and nutrients has direct feedbacks on biomass growth, significantly altering coupling of C, water, and other biogeochemical cycles (Fleischer et al., 2019; Trugman et al., 2019; Meyerholt et al., 2020), and mycorrhizal representation can also influence modeled soil C storage (Sulman et al., 2019). Traditionally, model development typically focuses on functions of either water or nutrients alone. Recent efforts indicate that P scarcity might be linked to tropical forest NPP susceptibility to drought, illustrating complex interactions among soil resources (Goll et al., 2018). Most nutrient-enabled models include C and N, and more are including P, but none to date include base cations (Thornton et al., 2007; Yang et al., 2014). Base cation availability and mobility in soils are distinct from phosphate (PO_4^{3-}) and other forms of P (Schlesinger and Bernhardt, 2020), so model development to incorporate P cycling is not a good proxy for base cation cycling. Because base cations appear to drive root traits and dynamics in many of the studies reviewed above, base cation cycling should be incorporated into vegetation models to improve simulation of tropical forest belowground dynamics.

Within models, root traits can be a parameter, a functional process, or an outcome – it is important to distinguish how root traits are represented in models in order to integrate them with field research. While improving representation of belowground processes is an area of active development in vegetation models, it lags behind more readily observed aboveground processes (Warren et al., 2015; Fisher et al., 2018). For example, belowground biomass is often an outcome of vegetation models, root depth distribution and hydraulic conductance are often set or adjustable parameters, and biomass allocation to roots can be a fixed parameter or is dynamically controlled by resource availability (**Table 1**). In the IPCC there have been up to 28 Earth system models, and many of these are linked to vegetation models (e.g., the TRENDY set of models) that include root dynamics (Arora et al., 2020). Typically, maximum rooting depth varies with PFT in vegetation models. For example, in a new version of Lund-Potsdam-Jena managed land vegetation model (LPJmL4.0), rooting depth varies from 0.5 to 18 m, depending on allocation of the PFT, but rooting depth also depends on ecosystem factors (Sakschewski et al., 2021). With dynamic C allocation schemes that respond to resource limitation, simulation of accurate root productivity is likely to improve, as indicated in this new version of LPJmL4.0.

Vegetation Models: Nutrient Uptake

While water uptake processes are dominated by gradient-driven mass fluxes in ecosystems, nutrients are mediated by more complex chemical and biological interactions within the soil. Thus, their incorporation into global models has been more gradual, with some large-scale efforts focusing on C, N, and P (Wang et al., 2010; Yang et al., 2014). Model development first focused on implementation of N cycling and acquisition in vegetation models, mostly based on process understanding and observations from temperate forests (Thornton et al., 2007; Bonan and Levis, 2010; Zaehle and Friend, 2010; Zaehle et al., 2014; Arora et al., 2020), with symbiotic N fixation often represented as an empirical function of evapotranspiration or NPP, rather than as a dynamic response to soil N availability (Wieder et al., 2015), but recent analyses have found this approach to have poor agreement with observations (Davies-Barnard and Friedlingstein, 2020). A more mechanistic representation of biological N fixation as a functional tradeoff in C cost among other uptake pathways is becoming more predominant in Earth system models (ESMs) (Fisher et al., 2010, 2019; Shi et al., 2016; Lawrence et al., 2019). At the same time, efforts to realistically represent P cycling and acquisition in vegetation models are surging, largely to improve representation of tropical forests (Yang et al., 2014). In their inter-model comparison, Fleischer et al. (2019) found that inclusion of P cycle constraints reduced biomass accumulation of a tropical site in response to elevated CO_2 by approximately 50% compared to C-only and C–N models. Considerable variability in model output among the CNP models was attributed to the different plant P acquisition and usage schemes utilized by the models, so constraining these processes is paramount. However, lack of process understanding and data for parameterization are hampering progress.

Nutrient acquisition schemes vary across model scale and type, and often are not explicitly tied to root traits or dynamics. In

most model schemes, nutrient demand by the plant is determined by: (1) fixed or dynamic stoichiometric ratios for each plant tissue type, and (2) allometric parameters that relate nutrients to C allocation among plant tissues (Thornton et al., 2007; Yang et al., 2014). Stoichiometric ratios can be allowed to vary within bounds, as in CABLE, QUINCY, and ORCHIDEE-CNP, reflecting field observations of plasticity in stoichiometric ratios (Meyerholt and Zaehle, 2018). In other models, stoichiometric ratios of C:N and N:P are fixed (e.g., JULES-CN), or vary without bounds (e.g., O-CN, GDAY) (Zaehle and Friend, 2010; Fleischer et al., 2019). Stoichiometric ratios are important features in vegetation models, because they govern plant demand for nutrients, and should be related to root nutrient uptake, nutrient resorption rates and tissue turnover times.

Within the context of plant demand and soil nutrient supply, root biomass and root uptake capacity additionally determine nutrient uptake rates in some vegetation models, such as ORCHIDEE-CNP and GDAY (Goll et al., 2017). Some models consider Michaelis-Menten kinetics of ammonium and nitrate uptake capacity per root biomass, for example O–CN (Zaehle and Friend, 2010), while others consider N uptake to be a function of plant N demand and cohort partitioning of fine root surface area, for example LPJ-GUESS (Smith et al., 2014). Among these models, none consider the functionality of fine root morphological traits like SRL for N or P uptake. Thus, more extensive data on root functionality, and how this relates to commonly measured root traits and to nutrient availability across tropical forests, could improve nutrient acquisition and allocation representation in vegetation models.

Vegetation models also implement a range of assumptions about competition for soil nutrients among plants, soil microbes, and mineral surfaces, which can modulate P availability in particular in tropical soils, as in CLM-ECA and the Jena Soil Model (JSM) (Zhu et al., 2016; Yu et al., 2020). For P acquisition, most models include the biochemical mineralization of organic P through phosphatase enzyme activity, but functional representation differs across models, with most models using a relatively simple control of plant demand or soil P availability over phosphatase-based mineralization (Fleischer et al., 2019). Yang et al. (2016) identified phosphatase as a critical response variable for vegetation biomass production under low fertility conditions. However, observations of tropical root phosphatase activity are scarce, and functional understanding of controls over phosphatase activity in tropical forests is limited. Some recent field data from Puerto Rico suggest that phosphatase activity in the rhizosphere and on root surfaces are more closely related to root P content and soil P availability than are bulk soil enzyme activities (Cabugao et al., 2021), so direct measures of enzyme activities on roots are needed. In most of these models, production of phosphatase enzymes and other investments in nutrient acquisition come at no extra C costs to plants. Approaches in models that focus more specifically on nutrient uptake determine N and P uptake rates as a balance of dynamically-varying C costs among different uptake pathways, including AMF and ECM symbioses, direct root uptake, leaf retranslocation, and biological N fixation, with pathways varying relative to demand for plant growth and maintenance, such as in

the Fixation and Uptake of Nutrients (FUN and FUN-P) nutrient uptake models (Fisher et al., 2010; Brzostek et al., 2014; Allen et al., 2020), which can be coupled to vegetation models and embedded in land surface models to improve nutrient uptake process-scale representation (Shi et al., 2016). The relationship of root nutrient uptake rate with other more commonly measured root traits, like morphological traits, production, and mortality, would be useful for improving nutrient uptake representation for tropical forests in vegetation models.

Vegetation Models: Water Uptake

Earth system models have classically represented water uptake as a function of atmospheric demand and root biomass, with water uptake constrained under dry soil conditions by a simple linear function (Feddes et al., 1976). While computationally inexpensive, this approach has been shown to underestimate water uptake under water-limited or drought conditions (Feddes et al., 2001). More recently, there has been a push for ESMs to incorporate more mechanistic plant hydraulics schemes (rather than empirical functions), which capture the plasticity of plant ecohydrology under drying conditions (e.g., hydraulic redistribution, compensatory uptake) (Eller et al., 2020), and can feedback to modify local climate, as indicated when Amazon hydraulic redistribution was incorporated into an atmospheric circulation model (Lee et al., 2005).

Root-mediated water uptake in larger land surface and climate models has evolved from purely zero-dimensional empirical functions that represent water uptake as a function of rooting depth, to one- and two-dimensional formulations which account for the vertical distribution of root biomass within the soil (Warren et al., 2015; Fatichi et al., 2016). Early implementations were biased toward the early onset of water limitation to plants, unable to fully resolve field observations under drying conditions (Feddes et al., 2001). Additional functions, or "correction factors," were later added to account for hydraulic redistribution and compensatory uptake, processes observationally shown to mediate plant water stress (Oliveira et al., 2005; Stahl et al., 2013), but these functions lack connection with measurable root traits (Feddes and Roats, 2004).

Recent work has demonstrated the importance of improving representation of fine roots to model ecosystem and regional-scale hydraulics (Fatichi et al., 2016; Xu and Trugman, 2021). Yet, aside from vertical root biomass and root depth distributions, approaches in terrestrial vegetation models are still largely decoupled from the measured root traits and dynamics reviewed above. These models typically rely on static model parameters inferred to match site-specific conditions and observed water fluxes. Recent advances in root representation in models include the addition of plant hydrodynamics modules to larger vegetation models, aimed at increasing the fidelity of feedbacks between water acquisition and plant growth (Christoffersen et al., 2016; Xu et al., 2016; Kennedy et al., 2019). Similar to finer scale models, water uptake is driven by water potential gradients within the soil-plant-atmosphere continuum in these modules, resolving processes like hydraulic redistribution and compensatory uptake. In these modules, which are relatively good at modeling plant mortality, important drivers of water uptake include: vertical root

depth distribution, and hydraulic resistance between soil and the rhizosphere (typically measured by root hydraulic conductance) (Christoffersen et al., 2016; Kennedy et al., 2019). Plant hydrodynamics implemented within CLM5 by Kennedy et al. (2019) quantified soil to root conductance as a function of root hydraulic conductivity and root surface area per unit ground area, so fine root SRL can play a role in these models. In FATES-Hydro (previously published as TFS v.1-Hydro; Christoffersen et al., 2016), the rhizosphere was distributed as shells layered around roots in the soil column, with soil to root hydraulic conductance scaled as a function of root biomass depth distribution, defined as an exponential decay function, as well as SRL and root hydraulic conductivity. Both approaches incorporate measurable root characteristics to improve representation of water uptake and effects on plant NPP, however, the paucity of tropical forest field observations has led to inference of parameters using more readily available aboveground proxies, with whole root conductance designated as a fraction of modeled aboveground biomass or resistance.

Beyond plant hydrodynamics models, which incorporate the entire soil-plant-atmospheric continuum, there are approaches which focus on resolving more detailed and mechanistic root structure and function with the computational scalability needed for larger scale simulations. These smaller scale models incorporate root morphology and physiology, with spatiotemporal patterns of water uptake emerging as a result of interactions between the physical soil environment and root biology (Doussan et al., 2006). These models capture spatial and temporal shifts in plant water sourcing driven by individual and competitive interactions among plants within the system (Manoli et al., 2014; Agee et al., 2021). A modeling study using 3 years of seasonal drought data from the Amazon suggested that deep roots with niche partitioning adaptations, which source water from different depths in the soil during different times of year, explained observational resilience to seasonal drought and vulnerability to severe episodic drought (Ivanov et al., 2012). This study added to previous representations by generating multiple root biomass depth distributions for different tree size classes, creating "root niche segregation" profiles, which are more closely aligned with site observations than earlier models without multiple root depth profiles.

Linking these smaller scale models to larger scale function, Couvreur et al. (2012) developed a hybrid micro-/macroscale scheme which reduces root system architecture and hydraulic traits (e.g., radial and axial root hydraulic conductivity) at the individual scale to develop scalable macroscale parameters which maintain important hydraulic information. This approach was implemented in HYDRUS (Baram et al., 2016; Cai et al., 2018), and CLM models (Sulis et al., 2019). However, these fine-scale approaches require large amounts of data to parameterize and validate model outcomes, constituting a significant challenge to scaling beyond a few individuals or a local region (Javaux et al., 2013). Linking small-scale root traits and root function representation into these larger scale models remains a frontier for accurate representation of root water uptake, particularly for biomes like tropical forests with scarce data.

Notably, fine root morphology is one of the more common sets of root traits used in hydraulically-enabled vegetation models. For example, SRL is used for converting fine root biomass values into total fine root length, which represents the surface area for resource uptake, and soil-root hydraulic resistance (Xu and Trugman, 2021). Thus, clarifying the functional relationships between fine root morphology and resource acquisition could be utilized within existing model frameworks to improve representation of tropical forests.

FRONTIERS IN TROPICAL ROOT ACQUISITION RESEARCH

Following the review of available literature above, we suggest research avenues that would be useful to better understand and model tropical root nutrient and water acquisition across tropical forests under global change scenarios of resource change.

What Are the Key Root Traits for Inferring Ecosystem Function in Tropical Forests?

Most of the vegetation modeling efforts to better represent nutrient uptake do not include root traits or function, and there remains a gulf between the data field ecologists collect and the parameters that drive models. The assumption that plant investments in different nutrient and water acquisition mechanisms depends on a C cost-benefit tradeoff. This assumption is currently *not* widely used in vegetation models, but C costs of resource uptake are increasingly considered (Fisher et al., 2010, 2018). In the field, determining the C cost per unit of nutrient or water acquired and how this varies along nutrient and moisture gradients is extremely difficult. However, studies reviewed here have already made advances in determining how plants are investing their C belowground (e.g., root length construction, phosphatase, organic acids exudation, and mycorrhizal associations at the community scale). These assessments are very helpful to constrain C investments in nutrient and water acquisition in vegetation models. Complementary studies in controlled settings could further assess the C cost of different resource acquisition strategies across soil fertility and moisture levels.

Also, key root traits related to nutrient uptake rate might not be the traits we commonly measure in the field, such as SRL and root N (Freschet et al., 2021), and root traits important in tropical forests might not be the same as the key root traits in temperate ecosystems. In particular, P is commonly a limiting nutrient in tropical forests, while N is generally limiting in temperate forests. The importance of accurately modeling P was demonstrated in an assessment of uncertainty among models for predicting Amazon forest biomass response to increased atmospheric CO_2 across 14 vegetation models. Among models that included the C, N, and P cycles, uncertainty in biomass C response to increased atmospheric CO_2 was attributed primarily to the representation of different P use and P acquisition strategies among models, which are challenging to constrain due to the lack of data

(Fleischer et al., 2019). For example, plant strategies for P uptake a very different from those for N uptake (e.g., root exudates and AMF association for P versus ECM and N fixing bacteria association for N) (Weemstra et al., 2016; Freschet et al., 2021), so models designed for forests with soil N scarcity cannot easily be used to simulate dynamics in tropical forests with P scarcity. The tropical field studies reviewed here indicate that fine root biomass can decline when soil P and base cations are plentiful, and that rock-derived nutrients, particularly P and K, drive root biomass stocks and depth distributions across tropical forests (**Table 1**; note that results from fertilization studies were more mixed). Thus, fine root biomass measures should be paired with measures of P and cation availability, cycling, and root uptake to increase process-level understanding that can be incorporated into model development.

Tradeoffs in morphological and physiological traits should be paired with more detailed studies in root anatomy in order to separate short-term functional changes from potentially longer-term structural changes. Changes in root morphology, architecture and physiology are ultimately regulated by the relative areal investment between cortical and stele (vascular) tissue, a trait scarcely included in root ecology studies, but which could be related to variation in fine root SRL, RTD, diameter, and N content (**Figure 3**). The fact that roots of tropical species showed relatively thicker, low SRL, and denser roots compared to other ecosystems suggests a greater dependency on mycorrhizal associations in this biome (Freschet et al., 2017; Wang et al., 2018), although there is a wide range of variation in tropical root morphological and architectural traits (Ma et al., 2018; Shen et al., 2019). This suggests that species can vary their allocation to cortical tissues according to local nutrient availability, as a way to decrease C investment in symbiotic associations and increase root surface area (Kong et al., 2021). In relation to water uptake, Eucalyptus roots in Brazil can present fewer xylem vessels but with larger diameter at depths greater than 10 m compared to shallow roots (Germon et al., 2020), which suggests that changes in anatomical traits in deeper soil layers might increase hydraulic efficiency for that species. Studies of grasses in Japan indicate that proportional allocation to different root tissues (e.g., stele, cortex, xylem, or aerenchyma) is one response to moisture gradients (Yamauchi et al., 2021). However, there is a lack of studies assessing root anatomical traits along nutrient or moisture gradients in tropical areas.

To identify key traits related to tropical forest function, and to address the recurring theme of general lack of field data for tropical forests, we suggest an assessment of the spatial patterns in community-scale traits across tropical bioregions and continents, and comparison with temperate patterns. Standardized root traits and metrics across studies would greatly help in assessment of the tropics as a whole. For example, multiple depths should be assessed for fine root biomass and morphological measures like diameter across studies, so that depth distribution differences can be assessed. These types of comparable and large-scale biogeographic study would help us understand whether a particular trait/response is a genuine pantropical forest pattern, versus a regional or forest type-specific process.

What Are Tropical Root Trait Tradeoffs and Synergies for Nutrient and Water Acquisition?

Key questions remain about tradeoffs and synergies among root traits involved in nutrient and water uptake across tropical forests. In assessing tradeoffs, studies should cover the full resource spectrum, low to high soil fertility and low to high water availability, to assess the full niche space (Silvertown et al., 2015). Many of the above studies investigate how morphological or physiological traits of tropical plants respond to drought, but far fewer investigate the response to flooding, thus omitting the high end of the water availability spectrum, i.e., flooded forests, peat swamp forests, etc. Greater investigation into tradeoffs and synergies among root traits could offer great mechanistic insight to strategies employed by tropical trees. For example, research on the timing and extent of root enzyme activities and/or root exudation, and water uptake, would also inform questions about root trait tradeoffs and synergies for nutrient and water uptake.

To assess these questions, we suggest coordinated studies and manipulation experiments that directly assess water versus nutrient uptake at the community level. For example, natural experiments across biogeographic gradients where rainfall and soil nutrient availability vary could be used more to examine key root traits related to water and nutrient uptake would be useful. Alternatively, large-scale nutrient and rainfall manipulation experiments could address responses to water limitation with changes in nutrient availability. The bulk of the evidence in this review comes from gradient studies and fertilization experiments, which are correlative. To understand functional tradeoffs and synergies among root traits, we also suggest greater emphasis on nutrient tracing experiments with isotopically-labeled nutrient additions to provide greater mechanistic information.

What Are the Cross-Scale Patterns of Root Trait Plasticity in Tropical Forests Undergoing Changing Water and Nutrient Availability?

The plasticity of root depth distribution in response to episodic drought, both at species and community scales, is likely to be crucial for survival in a future drier climate. Some tropical tree species appear to have limited capacity to shift root depth distribution in response to sudden moisture changes, as was shown in a stand-level irrigation experiment in Panama (Yavitt and Wright, 2001). A study in French Guiana using a dual isotope labeling approach found that half of the 65 trees from 47 species studied accessed deep soil water below 100 cm depth during dry periods, and nine individuals had great plasticity in their depth of water uptake, taking advantage of surface water and nutrients during rain events, and quickly switching to deep water stores during dry conditions (Stahl et al., 2013).

We suggest investigating the plasticity of root depth distributions and productivity in response to changes in water

availability over seasonal shifts in tropical forests, as well as in response to chronic drying (i.e., incremental reductions in annual rainfall), and increased intensity and frequency of extended drought. For example, studies could assess intraspecific variation in root trait plasticity across multiple species, and investigate the ability of different species to respond to changes in water and/or nutrient availability. One approach could be sampling root traits for individuals at the centers and edges of species' environmental distribution, and sampling rare species with distinct strategies. This approach could help us identify the range (the extremes) of the tropical belowground trait space.

Should Vegetation Models Represent Plasticity and Sensitivity of Individual Plants or Community-Level Trends for Water and Nutrient Acquisition?

A major question facing vegetation modelers seeking to accurately represent tropical forests is how to incorporate empirical process understanding at the species- or community-level, and use that to create an intermediate scale that aggregates responses of individual plants as functional strategies that can compete with one another within the ecosystem. Thus, functional strategies would be defined to represent the diversity of competitive strategies. Defining these functional types is a challenge, and one reason why many models have explored using belowground economic spectrum analogies. However, belowground empirical studies have demonstrated that simple economic spectrums similar to leaf economic spectrums are inadequate to describe root system tradeoffs (Bergmann et al., 2020). Appropriate groupings for root traits and functions would reproduce plant responses to resource gradients of water and nutrients in tropical forests. These groupings could then be used to forecast plant water, C, and nutrient dynamics under changing climate, as well as shifts in forest composition. A better representation of belowground functional strategy groups within diverse tropical forests would facilitate linkages to aboveground traits and processes. Because of the diversity of tropical forests, characterizing emergent trends in communities over seasonal timescales in the field is likely the most attainable and useful approach to link with modeling endeavors.

CONCLUSION

Fine roots represent the primary site of water and nutrient uptake in tropical forest trees. Because water and nutrients directly constrain plant growth, the traits and functions of fine roots are centrally important to tropical forest growth, nutrient cycling, and responses to climatic changes. This review assessed root traits through the lenses of biomass, depth distributions, phenology, morphology, physiology, and symbiosis, and modeling efforts to represent tropical root traits at small to large scales. We identified emerging trends in the literature that tropical fine root biomass and production

in surface soils are greatest under nutrient scarcity or water abundance. We also found that SRL, which is typically thought to increase under resource scarcity to expand the volume of soil explored, instead increased with greater base cation availability both across natural gradients and in fertilization experiments. The combined literature indicates that the response of the microbial-root symbiosis to changing nutrient levels across tropical forest gradients depends on baseline nutrient concentrations and relative nutrient or water limitation to plant and fungal production. For example, nutrient additions, rather than reducing mycorrhizal colonization of fine roots as might be expected, increased colonization rates under scenarios of water scarcity in some sites.

Efforts to model the traits and functions of fine roots have grown more sophisticated over time, yet there is a disconnect between the emphasis in models on characterizing nutrient and water uptake rates and C costs, and the strong emphasis in field experiments on measuring root biomass, production, and morphology in response to changes in resource availability. Empirical understanding of how water and nutrients, particularly base cations, influence root depth distributions, SRL, physiological root traits, and microbe-root symbioses across tropical forests is still limited, and yet the recent surge in tropical root trait studies provides enough evidence for process-based representation in vegetation models.

We highlight several frontiers for research on tropical forest root nutrient and water uptake: (1) identifying key root traits for predicting ecosystem function and aboveground linkages, (2) connecting commonly measured root morphological traits with physiological and anatomical traits such as hydraulic conductance and nutrient uptake rates for which they currently often serve as proxies, (3) elucidating fine root trait tradeoffs and synergies with microbial symbionts for nutrient and water acquisition, and (4) investigating the extent and scales of plasticity in root trait responses to environmental changes. Closer integration of field and modeling efforts could connect mechanistic investigation of fine-root dynamics to ecosystem-scale understanding of nutrient and water cycling, allowing us to better predict tropical forest-climate feedbacks.

ORCID

Daniela Francis Cusack
orcid.org/0000-0003-4681-7449
Shalom D. Addo-Danso
orcid.org/0000-0001-5074-1673
Elizabeth A. Agee
orcid.org/0000-0002-2331-3056
Kelly M. Andersen
orcid.org/0000-0002-1460-9904
Marie Arnaud
orcid.org/0000-0003-4001-6499
Sarah A. Batterman
orcid.org/0000-0002-7703-9873

Francis Q. Brearley
orcid.org/0000-0001-5053-5693
Amanda L. Cordeiro
orcid.org/0000-0001-7226-0133
Caroline Dallstream
orcid.org/0000-0002-9193-0611
Milton H. Diaz-Toribio
orcid.org/0000-0003-1675-2699
Lee H. Dietterich
orcid.org/0000-0003-4465-5845
Joshua B. Fisher
orcid.org/0000-0003-4734-9085
Katrin Fleischer
orcid.org/0000-0002-9093-9526
Claire Fortunel
orcid.org/0000-0002-8367-1605
Lucia Fuchslueger
orcid.org/0000-0002-9615-4439
Nathaly R. Guerrero-Ramírez
orcid.org/0000-0001-7311-9852
Martyna M. Kotowska
orcid.org/0000-0002-2283-5979
Laynara Figueiredo Lugli
orcid.org/0000-0001-8404-4841
César Marín
orcid.org/0000-0002-2529-8929
Lindsay A. McCulloch
orcid.org/0000-0001-6868-2632
Jean-Luc Maeght
orcid.org/0000-0002-7292-1955
Dan Metcalfe
orcid.org/0000-0001-6853-7072
Richard J. Norby
orcid.org/0000-0002-0238-9828
Rafael S. Oliveira
orcid.org/0000-0002-6392-2526
Jennifer S. Powers
orcid.org/0000-0003-3451-4803
Tatiana Reichert
orcid.org/0000-0002-6300-2084
Stuart W. Smith
orcid.org/0000-0001-9396-6610
Fiona M. Soper
orcid.org/0000-0002-9910-9377
Laura Toro
orcid.org/0000-0002-0550-3294
María N. Umaña
orcid.org/0000-0001-5876-7720
Oscar Valverde-Barrantes
orcid.org/0000-0002-7327-7647
Monique Weemstra
orcid.org/0000-0002-6994-2501
Leland K. Werden
orcid.org/0000-0002-3579-4352
Michelle Wong
orcid.org/0000-0002-7830-8035

Cynthia L. Wright
orcid.org/0000-0003-2571-7334
Stuart Joseph Wright
orcid.org/0000-0003-4260-5676
Daniela Yaffar
orcid.org/0000-0002-8090-7096

AUTHOR CONTRIBUTIONS

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