Journal of Tropical Ecology

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Belowground differentiation among trees in a degraded tropical dry forest landscape: no evidence of a collaboration gradient

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Research Article

Cite this article: Benavides-Tocarruncho JP, Paz H, Rodríguez N, Arrieta R, Pizano C, and Salgado-Negret B (2024). Belowground differentiation among trees in a degraded tropical dry forest landscape: no evidence of a collaboration gradient. *Journal of Tropical Ecology*. **40**(e15), 1–9. doi: https://doi.org/10.1017/S0266467424000129

Received: 14 February 2023
Revised: 20 March 2024
Accepted: 28 April 2024

Keywords:
Colombia; root diameter; root economic spectrum; mycorrhizae; trait probability density; TDF

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Abstract

Fine roots are specialized in nutrient and water acquisition and are critical for species performance and ecosystem functioning. Recent evidence has shown a broad root economic space determined by the orthogonal collaboration and conservation gradients related to resource acquisition and resource conservation, respectively. However, whether these gradients exist among tree species growing in degraded ecosystems where root growth is limited by soil conditions is much an open question. We measured six fine root traits (root diameter, specific root length, root dry matter content, root tissue density, branching intensity, and percentage of arbuscular mycorrhizal colonization) in 11 young tree species growing in sympatry for 9 years in degraded pastures in a tropical dry forest (TDF) in Colombia to determine (1) the covariation between fine root traits and (2) the patterns of belowground niche differentiation among 11 species coexisting under the same soil conditions. The covariation between fine root traits resembled the acquisitive-conservative, but not the collaboration gradient for this degraded habitat. The percentage of mycorrhizal colonization, a critical trait associated with the collaboration gradient, was unrelated to any fine root trait. Furthermore, we found a strong belowground differentiation among species, mainly across root diameter and branching intensity. Our results suggest that compacted degraded soils in TDF landscapes may affect the collaborative association with mycorrhizae, mostly allowing species differentiation along the do-it-yourself gradient. This finding suggests a hypothesis that needs to be tested with more species and sites. We discuss the importance of using root traits to aid species selection for restoration purposes.

Introduction

Soil and vegetation cover degradation resulting from anthropogenic practices such as cattle, agriculture, and urbanization have impacted the dynamics and functioning of forests worldwide (Jie et al. 2002). Land degradation has been extreme in tropical dry forests (TDF), which used to represent 42% of all the world's tropical forests (Brown & Lugo 1982), with more than 50% left in South America (Miles et al. 2006). In Colombia, around 90% of its cover was replaced by the end of the 20th century (Etter et al. 2008; García et al. 2014), and only 8% of TDF's original cover is left in land mosaics of early successional stages (González-M et al. 2018). In these degraded landscapes, natural regeneration is challenging, and planting trees is necessary for re-establishing local biodiversity and ecosystem functioning (Rodrigues et al. 2009; Garbowski et al. 2020; Werden et al. 2022). However, water limitation imposed by the pronounced dry season (3–6 dry months precipitation <100 mm·month^{-1}, Portillo-Quintero and Sánchez-Azofeifa, 2010; González-M. et al. 2019), which is exacerbated by soil compaction due to livestock grazing (Batey 2009; Tracy et al. 2011), represents a barrier to the successful restoration of degraded TDF. Under this scenario, exploring the variation and coordination of belowground traits among species will be fundamental for selecting species that can overcome the soil barriers dominant in dry degraded ecosystems.

Fine roots, which are the most distal orders of fine root systems (typically first- to third-order roots), are specialized in nutrient and water acquisition (McCormack et al. 2015) and therefore critical for species performance in degraded ecosystems (Paz et al. 2015; Garbowski et al. 2020; Werden et al. 2022). Recent studies have identified two main functional belowground gradients expressing globally (Bergmann et al. 2020). One gradient encompasses plants that optimize resource uptake by investing carbon in thin roots that efficiently explore the soil themselves ("do-it-yourself") to those that "outsource" resource acquisition via mycorrhizal associations, whereby an expanded cortical area of roots provides a wider intraradical habitat for their fungal partners (Raven & Edwards 2001; Brundrett 2002; Kong et al. 2014; Ma et al. 2018; Brundrett & Tedersoo 2018). The acquisition-conservation gradient, orthogonal to the collaboration

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Table 1. Tree species studied in a tropical dry forest in Huila, Colombia. Family, common name, code, leaf habitat, and wood density (WD) per species. Range (min-max) and mean (in parenthesis) for height (H) and diameter at breast height (DBH) of trees sampled per species. *Wood density was obtained from Gonzalez et al. (2021)

Specie	Family	Common name	Code	Leaf habit	WD (g/cm^3)*	H (m)	DBH (cm)
Ochroma pyramidale	Malvaceae	Balsa	Oc.py	Evergreen	0.25	4.3–5.6 (5.1)	6.5–9.7 (7.8)
Jacaranda caucana	Bignoniaceae	Gualanday	Ja.ca	Deciduous	0.45	4.3–5.5 (5.2)	2.9–4.7 (3.8)
Ceiba pentandra	Malvaceae	Ceiba	Ce.pe	Deciduous	0.33	2.4–5.1 (3.3)	3.6–13.8 (8.0)
Sapindus saponaria	Sapindaceae	Chambimbe	Sa.sa	Deciduous	0.59	1.8–5.5 (3.4)	1.4–4.4 (2.4)
Pseudobombax septenatum	Malvaceae	Ceibo	Pse.sep	Deciduous	0.30	2–4.2 (2.9)	1.9–6.6 (4.4)
Machaerium capote	Fabaceae	Capote	Ma.ca	Deciduous	0.62	1.8–3.3 (2.2)	1.2–2.5 (1.8)
Casearia corymbosa	Salicaceae	Varazón	Ca.co	Evergreen	0.74	1.7–2.1 (1.9)	2.1–3.3 (2.8)
Guazuma ulmifolia	Malvaceae	Guazimo	Gu.ul	Deciduous	0.39	1.9–6 (4.0)	1.6–8.2 (4.6)
Celtis iguanaea	Cannabaceae	Uña de gato	Ce.ig	Deciduous	0.52	2.5–6 (4.0)	1.8–3.5 (2.4)
Chloroleucon mangense	Fabaceae	Raspayuco	Ch.ma	Deciduous	–	3.2–5 (3.9)	3.4–5.9 (4.8)
Tabebuia rosea	Bignoniaceae	Ocobo	Ta.ro	Deciduous	0.65	2.1–4.1 (3.0)	2.2–3.3 (2.7)

gradient, represents a trade-off between traits linked to high metabolic activity (e.g., root nitrogen) and those associated with the costs of root construction (e.g., root tissue density [RTD] or root dry matter content [RDMC]) (McCormack & Iversen 2019; Bergmann et al. 2020). These gradients have been reported across natural ecosystems worldwide (Bergmann et al. 2020). However, the exploration of root traits covariation and its importance for the belowground niche partitioning among species is infrequently studied in degraded habitats. For example, the dry compacted soils typical of degraded TDFs may affect root exploration capabilities (Alameda & Villar 2012), their morphology, and root partnership with mycorrhizae as they are mostly involved in P but not in water acquisition (Smith & Read 2009). These factors may limit belowground niche partitioning along the collaborative more than across the conservative gradient as water acquisition may critically depend on root morphology and mass deployment.

In the present study, we used six fine root traits (root diameter [D], specific root length [SRL], RDMC, RTD, branching intensity [BI], and percentage of arbuscular mycorrhizal colonization [% M]) measured in young individuals of 11 TDF tree species growing in sympatry for 9 years in a degraded TDF landscape. Our aims were (1) to define covariation between fine root traits and (2) to explore the belowground niche partitioning among 11 species coexisting under the same compacted soil conditions.

Methods

Study site and species

The study area is located in the restoration area of El Quimbo in the department of Huila, Colombia (75°41' W, 2°18' N), between 700 and 800 m of altitude. The zone is classified as a TDF with a mean annual temperature of 24°C and an annual mean precipitation of 1036 mm in a bimodal regime, with dry seasons from June to August and from December to January (Avella-M. et al. 2019). We took advantage of a restoration experiment established 9 years ago in abandoned pasture lands in which 11 common tree species (Table 1) were transplanted to plots containing individuals of all species randomly distributed, thus controlling for individual age and soil conditions (Torres-Rodríguez et al. 2019). Soil bulk density varies between 0.8 and 1.2 (1.1 on average; unpubl. data) grams per cm^3, slopes vary between 0.1° and 14°, and the soils are classified as inceptisols and mollisols with low P, K, and organic matter content due to cattle ranching (Torres-Rodríguez et al. 2019).

Functional traits

Five individuals of each species were sampled in 2021, nine years after they were planted as saplings. Individual height varied between 1.7 m (*Casearia corymbosa*) and 6 m (*Guazuma ulmifolia* and *Celtis iguanaea*). For each individual tree, fine roots were sampled by following lateral roots growing radially from the main shoot until fine roots (2 mm or less in thickness) were found. Then, following the order-based classification (McCormack et al. 2015), the fine roots were separated into individual root orders, prioritizing the collection of the first three orders. The diameter of our fine roots ranged from 0.25 to 0.71 mm (Table S1). The fresh weight of the sampled roots for each individual varied between 0.8 and 1.0 g.

In the field, fine roots were carefully collected, washed, and stored in plastic bags filled with water inside a cooler for transportation to the field station laboratory. Upon arrival at the laboratory, the fresh roots were cleaned, weighed, and scanned at

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Table 2. Functional traits measured and their functional significance

Trait	Units	Functional description
Average root diameter (D)	mm	Storage (Weemstra et al. 2016) and transport of water and organic compounds; mycorrhizal associations for resource absorption (Eissenstat et al. 2015)
Specific root length (SRL)	m g^{-1}	Foraging and resource acquisition capacity (Weemstra et al. 2016).
Root dry matter content (RDMC)	mg g^{-1}	Biomass storage, structural defense, and decomposition rate (Freschet et al. 2021; Salgado-Negret et al. 2016)
Root tissue density (RTD)	g cm^{-3}	Biomass storage, resistance to rupture and herbivores, increased root lifespan (Salgado-Negret et al. 2016; Freschet et al. 2021)
Branching intensity (BI)	mm^{-1}	Architectural investment for foraging and resource acquisition capacity (Eissenstat et al. 2015; Freschet et al. 2021)
Percentage of mycorrhizal colonization (%M)	%	Resources acquisition and outsourcing strategy (Eissenstat et al. 2015; Bergmann et al. 2020)

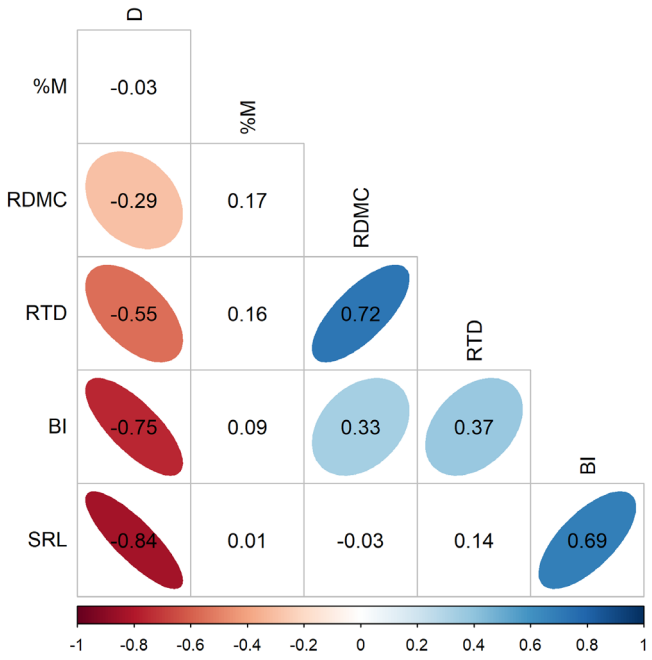

Figure 1. Pearson correlation coefficients with Bonferroni correction for pairwise relationships among six fine root traits. Significant correlations are indicated as red (negative) and blue (positive) ovals. Trait abbreviations: D: root diameter, %M: mycorrhizal colonization, RDMC: root dry matter content, RTD: root tissue density, BI: branching intensity, SRL: specific root length.

300 dpi (Epson Perfection V700 Photo scanner). Then, the roots were dried in an oven at 70°C for 48 hours and weighed to estimate the dry weight. The images were analyzed with RhizoVision Explorer, an open-source software for root trait measurement (Seethepalli et al. 2021). We obtained six morphological traits (Table 2) using the weights and the measurements from the scanned roots: (1) average root diameter (D, mm) computed as the mean of all diameters in each skeleton pixel, (2) Specific root length (SRL, m g^{-1}) calculated by dividing total length by the dry weight, (3) root dry matter content (RDMC, mg g^{-1}) calculated by dividing the dry weight by the fresh weight, and (4) root tissue density (RTD, g cm^{-3}) calculated by dividing the dry weight by root volume, assuming root tissues to be cylindrical in shape (Freschet et al. 2021). (5) Branching intensity (BI, mm^{-1}) was calculated as the total number of root branching points ("links," where a lateral root is linked to its parent root) divided by the total length (Eissenstat et al. 2015; Seethepalli et al. 2021). (6) The percentage of arbuscular mycorrhizal colonization (%M) was calculated by clearing fine roots with 3% KOH and 3% H_2O_2 acidified with 3% HCl, washed with distilled water and stained with 0.05% aniline blue in lactoglycerol solution (Zangaro et al. 2000). Stained root segments of each harvested plant were then mounted on a slide, and the presence/absence of Arbuscular mycorrhizal fungi (AMF) was recorded at 100 intersect points for each slide (McGonigle et al. 1990). Although RDMC and D are claimed to be tightly correlated with each other and with SRL, we decided to include all of them because for the TDF, these relationships remain unclear. There, species with high SRL have been reported to exhibit either high diameter but succulent low tissue density or the opposite (Sanaphre-Villanueva et al. 2022).

Data analysis

To explore the patterns of covariation among fine root traits (first aim), we performed Pearson correlation with Bonferroni correction using the R Stats package (R Core Team 2021). To explore the belowground niche partitioning among 11 species (second aim), we followed 2 approaches (univariate and multivariate) using trait probability density (TPD) (Carmona et al. 2016). The TPD approach is based on estimating Gaussian kernel density functions around each observation (Carmona et al. 2016, 2019). The TPD function of a given species represents the probability of observing different trait values in that species considering all sampled individuals (Carmona et al. 2016). For the multivariate approach, we first generated a multivariate functional space among species by applying a Principal Component Analysis (PCA) on all plants measured per species and selecting the first two PCA axes as suggested by the Horn's test for our data (Horn 1965; Dinno 2018). Then taking the scores of each plant of every species along the first and second PCA axes, we calculated the multivariate functional niche of each species by using the TPD (Carmona et al. 2016), implemented in the TPD's function of the R package "TPD" (Carmona et al. 2019). To explore belowground niche partitioning among species, we used the dissimilarity index (dissim function provided by the TPD package and TPD dissimilarity <0.05; Carmona et al. 2019) that measures the overlapping probability in the functional space between two species (TPD distributions). In addition, to better understand which functional traits differed most between species (univariate approach), we calculated functional niches based on single traits and compared them, following the same procedures described above. All statistical analyses were performed using R statistical software (R Core Team 2021).

Results

We found a negative correlation between root diameter (D) and all root traits except for %M which was not significantly correlated with D (Figure 1, Table S2). Additionally, we found a positive

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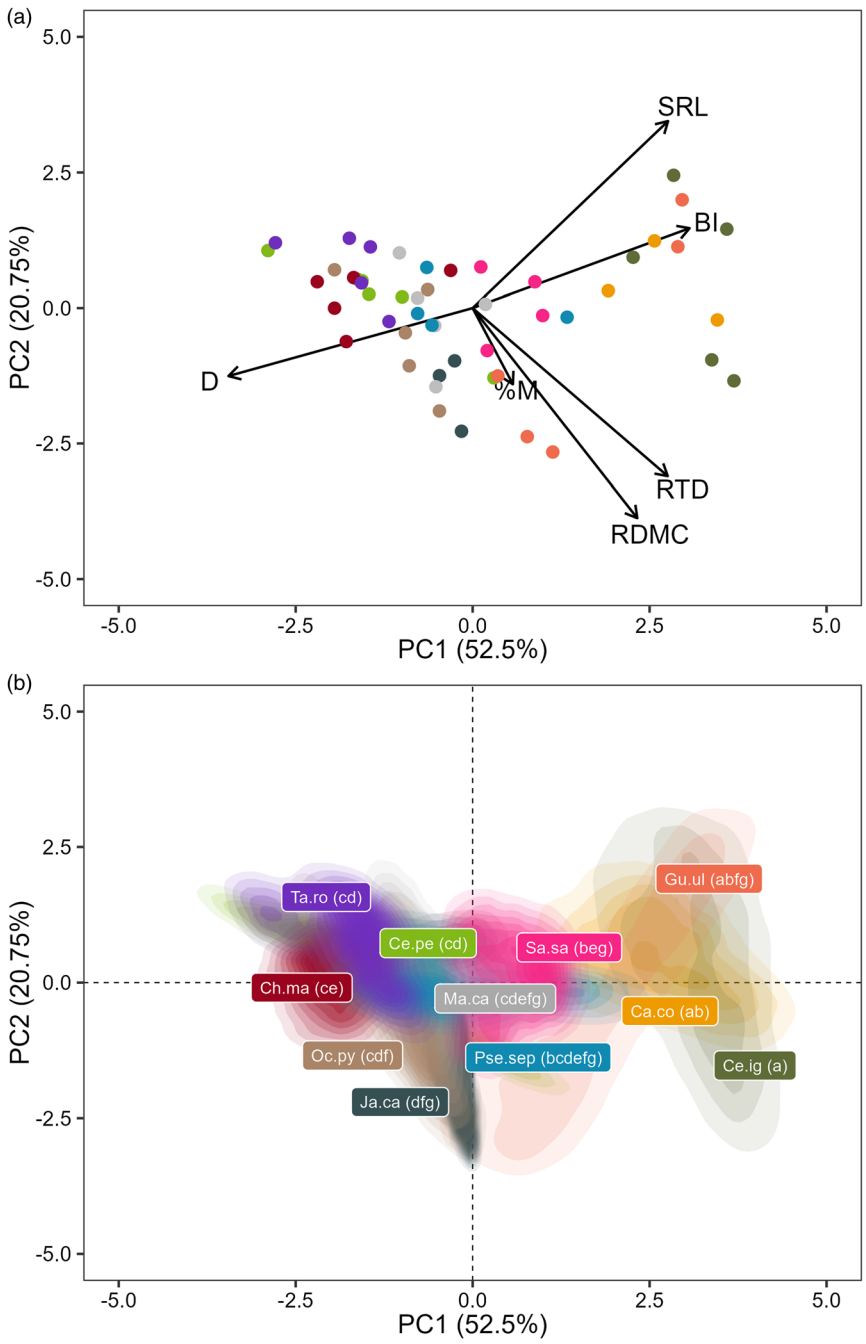

Figure 2. Multivariate trait analysis. (a) PCA of six fine root traits. Each point in the PCA is an individual of a given species; color codes are shown in panel (b). Trait abbreviations: D: root diameter, BI: branching intensity, SRL: specific root length, RDMC: root dry matter content, RTD: root tissue density, %M: mycorrhizal colonization. (b) Trait probability densities (TPD) showing the functional trait combinations for eleven tree species. Species abbreviations are in Table 1; each species has a distinctive color in the PCA and TPD plots. Different letters in parenthesis next to the species abbreviation indicate significant differences between species using the dissimilarity index (>95% non-shared probability).

correlation between traits associated with construction root costs, RTD or RDMC, and BI (Figure 1, Table S2).

The bivariate relationships between traits were supported by the multivariate approach (Figure 2). The belowground trait space of the 11 tree species was summarized by the first 2 dimensions of the PCA (Figure 2a, Table S3), which together explained 73.3% of the among-individuals variation and were the only 2 significant components according to Horn's test (Horn's test adjusted eigenvalues greater than 1: 2.657 and 1.004, respectively). The first PCA axis (PC1 explaining 52.5%) suggested a trade-off between high BI and SRL (loading positively on PC1) and a high D (loading negatively on PC1). The contribution of %M to the first axis was low (Figure 2a, Table S3). The second PCA axis (PC2 explaining 20.8%) separated species with high tissue densities (i.e., high values of RTD and RDMC) located on the negative side from species with high SRL on the positive side (Figure 2a). However, it is important to note that both SRL and tissue density also partially contributed to PC1. The multivariate approach showed strong belowground niche partitioning among species, mainly across the D and BI gradient (PC1) (Figure 2b, Table S4). Species such as *Celtis iguanaea* (Ce.ig), *Casearia corymbosa* (Ca.co), and *Guazuma ulmifolia* (Gu.ul) with high scores on PC1 were significantly different from species with high values of D, such as *Ceiba pentandra* (Ce.pe), *Tabebuia rosea* (Ta.ro), *Chloroleucon mangense* (Ch.ma), and *Ochroma pyramidale* (Oc.py) (Figure 2b). We did not find differences between trees of different species along the PC2 (Figure 2b, Table S4).

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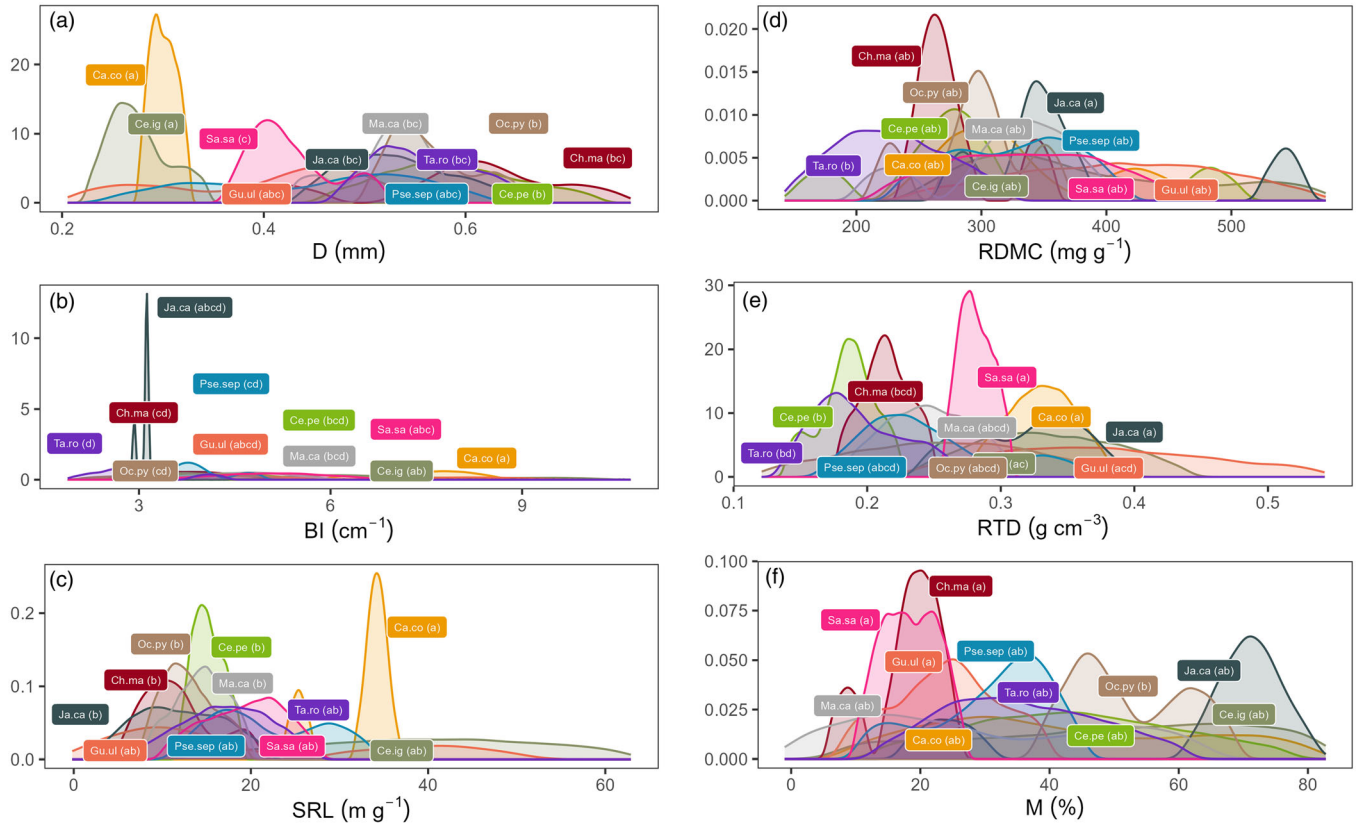

Figure 3. Trait probability density for each of the 6 fine root traits and for the 11 tree species. The *Y* axis is the density. Trait abbreviations: D: root diameter, BI: branching intensity, SRL: specific root length, RDMC: root dry matter content, RTD: root tissue density, %M: mycorrhizal colonization. Species abbreviations are in Table 1. Different letters in parenthesis next to species abbreviations indicate significant differences between species according to the similarity index.

The multivariate divergences for the individual traits among species were supported by the univariate approach (Figure 3, Table S5–S10). The species differentiation was mainly explained by D, with Ca.co and Ce.ig showing the thinnest roots and differing significantly from the other species (except Gu.ul and Pse.sep) (Figure 3a). Regarding BI, Ca.co showed the highest values and were statistically different from the other species (except for Ce.ig, *Sapindus Saponaria* (Sa.sa) and Gu.ul and *Jacaranda caucana* (Ja.ca) (Figure 3b). Ta.ro showed the lowest BI values and varied from Sa.sa, Ce.ig, and Ca.co, which had the highest values (Figure 3b). Concerning SRL, Ca.co showed the highest values and significantly differed from Oc.py, Ce.pe, Ch.ma, Ja.ca, and *Machaerium capote* (Ma.ca) (Figure 3c). We detected little differentiation among species for RDMC, RTD, and %M, probably associated with strong functional intraspecific variability (Figure 3d–f, Table S8–S10).

Discussion

Using 6 fine root traits measured in young individuals of 11 TDF tree species growing in degraded pastures in Colombia, we found ample variation in root traits that does not resemble the expectations from the collaboration gradient. The percentage of mycorrhizal colonization, an essential trait associated with the collaboration gradient, was unrelated to any fine root trait. Furthermore, we found strong species' belowground differentiation mainly determined by the gradient between D versus BI and SRL rather than the acquisitive-conservative gradient. The differences in belowground niche among species highlighted their multiple strategies to deal with drought and penetrate compacted soils, essential information to understand species' responses to climate change and to prioritize species for restoration purposes.

In principle, D and %M are expected to be tightly associated due to the limited intrinsic ability to acquire soil resources of thick roots (Bates & Lynch 2001); however, in our study, such traits varied independently. The lack of such correlation is not exclusive to our study, though no clear explanations have been claimed (Siqueira & Saggin-Júnior 2001; Lugli et al. 2020). One possibility is that under habitats with dry soils, since mycorrhizal association enhances mainly P capture but not water (Gavito et al. 2008; Smith & Read 2009, but see Bahadur et al. 2019), the root's abilities to forage water may be more dependent on root morphology itself than on microbial associations. Alternatively, under low phosphorous availability, typical from old and weathered tropical soils (Vitousek 2004), even finely branched roots may not ensure sufficient nutrient uptake by themselves, making them very responsive to and dependent on AMF (Siqueira & Saggin-Júnior 2001). For instance, in our study, the species with the thinnest roots (*Celtis iguanaea* and *Casearia corymbosa*) exhibited mycorrhizal colonization percentages exceeding 42% on average. It is essential to recognize that the informative value of %M may be reduced, and identifying specific fungal groups through molecular techniques that better capture the functional nature of the symbiosis is needed (Cusack et al. 2021). As we did not report a positive relationship between D and %M and, therefore, did not find a collaboration gradient, the negative relationship between D and SRL may reflect a mathematical autocorrelation more than ecological meaning (Ostonen et al. 2007). However, in TDFs, the previous observations

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of species with high SRL and high root diameters with low-density succulent tissues (Sanaphre-Villanueva et al. 2022) call for a functional role of both traits that still need to be studied in depth. Given the importance of mycorrhizal symbiosis for promoting the survival and growth of trees and shrubs within restoration experiments (Asmelash et al. 2019), an in-depth exploration of their role under degraded and dry soils becomes imperative.

The second gradient was related to resource acquisition-conservation, supported by a high RTD and RDMC (although we did not measure root N concentration). These results are consistent with other studies (Bergmann et al. 2020; Arrieta-González et al. 2021; Weemstra et al. 2023). Surprisingly, conservative traits such as RTD and RDMC were negatively related to D (Werden et al. 2022), challenging the traditional idea that D increases with RTD for carbon conservation (McCormack et al. 2012; Weemstra et al. 2016). This negative correlation may reflect that D increases through the root cortex, a parenchymatous tissue with low carbon content and dry weight, faster than the stele area, a tissue specialized in transporting nutrients and water through lignified cells (Kong et al. 2014; Valverde-Barrantes et al. 2017). The common observation of thick roots with low tissue density in other TDFs suggests a potential role of water storage in fat roots in maintaining tissue hydration within a dry soil matrix (Paz et al. 2015; Sanaphre-Villanueva et al. 2022). Interestingly, according to the PCA, in our study, SRL was an important trait contributing to both root gradients, which has already been reported by other studies (Cusack et al. 2021; Weemstra et al. 2023; but only in pairwise correlations in Bergmann et al. 2020). The longer and thinner fine roots can increase overall absorptive capacity ("do-it-yourself" strategy), but the negative correlation with conservative traits could be explained mathematically (as long as the volume is filled with dry mass and not water or air), as high RTD implies more root mass per unit root volume and generally decreases the root mass per unit root length (Weemstra et al. 2023).

Although our species were planted in a pasture with similar soils and drought conditions, we found strong belowground differentiation among species mainly through the D-BI gradient rather than the acquisitive-conservative gradient. The compacted soils, typical of degraded pastures in dry ecosystems, could promote strong differentiation in traits associated with resource acquisition strategies (D vs BI and SRL). Under compacted soils, cortical cells tend to become broader and shorter as a strategy to penetrate soils, protecting the stele and causing thicker roots (Atwell 1993). Conversely, mechanical damage caused by soil compaction may also alter the root system architecture in some species, forcing lateral roots to alter their direction of growth and resulting in an increase in lateral root branching (Chen et al. 2014), which is particularly important in those species unable to develop thick roots. Additionally, thick roots have higher storage space for accumulating water and starch (cortical cells, Lux et al. 2004); both resources are fundamental for drought responses under stomatal closure (Sala et al. 2010). On the contrary, the absence of belowground niche differentiation among species in conservative traits (RDMC and RTD) and %M could be explained by the high intraspecific variability in these traits. This variability may result from the high spatial heterogeneity of soil resources (Weemstra et al. 2016). For example, the spatial distribution of root-mycorrhizal associations is expected to be driven by P content, a highly variable nutrient in the soil (Cui & Caldwell 1996). Furthermore, compaction may exert strong selective pressure, leading a reduced intraspecific variability in D and BI (as mentioned earlier). However, it appears that compaction does not influence conservative traits (RDMC and RTD), which are more associated with resource conservation. As a result, there is no single optimal phenotype of conservative traits (with low intraspecific variability) that responds to compacted soils.

More information is needed to better understand how variations in root traits within and between species contribute to niche differentiation and prioritization of restoration efforts in TDF communities. For example, species such as *Ochroma pyramidale* (Oh.py), *Pseudobombax septenatum* (Pse.sep), and *Ceiba pentandra* (Ce.pe), known for their low wood density and fast growth rates, exhibited thick roots with low density. This efficient strategy allows them to store water and carbohydrates, which is advantageous in dry forest environments (Pineda-García, Paz & Tinoco-Ojanguren, 2011; Sanaphre-Villanueva et al. 2022). However, it is worth noting that dense wood species like *Celtis iguanaea* (Ce.ig) and *Tabebuia rosea* (Ta.ro) also exhibited a similar combination of traits. This suggests that further exploration and study of a wide functional space of species are needed to fully understand the patterns of variation in root traits.

Root traits such as root diameter and branching intensity may be useful for prioritizing species to restore abandoned pastures of TDF regions. For instance, in *Ceiba pentandra* (Ce.pe), thick roots and low tissue density were associated with water storage. This may be important for the maintenance of root xylem hydration and the water stream from roots to leaves, allowing photosynthesis and growth rates during dry periods at the seasonal or daily scale, during the hours of greatest transpiration (Čermák et al. 2007; Poorter & Markesteijn 2008). Several studies have suggested that the large diameter of growing tips helps to deform and separate soil particles, enhancing mechanical force and soil penetration ability (Materechera et al. 1992; Atwell 1993; Clarkl et al. 2003; Bengough et al. 2006; Weemstra et al. 2016), which makes species with thick roots promising candidates for establishing at initial stages of forest cover. A perfect example is *Chloroleucon mangense* (Ch.ma), with thick roots and high fiber and structural carbohydrate contents (Paz obs. Pers.). Additionally, Ch.ma is a nitrogen-fixing legume (Sprent 2001), which may restore soil fertility in degraded drylands, frequently seen in TDF (Avendaño-Yáñez et al. 2018). Conversely, *Casearia corymbosa* (Ca.co), *Celtis iguanaea* (Ce.ig), and *Guazuma ulmifolia* (Gu.ul), with branched, thin, and high-density roots, are predicted to be efficient in exploring soils and acquiring resources, allowing them to supply the high-water demand of the leaves, as these species have low water potentials during drought periods (Werden et al. 2018). However, those species may not develop in compacted soils because their roots cannot easily penetrate dense soils (Clarkl et al. 2003); therefore, they are good candidates for restoring sites with low soil compaction.

Here, we highlight these results as essential insights about what traits should be used to select and what can be the possible relations with restoration effectiveness. However, other belowground traits need to be explored. Root depth, elongation rate, and other physiological traits have been identified as critical determinants of plant performance under drought due to allowing access to unexploited soil moisture (Garbowski et al. 2020). Additionally, in TDF, the introduction of exotic grasses and legumes to promote and improve animal forage (Vasquez-Valderrama et al. 2020) may reduce the establishment probability of tree species. Therefore, to explore traits associated with the competitive exclusion of those exotic species may be essential to improve the restoration success (Garbowski et al. 2020). Finally, tree species selection for restoration should not rely only on root traits analysis, but these

https://doi.org/10.1017/S0266467424000129 Published online by Cambridge University Press

results must be confirmed by demographic analyses that relate these strategies to species' performance in the field.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0266467424000129.

Acknowledgments. We acknowledge Enel Colombia and Natura Foundation and its local team from the "Ecological restoration plan of the tropical dry forest of the El Quimbo Hydroelectric plant" ("Plan de restauración ecológica de bosque seco tropical de la Central Hidroeléctrica El Quimbo") for all of their support in carrying out this investigation.

Financial support. This research was supported by the project "¿Cómo optimizar los esfuerzos de restauración del bosque seco? un análisis desde el paisaje y los rasgos funcionales de las especies" funded by the "Convocatoria nacional para el fomento de alianzas interdisciplinarias que articulen investigación, creación, extensión y formación", grant of the Universidad Nacional de Colombia 20192021. Rosa Arrieta was supported by the "Colombia Biodiversa" grant no 09-2021 provided by the Alejandro Angel Escobar Foundation.

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