# Tree growth is better explained by absorptive fine roots than transport fine roots

Anvar Sanaei[1*], Fons van der Plas[1,2], Hongmei Chen[1,3], Sophie Davids[1], Susanne Eckhardt[1], Justus Hennecke[1,4], Anja Kahl[1], Yasmin Möller[1], Ronny Richter[1,4], Jana Schütze[1], Christian Wirth[1,4,5], Alexandra Weigelt[1,4]

[1] Institute of Biology, Leipzig University, 04103 Leipzig, Germany

[2] Plant Ecology and Nature Conservation Group, Wageningen University, P.O. Box 47, Wageningen, The Netherlands

[3] Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

[4] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany

[5] Max-Planck-Institute for Biogeochemistry, 07745 Jena, Germany

* Address for correspondence. Email: anvar.sanaei@uni-leipzig.de

**Abstract**

1. Quantifying plant trait variation yields insights into trade-offs inherent in the ecological strategies of plants and is the basis for a trait-based prediction of plant performance and ecosystem functioning. Although the interest in root traits has increased in recent years, we still have limited knowledge of i) whether functionally discrete fine roots—absorptive versus transport roots—have similar trait coordination and ii) how they help to explain plant performance, such as growth.
2. We measured traits of 28 European broadleaved tree species growing in a research arboretum to study i) the coordination within absorptive and transport fine root traits and ii) the degree of trait-tree growth relationships. To do so, we combined a suite of morphological (root diameter, specific root length and root tissue density) and anatomical (cortex to stele ratio and mycorrhizal colonization rate) traits for each of the absorptive and transport roots.
3. Despite remarkable differences in average trait values between absorptive and transport roots, our study shows that trait coordination within absorptive and transport roots is comparable. Our results also show that tree growth is better explained by absorptive root traits than by transport roots and is higher in species with a thinner root diameter.
4. Synthesis. The significant relationship between absorptive roots and tree growth and the lack of such a relationship for transport highlight that roots mostly involved with resource absorption are more important in explaining tree growth than roots involved in transport.

**Keywords:** absorptive roots, basal area increment, broadleaved tree species, leaves, plant functional traits, root economic space, transport roots

## 1. Introduction

Functional traits of plants are being used to comprehend plant community structure, assembly and functions (Lavorel & Grigulis, 2012; Westoby & Wright, 2006). Plant traits reflect different plant strategies and illustrate how plants respond to the environment (Westoby & Wright, 2006); hence, they have the promise to answer how and why plant performance differs among species (Poorter & Bongers, 2006). A suite of associated plant traits known as the leaf economics spectrum (LES) has been established at the leaf level (Reich, 2014; Wright et al., 2004). The LES defines a functional gradient from leaves with conservative resource use to those with an acquisitive strategy, the latter providing a high return on investment, thus being associated with high growth rates. The success of the LES in elucidating variations in leaf traits and predicting plant performance has stimulated researchers to expand the economic theory to 'fine roots', proposing a two-dimensional space of roots known as the root economics space (RES; Bergmann et al., 2020). The first dimension is known as the collaboration gradient, and that ranges from species with high root diameter offering space for arbuscular mycorrhizal fungi to species with greater specific root length (SRL). The second RES dimension, known as the conservation gradient, is equivalent to the classical LES with high root nitrogen representing a fast-growth strategy and low root tissue density (RTD) representing a slow-growth strategy. Importantly, while the classical working definition of fine roots, as roots ≤ 2 mm in diameter, has been widely used, it does not well reflect the differences in the functional roles of fine roots. Therefore, fine roots have been recently classified into two functional groups: absorptive and transport roots (McCormack et al., 2015). However, it is still poorly understood whether coordination of fine root traits along the RES is the same for absorptive and transport roots, and whether these different root types differ in their contribution to predicting plant functioning such as tree growth.

Many ecological studies on root traits define fine roots based on an arbitrary diameter size, and often implicitly assume roots within this size class to be homogenous in their functioning (Pregitzer et al., 2002). However, plant species typically possess hierarchical root systems, so that in reality fine roots are composed of a collection of very heterogeneous orders and branches differing in morphology, architecture, anatomy and longevity (Guo, Li, et al., 2008; Guo, Xia, et al., 2008; McCormack et al., 2015; Pregitzer et al., 2002) as well as in microbial associations (King et al., 2023). Given this, the trait data obtained from different root orders of the same species could be structurally and anatomically different and hence perform different functions (Laliberté, 2017; McCormack et al., 2015). Through this understanding, fine roots have been classified into two distinct groups based on their

functional roles. The first group, absorptive roots (order ≤ 3), is responsible for soil-based resource uptake and serves as a hotspot for biotic interactions with microbes and mycorrhizal activity (Freschet & Roumet, 2017; McCormack et al., 2015). The second group, transport roots (order > 3), is most important for transport and storage (Freschet & Roumet, 2017; McCormack et al., 2015). Thus, the capacity of resource transportation increases while absorption capacity decreases with increasing root order (McCormack et al., 2015). Moreover, the lifespan and root diameter of root segments are tied to the location within the branching root system, and consistently increase from the distal to the proximal end (Pregitzer, 2002; Pregitzer et al., 2002). Given this, absorptive roots located at the distal end have a smaller diameter and greater SRL compared to transport roots, and exhibit a shorter lifespan (Pregitzer, 2002; Xia et al., 2010). On the other hand, transport roots, characterised by a larger diameter and longer lifespan, emerge later in the developmental process as a consequence of secondary growth, resulting in greater RTD and lower SRL (Pregitzer, 2002; Xia et al., 2010). In addition, in a root system, anatomical changes across root orders occur mainly due to shifts in physiological functions from resource uptake to transport and storage (Gambetta et al., 2013; Guo, Xia, et al., 2008). As such, a higher percentage of cortex area, or cortex-to-stele ratio, which is characteristic of absorptive roots, is considered an indication of resource absorption and mycorrhizal colonization (Comas et al., 2012; Kong et al., 2017; Zhou et al., 2022). Conversely, a higher stele diameter is known as an indicator of resource transportation in transport roots (Feild & Arens, 2007; Guo, Xia, et al., 2008; Zhou et al., 2022). There is mounting evidence that higher root orders have no cortex due to secondary growth (Endo et al., 2021; Guo, Xia, et al., 2008; Long et al., 2013), thereby reducing mycorrhizal colonization rate (King et al., 2023). Despite this heterogeneity in absorptive and transport root traits, the relative importance of absorptive and transport roots for ecosystem functions such as tree growth is still unexplored.

Forest ecosystem functioning directly and indirectly depends on variation in plant functional traits across the globe (Gibert et al., 2016; Paine et al., 2015); thus, studying the link between plant functional traits and ecosystem functioning is important for a mechanistic understanding of forest functioning (Díaz et al., 2016; McGill et al., 2006). Indeed, the effective acquisition and utilization of limited resources are optimized by the functional coordination of roots and leaves and thus their traits (Reich, 2014). Consequently, there has been a lot of interest in identifying the relationship between leaf functional traits and forest functioning (Gibert et al., 2016; Paine et al., 2015; Poorter & Bongers, 2006). For instance, along with the leaf economic spectrum, tree annual growth was positively related to

acquisitive traits, characterised by a high specific leaf area (SLA) and stomatal density in subtropical forests (Liu et al., 2015), and a high leaf nitrogen content and SLA in temperate forests (Da et al., 2023). In principle, such relationships have been attributed to higher photosynthetic capacity and a higher potential for a quick return on investment of resources in fast-growing species, leading to a higher growth rate (Reich, 2014; Wright et al., 2004). Even though linking functional traits and plant performance is important, the majority of the studies have reported rather weak links between plant functional traits and plant performance. For example, only 3.1% of variance in tree growth was explained by leaf traits at the global scale in forests (Paine et al., 2015) and 4.8% of variance across functions by leaf and root traits together in grasslands (van der Plas et al., 2020). The reasons for such weak links could be due to the use of species-level mean trait data rather than individual-level trait data and/or using single traits rather than multiple traits, thereby weakening the strength of the relationships between plant functional traits and plant performance. The former might be attributed to the fact that different individuals of the same species respond differently to environmental variables (Siefert et al., 2015); for example, there is some evidence that individual-level trait data improves the degree of trait-growth relationships (Liu et al., 2016; Umaña et al., 2018). Fine roots serve a variety of functions, such as acquiring resources and interacting with soil organisms, all of which influence plant performance (Bardgett et al., 2014; Freschet, Roumet, et al., 2021; McCormack et al., 2015; Smith & Read, 2002). However, our understanding of the relative importance of fine root traits for tree growth lags behind that of leaf traits, partly due to the difficulty of sampling and/or measuring root traits (Freschet, Roumet, et al., 2021). A few recent studies have examined the explanatory power of root traits—in combination with leaf traits—on tree growth, in which for fine roots they focused only on the first three root orders (Shen et al., 2022; Weemstra et al., 2021) or the first two root orders (Da et al., 2023). Shen et al. (2022) showed that acquisitive leaf traits had a higher explanatory power than fine root traits for relative growth rates for height across tree species, even though SRL and RTD were significantly correlated with the relative growth rates for height of individuals. By contrast, Da et al. (2023) found that the conservation gradient of absorptive root traits explained forest aboveground carbon storage and woody biomass productivity better than conservation gradients in leaves and absorptive root collaboration gradients. Hence, the question is, why these previous studies found contrasting relationships between fine root traits and tree growth. A possibility, that has so far been unexplored, is that these contrasting relationships are driven by functional differences between absorptive and transport roots, whereby trait coordination, as well as their effects on

tree growth, differ between these two root types. Altogether, this highlights the necessity of examining the trait coordination within functionally discrete fine roots—absorptive and transport roots—as well as examining their relative importance for tree growth, either with or without the combination leaf traits.

By using 28 European broadleaved tree species growing in a research arboretum in Germany, this study aims to quantify the coordination within absorptive and transport fine roots and determine their explanatory power for tree growth, either with or without the combination of leaf traits. More specifically, this study tests the following three hypotheses: First, due to differences in the morphology and anatomical structures of the absorptive and transport roots (Guo, Xia, et al., 2008; McCormack et al., 2015; Pregitzer et al., 2002), we hypothesized (H1) that absorptive and transport roots do not necessarily demonstrate similar trait covariation patterns. Second, given the distinct functions of absorptive and transport roots in below-ground processes and functioning (King et al., 2023; McCormack et al., 2015), we hypothesized (H2) that absorptive root traits have a more substantial influence on tree growth due to their key role in resource uptake. Third, considering that tree growth relies on concurrent acquisition of above- and below-ground resources, which can be provided through both leaves and roots (Bardgett et al., 2014; Wright et al., 2004), we hypothesized (H3) that incorporation of leaf traits would increase the explanatory power of estimating tree growth.

## 2. Materials and Methods

### 2.1. Study area and experimental design

This study was carried out in the research arboretum ARBOfun located near Leipzig, Germany (51°16′N, 12°30′E; 150 m a.s.l.). The arboretum was established between 2012 and 2014 and is designed for 100 tree species belonging to 39 families planted 5.8 m apart. The 2.5 ha of the arboretum is subdivided into five blocks, with each block containing one individual of each species. The mean annual precipitation is approximately 534.3 mm, and the mean annual temperature is 9.4 °C (Deutscher Wetterdienst (DWD), 2024). The soil type of the arboretum, which was previously used as a managed arable field, is Luvisol, and it has a pH of 5.7 (Ferlian et al., 2017).

### 2.2. Root sampling and measurement

In 2018 and 2019, roots of three individuals per species were sampled. First, the soil around the targeted tree was loosened using a digging fork, and then roots were uncovered carefully by hand and with smaller gardening tools. If a root of higher order was found, it was traced

towards the main stem of the target tree to confirm its identity. Then intact root branches containing at least the first five root orders, with the most distal root tip as the first root order, were collected. The root samples, including adherent soil, were wrapped in moist paper, sealed in a plastic bag and stored in a cooling box before being transported to the laboratory. After washing root samples, the sample of each individual tree was divided into two portions: one small portion for examining anatomical traits and another for examining morphological traits. Each subsample comprised fine roots spanning the first to fifth root orders. Finer cleaning was conducted using tweezers under the stereo microscope. After cleaning, the different root orders of the fine root samples were identified and then dissected for trait examination, with each root order being analysed separately. Dissection of root orders was done under a stereo microscope with a scalpel, starting with the root tips as the first root order and categorizing higher root orders towards the stem. From each root sample, 60 root pieces of the first and second root orders, 20 root pieces of the third root order and 10 root pieces of the fourth and fifth root orders were dissected and stored separately in 1.5 ml Eppendorf tubes with water until further processing. The samples of each root order were scanned using a flatbed scanner (Epson Expression 11000XL, UK) at a resolution of 600 dpi, then root pieces were collected, oven-dried at 60°C for over 48 h and weighed to obtain the root dry weight.

All morphological root traits by root orders at individual tree level were quantified using root scans, which were analysed in a batch using the RhizoVision Explorer (Seethepalli et al., 2021). Using the provided data in RhizoVisison—mainly the total root length and volume —alongside the root dry weight data, RTD (root dry weight/root volume) and SRL (total root length/root dry weight) were calculated.

For the measurement of anatomical root traits, root subsamples were cleaned similarly as above, separated by root orders, and placed in scintillation vails containing fixing solution Roti®-Histofix 4% formaldehyde. The samples were left at room temperature for two hours and then refrigerated overnight. The next day, root samples were dehydrated with a series of ethanol with steps of 10%, 30%, 50% and 70%, in which the root samples rested for one hour each to gradually remove the water remained in the root tissue (Zadworny et al., 2016). Samples were kept in the refrigerator in another 70% ethanol solution until further processing. We used an automated tissue processing system (Donatello, Diapath) with (i) 45 min each at 38°C: twice 80% ethanol and twice 96% ethanol, (ii) 60 min each at 38°C and at 40°C xylol and (iii) 80 min each at 62°C three times paraffin, followed by manual embedding of root fragments using a paraffin embedding center (TES 99, Medite). Embedded samples were

cross-cut to 1-3 µm with a sledge microtome (DDMP, Medim), put on a slide, processed twice for 10 min in xylol, followed by each 5 min 96%, 80% and 70% ethanol, and finally distilled water before staining for 2 min in 0.01% toluidine blue solution (Aldrich). Slides were permanently fixed with a Tissue Tek system (Sakura). Then, the images of cross-sections per root order were recorded with a microscope (Axiostar plus, Zeiss, Germany) and microscope camera companied with the program AxioVision (Zeiss, Oberkochen, Germany). We ensured that the entire cross-section as well as a representative section of higher resolution was depicted in the cross-section image. Analysis of the images for measuring root area, stele area (SA), cortex area (CA) and cortex area to stele area ratio (C:S ratio) was done with ImageJ (Schneider et al., 2012).

The rate of arbuscular mycorrhizal colonization (MCR) was investigated using the magnified intersection method (McGonigle et al., 1990). Root pieces were bleached in 10% potassium hydroxide for 18 h. Next, roots were rinsed using DI water and stained in a 10% ink-vinegar solution (Vierheilig et al., 1998) for 15 min at 90 °C in a water bath. Stained root samples were stored in lactoglycerol until processing. MCR of root pieces was quantified by examining hyphae, arbuscules, hyphal coils, vesicles, and arbuscular mycorrhizal fungi according to the magnified intersection method (McGonigle et al., 1990) with a microscope slide at a magnification of 200x.

We assigned the mycorrhizal type, i.e., arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi, to each species based on the recent symbiotic guild assignments (Steidinger et al., 2019). As a result, of the 28 tree species, 13 are AM species and 15 are EM species (Table S1). In this study, we used functional fine root role classification, where the first three root orders are defined as absorptive roots, while the fourth to fifth root orders are defined as transport roots (McCormack et al., 2015). We acknowledge that the transition from absorptive to transport is species-specific, and that transition might occur gradually, so it is difficult to fix the function of different root orders. More specifically, the third-order fine roots are classified as transport roots in some species, and they might be a transitionary root type in some species. Thus, we ran an additional analysis with the average of the first and second root orders as absorptive roots and the average of the fourth and fifth root orders as transport roots. The results of these additional analyses are presented in supplementary information (Figures S6 and S7), where our main findings and conclusion remain the same. Potential causes of variation in root order function might be due to plant phylogenetic clades, age and environmental conditions (McCormack et al., 2015; Li et al., 2022), which are not

relevant in our study due to the experimental design and the selected broadleaved species. Finally, we used the average of the first three root-order traits to represent absorptive roots and the average of the fourth to fifth root-order traits to represent transport roots for further analyses.

### 2.3. Leaf sampling and measurement

13 fully expanded and intact sun-exposed leaves were randomly selected and collected from each individual tree species between 2018 and 2022, following the standard protocol (Cornelissen et al., 2003). Of the 13 leaves, five were scanned at 600 dpi with flatbed Expression 11000XL, and the images were analysed using WinFolia (Regent Instrument, Canada) to get the fresh leaf area. After scanning, the lamina and petiole were separated, blot-dried, and weighed to get their fresh weights. Then the samples were oven-dried at 60°C for five days and weighed. The leaf mass per area (LMA) was computed by dividing the dry mass of the five leaves (including both lamina and petiole) by their total fresh area. The leaf dry matter content (LDMC) was determined by dividing the mean leaf dry weight to the mean leaf fresh lamina weight. We measured force to punch using a motorised vertical test stand along with a Sauter FH50 with dynamometer combined with a flat-sided needle on three positions of three leaves per species. Additionally, three leaves per species were manually crosscut using a blade to obtain thin sections in the central area of the leaf. The resulting cross sections were then placed in a drop of water on an object slide and examined under a microscope. Then, the mean leaf thickness was determined using the Axiocam (Zeiss, Germany) and the software ZEN 2 core. We then calculated the leaf toughness for each leaf by dividing force to punch of the leaf by the leaf thickness and then computed the individual mean leaf toughness (Westbrook et al., 2011).

### 2.4. Quantification of tree growth

In February 2023, we measured the diameter at breast height (DBH) of each tree individual using a caliper. We then calculated basal area increment as a proxy for tree growth using the sum of DBH data for individual tree species. As such, we calculated the average absolute basal area increment by dividing the 2022 basal area data of each individual tree by its age since planting. Hence, the average basal area increment was calculated according to the following equation:

$$\text{Average basal area increment } = ln\left(\frac{\sum_{j=1}^{n}\left(\frac{\pi}{4} * DBH_{j(2022)}^{2}\right)}{\text{tree age since planting}}\right)$$

where DBH is the diameter at breath height measured at the 1.3-meter height of an individual, *j* is an index for the *n* stems of the individual, and 2022 is the year when DBH of the individual tree was measured, which overlap the years (2018-2022) during which the trait measurements were done.

### 2.5. Statistical analyses

To assess the variation and coordination of the absorptive and transport root traits, we performed principal component analyses (PCAs) using stepwise inclusion of traits. To do so, the first set of PCAs were performed on morphological root traits, including specific root length (SRL), root tissue density (RTD) and root diameter for absorptive and transport roots separately. Hence, in this first step we focused on those morphological traits that were also analysed in recent studies investigating root trait coordination (Bergmann et al., 2020; Weigelt et al., 2021). The second set of PCA were extended to the whole set of root traits, adding root anatomical (cortex to stele ratio; C:S and mycorrhizal colonization rate; MCR) traits on top of root morphological traits for absorptive and transport roots separately. A third set of PCAs were performed on the whole set of root traits as well as leaf traits (LDMC, LMA and LT). The PCAs were performed using the *prcomp* function of the ‘stats’ package on scaled trait data and without axis rotation. To aid interpretation, we inverted the PCA axis of the transport root traits by multiplying by minus one whenever required. We further examined the effect of the mycorrhizal type (AM vs. EM) on the position of tree individual within root trait space by employing a permutational multivariate analysis of variance (PERMANOVA) with root trait space constructed based on Euclidean trait distances using the *adonis2* function of the ‘vegan’ package (Oksanen et al., 2021). Next, as the first two PCA axes captured most of the variance, we extracted the loading scores of traits on first and second PCA axes and used them as continuous variables to explain variation in tree growth estimation. Specifically, we performed linear regression to quantify the relationships between average basal area increment (as a dependent variable) and the first and second PCA axes scores (as the explanatory variables) of each PCA coordination using the *lm* function of the ‘stats’ package. We used a dependent t-test to compare root traits between absorptive and transport roots. To complement the results of PCAs on traits, we subsequently explored the pairwise correlations by performing Pearson's correlations between absorptive or transport root traits and leaf traits using the *ggraph* function of the ‘ggraph’ package (Pedersen, 2022). To assess each single root and leaf trait as an explanatory predictor for tree growth, we further performed bivariate linear regression separately across absorptive or transport root and leaf traits. To meet the

linear regression assumptions, all traits were log-transformed before the regression analysis. All analyses were done using the R v.4.1.3 platform (R Core Team, 2022).

## 3. Results

### 3.1. Covariation in absorptive and transport root traits

The PCA of absorptive root morphological traits showed that the first two axes together captured 91% of the variability (Figure 1a, Table S2). The first principal component (PCA1) axis is positively associated with root diameter, and the second principal component (PCA2) axis is positively and negatively related to SRL and RTD, respectively (Figure 1a, Table S2). The first two PCA axes of transport root morphological traits together explained 87% of the variability (Figure 1d, Table S2). The PCA1 axis of the transport root morphological traits was also negatively associated with root diameter, but unlike with absorptive root morphological traits, was in addition negatively associated with SRL (root collaboration gradient), while the PCA2 axis was positively related to RTD as a part of the root conservation gradient (Figure 1d, Table S2). For absorptive roots, a PCA based on a combination of morphological and anatomical (C:S and MCR) traits showed that the first two PCA axes explained 70% of variation in root traits, in which root diameter and MCR tended to load positively on the PCA1, while RTD and SRL tended to load negatively and positively on the PCA2, respectively (Figure 1b, Table S2). For transport roots, a PCA based on the combination of morphological and anatomical traits showed that the PCA1 and PCA2 axes together explained 63% of variation, in which MCR, C:S and root diameter loaded positively on PCA1, and SRL loaded positively on PCA2 (Figure 1e, Table S2). The results of the PCA based on the whole set of absorptive root and leaf traits showed that PCA1 and PCA2 accounted for 55% of variation (Figure 1e, Table S2): PCA1 was positively related to the root diameter and MCR while negatively related to LDMC and PCA2 was mainly positively related to SRL (Figure 1c, Table S2). The results based on the whole set of transport root and leaf traits showed that PCA1 and PCA2 accounted for 49% of variation. PCA1 was negatively related to MCR, while it was positively associated with LDMC and LMA (Figure 1f, Table S2) and PCA2 was positively associated with SRL, while being negatively related to root diameter (Figure 1f, Table S2). While the mean trait values significantly differ between absorptive and transport roots (Figure S1), except for MCR, the trait coordination of the absorptive and transport roots remains similar. However, when root and leaf traits were pooled, more specifically, root diameter shifted to the second PCA axis in transport roots (Figure 1e,f). In addition, pairwise correlations show a much stronger negative correlation

between root diameter with RTD and LDMC and also between MCR and SRL in absorptive roots, and a much stronger positive correlation between root diameter and MCR in absorptive roots (Figure S2).

While mycorrhizal-type separation was much clearer in absorptive root morphological traits compared to transport root morphological traits, incorporation of C:S and MCR led to better mycorrhizal-type separation even in transport roots (Figure 1). In line with these results, the per-MANOVA test revealed significant differences between AM vs. EM species across all trait combinations ($P < 0.001$; Figure 1a,b,c,e,f), except for transport root morphological traits ($P = 0.605$; Figure 1d). More specifically, AM species were associated with higher root diameter, C:S and MCR, while EM species were associated with higher RTD, LDMC and LMA (Figure 1).

Considering only leaf traits, the PCA showed that the first two axes together captured 88% of leaf trait variation (Figure S4a). PCA1 axis is negatively associated with LDMC, and PCA2 was positively associated with LT while being negatively related to LMA (Figure S4a).

### 3.2. The relationships between fine root and leaf traits and tree growth

Our results of linear regressions between PCA1 and average basal tree area increment reveal that absorptive root morphological traits were negatively associated with tree growth ($R^2 = 0.13$, $P < 0.01$; Figure 2a), showing a higher growth for trees with thinner absorptive roots (lower root diameter), while no relationship was found for morphological transport roots (Figure 2d). Morphological combined with anatomical traits of absorptive roots showed an even higher explanatory power for tree growth ($R^2 = 0.18$, $P < 0.001$; Figure 2b), where trees with lower root diameter, and MCR showed higher growth rates (Figure 1; Table S2). In contrast, there were no significant relationship between tree growth and morphological combined with anatomical transport roots (Figure 2d). Finally, absorptive root and leaf traits together explained even more variance in tree growth ($R^2 = 0.20$, $P < 0.001$; Figure 2c), where trees with higher root diameter and MCR but with lower LDMC showed lower growth (Figure 1; Table S2). The combination of transport root traits and leaf traits also revealed a significant relationship with tree growth ($R^2 = 0.09$, $P < 0.05$; Figure 2f), where trees with lower MCR but with higher LDMC and LMA showed higher growth (Figure 1; Table S2). The explanatory power of absorptive root and leaf traits on tree growth was stronger (Figure 2c) than transport root and leaf traits (Figure 2f). Surprisingly, none of the PCA2 axes showed a significant relationship with tree growth (Figure S3), despite their high loadings of 18% to 38%. In line with the PCA results on multiple traits, single root and leaf traits were also

correlated with tree growth (Figure S5). As such, absorptive root traits were significantly negatively correlated with tree growth ($P < 0.01$; Figure 5c,d,e), while SRL was marginally positively correlated with tree growth ($P = 0.09$; Figure S5b). For transport roots, only MCR was significantly negatively associated with tree growth ($P < 0.01$; Figure S5j).

The linear regressions between PCA1 of leaf traits and average basal tree area increment show that leaf traits were related to tree growth ($R^2 = 0.10$, $P < 0.01$; Figure S4b), showing a higher growth for trees with higher LDMC. Single leaf traits, i.e., LMA and LT, but not LDMC, were significantly positively related to tree growth ($P < 0.05$ to $P < 0.01$; Figure S5l,m).

## 4. Discussion

By functionally separating fine roots into absorptive and transport roots and also by stepwise inclusion of root traits in PCA, we explored the coordination within absorptive and transport fine roots, which, based on our knowledge, has not been tested so far. Overall, we found that trait coordination within absorptive and transport roots is comparable. Specifically, mycorrhizal colonization, root diameter, and cortex-to-stele ratio were the key traits loading on the first PCA axis, where the two mycorrhizal types clearly separated. Furthermore, tree growth is better explained by absorptive root traits than by transport roots and was higher in species with thinner root diameter that were less colonized by arbuscular mycorrhizae, highlighting the role of efficient and independent exploration of soil resources.

### 4.1. Covariation in absorptive and transport root traits

Despite significant differences between absorptive and transport root traits (Figure S1), we found that, contrary to our first hypothesis (H1), coordination within absorptive and transport root traits was quite similar to each other and similar to the collaboration gradient published previously; whereby species with higher root diameter were highly related to mycorrhizal association (Bergmann et al., 2020). In partial disagreement with our results, in another study different economic strategies were observed for thin (< 247 μm) and thick (> 247 μm) fine roots, where thin roots followed the resource acquisition-conservation strategy but thick roots did not (Kong et al., 2016). It must be mentioned that Kong et al. (2016) applied univariate regression analysis between root traits, not PCA for the trait coordination. The specific fine root diameter cutoff, limited number of species, and/or including root nitrogen concentration, which we did not measure, can contribute to the different observed patterns. This again highlights the importance of trait selection for the outcome of studies on trait coordination patterns (Weigelt et al., 2023).

Against our expectation, there was no significant difference in mycorrhizal colonization between absorptive and transport roots (Figure S1), which is contrary to the generally acknowledged notion that higher root orders (or transport roots) are not or less colonized by mycorrhizae (King et al., 2023; McCormack et al., 2015). Indeed, transport roots possess lower potential for mycorrhizal colonization due to their thinner cortex (or presence of periderm), providing smaller space for mycorrhizal colonization (Eissenstat et al., 2015; Kong et al., 2017; McCormack et al., 2015). Our inconsistent results might be partly attributed to topological root order classification, in which a higher proportion of thinner roots (absorptive roots) are classified as having higher root orders (transport roots); therefore, the percentage of transport roots is higher than in the morphometric root order classification method (Freschet, Pagès, et al., 2021). Moreover, species-specific differences in mycorrhizal dependence might affect the overall colonization of the roots with mycorrhizae (Zhou et al., 2022). There is some evidence that, for example, *Fraxinus rhynchophylla* Hance. has mycorrhizal colonization in fourth order roots and *Acacia auriculiformis* A.Cunn. ex Benth. is colonized even in fifth order roots, meaning that some species are more colonized by mycorrhizae than others even in higher root orders (Guo, Xia, et al., 2008; Long et al., 2013). This is because plant species differ in the secondary growth development, and mycorrhizal colonization in higher root orders also confirms a higher dependency of those species on mycorrhizae for nutrient uptake (Zhou et al., 2022). This was the case in our mycorrhizal colonization data. As such, order-based root mycorrhizal colonization data showed that for the majority of species, mycorrhizal colonization was greater in the lower root orders or remained on the same level in the higher root orders. Yet, in some species, like *Fraxinus excelsior* L., *Euonymus europaeus* L. and *Frangula alnus* L. mycorrhizal colonization slightly increased with increasing root orders. Altogether, this might lessen the overall mycorrhizal colonization rate differences between absorptive and transport roots.

Our results further corroborate previous studies that AM species are thought to have thicker roots with a thicker cortex, supporting higher rates of mycorrhizal colonization compared to EM species (Laliberté, 2017). In contrast, EM species possess thinner, higher branching intensity and longer roots, allowing them to independently explore a larger volume of below-ground resources without relying on the root cortex (Cheng et al., 2016; Yan et al., 2022). Segregation of AM and EM species across trait coordination shows their strong differences in root traits, distinctions in life-history strategy and distinct nutrient sources in the root economics space (Averill et al., 2019; Yan et al., 2022).

By incorporating leaf traits into PCAs with absorptive and transport roots, trait coordination showed that conservative leaf traits were closely aligned with conservative root traits, reaffirming that the conservation gradients of both leaf economic spectrum and root economic space are correlated (Reich, 2014). Similar results have been reported when leaf and root traits were pooled, indicating the same trade-offs between the fast–slow conservation gradient in root and leaf traits (Kramer-Walter et al., 2016; Weigelt et al., 2021).

**4.2. Absorptive root traits better explain tree growth than transport root traits**

Past attempts at exploring the contribution of fine root traits to plant performance have considered fine roots as a homogenous pool without regard to their distinct functional roles (Orwin et al., 2018; van der Plas et al., 2020). Thus far, our understanding of how fine roots contribute to tree growth stems from studies testing either the first two or three root orders (Da et al., 2023; Shen et al., 2022; Weemstra et al., 2021), but there is no study testing the effects of functionally discrete fine roots on tree growth. By separating fine roots into absorptive and transport roots, we found that absorptive fine root traits are highly correlated with tree growth, consistent with our second hypothesis (H2). The greater contribution of absorptive root traits to tree growth compared to transport root traits can be attributed to the functioning role of absorptive roots within the plant system (Freschet & Roumet, 2017; McCormack et al., 2015). Within the plant, absorptive roots are mainly involved in soil-based resource acquisition (e.g., nutrients and water), which is directly linked to tree growth. More specifically, the absorptive root traits loaded on the PCA1 (MCR, root diameter and C:S ratio) were the key traits associated with tree growth, highlighting the importance of root anatomical and mycorrhizal associations for tree growth (Lynch et al., 2021). Indeed, the positive associations among mycorrhizal colonization, root diameter and cortex-to-stele ratio are characteristic of absorptive roots (Smith & Read, 2002), and we observed that those traits have stronger correlations in absorptive roots (Figure S2). More precisely, our results showed that species with thicker roots that are more colonised by mycorrhizal fungi (Comas et al., 2012; Eissenstat et al., 2015) were negatively correlated with tree growth. Indeed, plants with thicker roots tend to have a longer lifespan and a smaller surface area, resulting in a smaller volume of below-ground resources explored and thus a high dependence on mycorrhizal colonization (McCormack & Iversen, 2019; Pregitzer et al., 2002). In contrast, SRL, as a part of root collaboration gradient in root economic space, was positively correlated with tree growth, meaning that species with the ability to independently explore soil for resources efficiently produce higher growth. Similar results were obtained based on single-trait bivariate

relationships, where mycorrhizal colonization, root diameter, and cortex-to-stele ratio are significantly and negatively correlated with tree growth, while SRL is marginally positively correlated with tree growth (Figure S5). In addition, tree species in Leipzig are experiencing drought from 2018 to 2020 (Schnabel et al., 2022), so it seems that thinner and smaller root diameters, i.e., potentially reaching smaller pores of soil, are more beneficial, particularly during dry years (Comas et al., 2013), thereby enabling the acquisition of higher nutrients and water with low investment. A higher SRL and smaller root diameter are associated with higher hydraulic conductivity, which reflects drought tolerance capacity (Comas et al., 2012, 2013; Hernández et al., 2010).

Contrary to our expectations, we found a higher average growth increment over time in EM species than AM species, which might be explained by their differences in carbon balance between return and investment over time. Specifically, EM species are more likely to show a slow-growth strategy, while AM species are known to have a fast-growth strategy (Averill et al., 2019; Phillips et al., 2013), thus suggesting a higher growth rate. In partial agreement with our results, in a more recent study, Dietrich et al. (2023) reported an increase in growth increment over time for EM species, while AM species tend to decrease growth increment over time, and they argued that it might be attributable to their distinct nutrient resources and soil mutualistic relationships. More precisely, compared to AM species, EM species tend to grow more slowly in the beginning, but then their growth increments increase over time (Dietrich et al., 2023). Another possible explanation could be a higher SRL for EM species (Figures 1 and S5), which again highlights efficiently exploring a substantial soil volume, resulting in greater resource uptake (Comas et al., 2012; Ostonen et al., 2007). In the same direction, mycelium of the EM species efficiently penetrates the capillary pores and explores water-depleted zones around the root, resulting in the utilization of soil water reservoirs (Boczoń et al., 2021).

It was not surprising that incorporation of leaf traits to the whole set of absorptive roots improved the strength of relationships between tree growth and traits, in support of our third hypothesis (H3). It is certain that leaves play crucial roles in plants by converting sunlight energy and carbon dioxide and water into organic carbon through photosynthesis (Reich, 2014; Schulze, 2006; Wright et al., 2004), thereby influencing growth. Our results corroborate previous studies showing the importance of leaf traits and their contribution to forest functioning (Cornelissen et al., 1996; Poorter & Bongers, 2006). Our results showed that thinner roots that are less colonized with mycorrhiza were related to high tree growth, but

this was the case only for species with higher LDMC and LMA. More specifically, species with a slow-growing strategy (higher LDMC and LMA) tend to have higher growth, indicating a decoupled root and leaf trait strategy explaining tree growth. The opposite pattern has been reported where species with high root diameter but a lower specific leaf area enhanced tree growth (Weemstra et al., 2021). Taken together, these findings confirm that traits more directly related to resource uptake above- and below-ground are important indicators of tree growth (Weemstra et al., 2021; Weigelt et al., 2021). In addition, incorporation of leaf traits to transport root traits significantly explained tree growth estimation. Based on the trait loading on the PCA axes (Table S2), we believe that this contribution arises from leaf traits rather than transport root traits, as LDMC and LMA are primarily loaded on the first PCA axis, however mycorrhizal colonization rate was the only absorptive root trait loaded on the first PCA axis (Figure 1f, Table S2). This is also supported by the fact that leaf traits alone explain tree growth equally well as, if not better than, leaf and transport roots together (Figure S4). This is not surprising and confirms that transport roots are mainly involved in the transport and storage of resources and also play crucial roles in protecting plants against pathogens and from dehydration (Enstone et al., 2002; Lynch et al., 2021) rather than resource acquisitions that are directly related to growth (McCormack et al., 2015).

By functionally separating fine roots into absorptive and transport roots, our results show a strong association between absorptive fine roots and broadleaved tree growth in a research arboretum. A higher contribution of absorptive root traits to predicting tree growth suggests that variation in absorptive root traits, rather than transport root traits, better explains tree growth variation via presumably providing soil-based resources, e.g., nutrients and water, directly influencing overall tree growth. We argue that by considering fine roots (≤ 2 mm in diameter) as a homogenous pool, the variance of root traits along root orders might be underestimated and might not clearly show root functioning signals. We also acknowledge that further research assessing the role of root and leaf nutrient concentrations as well as considering transport root-related functions may be particularly illuminating.

**Acknowledgments**

We thank Roman Patzak, Imke Pelloth, Lea von Sivers, Tom Künne and Julia Leonore van Braak for their help with the field and lab measurements. We also thank Maritta Wipplinger from the institute of veterinary pathology at Leipzig University for her help in root cross-section preparation. We are especially grateful to Florian Schnabel, Lena Kretz and David

Schellenberger Costa for helping with discussing ideas. A.S is supported by the Saxon State Ministry for Science, Culture and Tourism (SMWK) – [3-7304/35/6-2021/48880].

## Conflict of Interest Statement

The authors declare that they have no competing interests.

## Author Contributions

A.W., C.W. and A.S. conceived the ideas and developed the concept of the study. F.v.d.P., H.C., S.D., S.E., A.K., J.M., J.S. and A.W. contributed to data collection. A.S. analysed the data and led the writing of the manuscript. F.v.d.P., H.C., R.R., J.H., C.W. and A.W. contributed to the writing in several manuscript interactions. All authors contributed critically to the drafts and gave final approval for publication.

## Data Availability Statement

We will store the dataset in the public repository once the paper is accepted.

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## Figure captions

**Figure 1.** Principal component analyses (PCA) of individual-levels of (a,d) morphological root traits (b,e) morphological and anatomical root traits, (c,f) and all root and leaf traits (d,e) for both absorptive and transport root traits. Abbreviations for traits are as follows: RD, root diameter; RTD, root tissue density; SRL, specific root length; C:S, cortex to stele ratio; MCR, mycorrhizal colonization rate; LMA, leaf mass per area; LT, leaf toughness; LDMC, leaf dry matter content; AM, arbuscular mycorrhizal species; and EM, ectomycorrhizal species. The second PCA axis of absorptive morphological traits (d) and the first PCA axis of the whole set of transport root and leaf traits (f) are flipped.

**Figure 2.** Relationships between the first axis of the PCA and average basal area increment across stepwise inclusion of root and leaf traits for absorptive roots (a–c) and transport roots (d–f). Shown are the $R^2$ and $P$-values of the linear regressions. Significant relationships between basal area increment and PCA axes are denoted by * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$). The x-axis of the whole set of transport root and leaf traits (f) is flipped.

**Figure 1.**

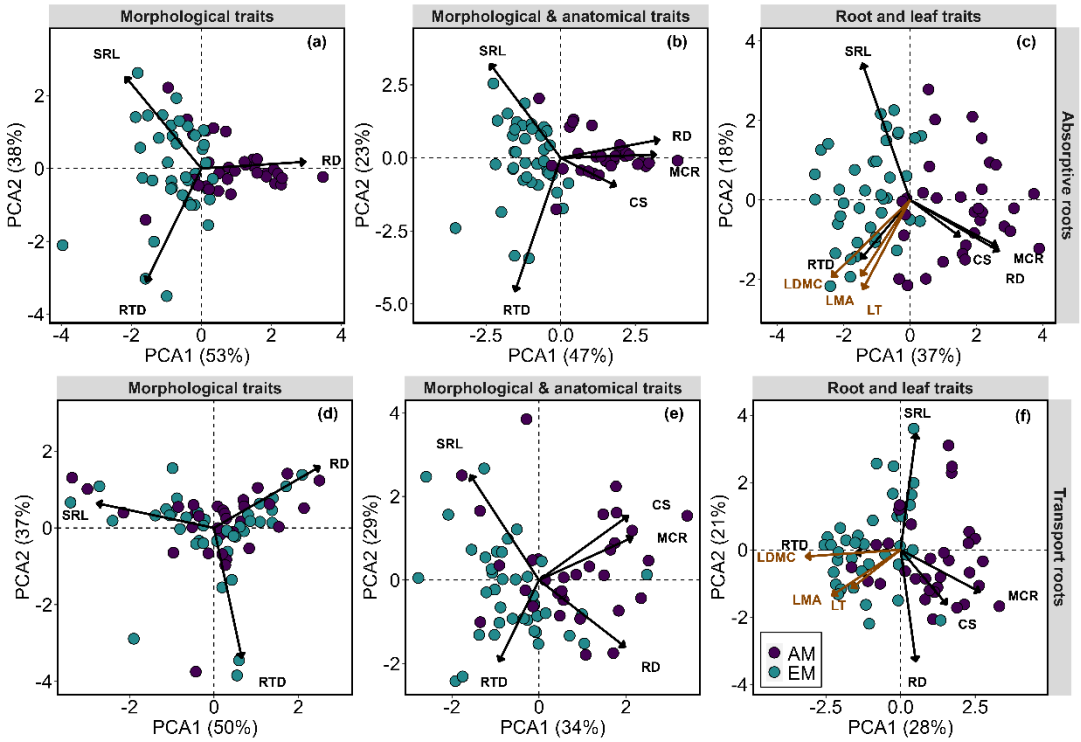
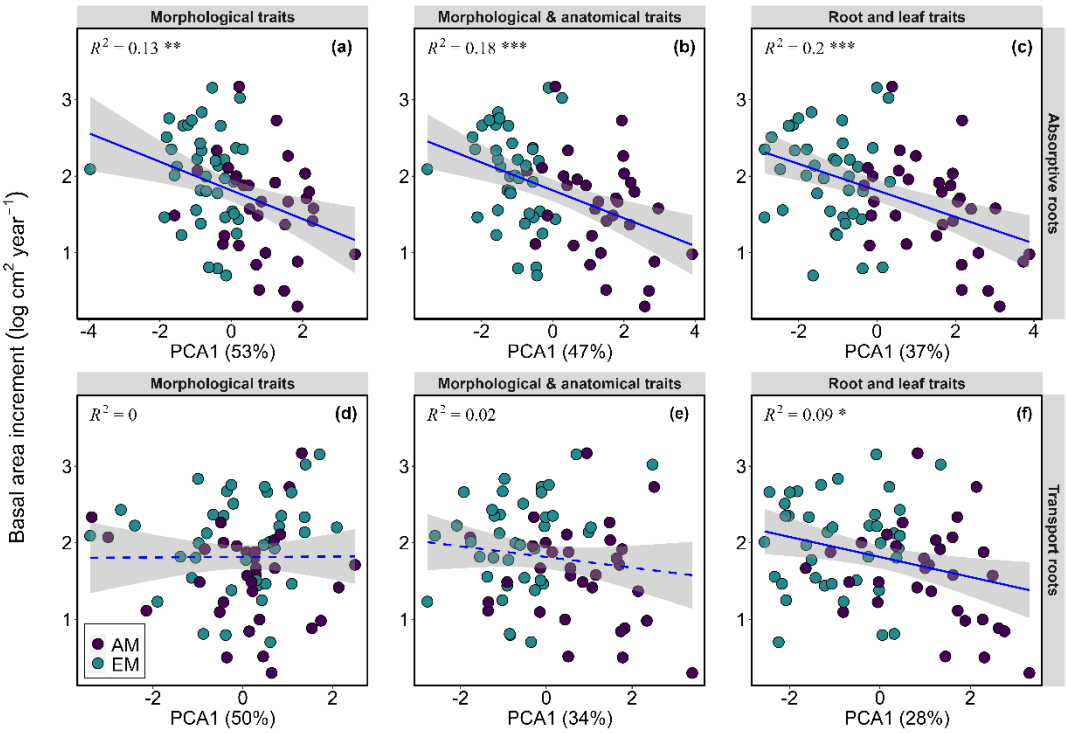

Morphological traits
Morphological & anatomical traits
Root and leaf traits
Absorptive roots
Transport roots
(a)
(b)
(c)
(d)
(e)
(f)
SRL
RD
RTD
CS
MCR
LDMC
LMA
LT
PCA1 (53%)
PCA2 (38%)
PCA1 (47%)
PCA2 (23%)
PCA1 (37%)
PCA2 (18%)
PCA1 (50%)
PCA2 (37%)
PCA1 (34%)
PCA2 (29%)
PCA1 (28%)
PCA2 (21%)
AM
EM

**Figure 2.**


Morphological traits
Morphological & anatomical traits
Root and leaf traits
$R^2 = 0.13$ **
(a)
$R^2 = 0.18$ ***
(b)
$R^2 = 0.2$ ***
(c)
Absorptive roots
$R^2 = 0$
(d)
$R^2 = 0.02$
(e)
$R^2 = 0.09$ *
(f)
Transport roots
AM
EM
Basal area increment (log cm$^2$ year$^{-1}$)
PCA1 (53%)
PCA1 (47%)
PCA1 (37%)
PCA1 (50%)
PCA1 (34%)
PCA1 (28%)