

1 **Tree growth is better explained by absorptive fine roots than transport fine**
2 **roots**

3

4 Anvar Sanaei^{1*}, Fons van der Plas^{1,2}, Hongmei Chen^{1,3}, Sophie Davids¹, Susanne Eckhardt¹,
5 Justus Hennecke^{1,4}, Anja Kahl¹, Yasmin Möller¹, Ronny Richter^{1,4}, Jana Schütze¹, Christian
6 Wirth^{1,4,5}, Alexandra Weigelt^{1,4}

7

8 ¹ Institute of Biology, Leipzig University, 04103 Leipzig, Germany

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

11 ³ Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

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

14 ⁵ Max-Planck-Institute for Biogeochemistry, 07745 Jena, Germany

15

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

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31

32

33

34 **Abstract**

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

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

58

59

60

61

62

63

64

65

66 **1. Introduction**

67 Functional traits of plants are being used to comprehend plant community structure, assembly
68 and functions (Lavorel & Grigulis, 2012; Westoby & Wright, 2006). Plant traits reflect
69 different plant strategies and illustrate how plants respond to the environment (Westoby &
70 Wright, 2006); hence, they have the promise to answer how and why plant performance
71 differs among species (Poorter & Bongers, 2006). A suite of associated plant traits known as
72 the leaf economics spectrum (LES) has been established at the leaf level (Reich, 2014; Wright
73 et al., 2004). The LES defines a functional gradient from leaves with conservative resource
74 use to those with an acquisitive strategy, the latter providing a high return on investment, thus
75 being associated with high growth rates. The success of the LES in elucidating variations in
76 leaf traits and predicting plant performance has stimulated researchers to expand the
77 economic theory to ‘fine roots’, proposing a two-dimensional space of roots known as the root
78 economics space (RES; Bergmann et al., 2020). The first dimension is known as the
79 collaboration gradient, and that ranges from species with high root diameter offering space for
80 arbuscular mycorrhizal fungi to species with greater specific root length (SRL). The second
81 RES dimension, known as the conservation gradient, is equivalent to the classical LES with
82 high root nitrogen representing a fast-growth strategy and low root tissue density (RTD)
83 representing a slow-growth strategy. Importantly, while the classical working definition of
84 fine roots, as roots ≤ 2 mm in diameter, has been widely used, it does not well reflect the
85 differences in the functional roles of fine roots. Therefore, fine roots have been recently
86 classified into two functional groups: absorptive and transport roots (McCormack et al.,
87 2015). However, it is still poorly understood whether coordination of fine root traits along the
88 RES is the same for absorptive and transport roots, and whether these different root types
89 differ in their contribution to predicting plant functioning such as tree growth.

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

100 functional roles. The first group, absorptive roots (order ≤ 3), is responsible for soil-based
101 resource uptake and serves as a hotspot for biotic interactions with microbes and mycorrhizal
102 activity (Freschet & Roumet, 2017; McCormack et al., 2015). The second group, transport
103 roots (order > 3), is most important for transport and storage (Freschet & Roumet, 2017;
104 McCormack et al., 2015). Thus, the capacity of resource transportation increases while
105 absorption capacity decreases with increasing root order (McCormack et al., 2015). Moreover,
106 the lifespan and root diameter of root segments are tied to the location within the branching
107 root system, and consistently increase from the distal to the proximal end (Pregitzer, 2002;
108 Pregitzer et al., 2002). Given this, absorptive roots located at the distal end have a smaller
109 diameter and greater SRL compared to transport roots, and exhibit a shorter lifespan
110 (Pregitzer, 2002; Xia et al., 2010). On the other hand, transport roots, characterised by a larger
111 diameter and longer lifespan, emerge later in the developmental process as a consequence of
112 secondary growth, resulting in greater RTD and lower SRL (Pregitzer, 2002; Xia et al., 2010).
113 In addition, in a root system, anatomical changes across root orders occur mainly due to shifts
114 in physiological functions from resource uptake to transport and storage (Gambetta et al.,
115 2013; Guo, Xia, et al., 2008). As such, a higher percentage of cortex area, or cortex-to-stele
116 ratio, which is characteristic of absorptive roots, is considered an indication of resource
117 absorption and mycorrhizal colonization (Comas et al., 2012; Kong et al., 2017; Zhou et al.,
118 2022). Conversely, a higher stele diameter is known as an indicator of resource transportation
119 in transport roots (Feild & Arens, 2007; Guo, Xia, et al., 2008; Zhou et al., 2022). There is
120 mounting evidence that higher root orders have no cortex due to secondary growth (Endo et
121 al., 2021; Guo, Xia, et al., 2008; Long et al., 2013), thereby reducing mycorrhizal colonization
122 rate (King et al., 2023). Despite this heterogeneity in absorptive and transport root traits, the
123 relative importance of absorptive and transport roots for ecosystem functions such as tree
124 growth is still unexplored.

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

134 acquisitive traits, characterised by a high specific leaf area (SLA) and stomatal density in
135 subtropical forests (Liu et al., 2015), and a high leaf nitrogen content and SLA in temperate
136 forests (Da et al., 2023). In principle, such relationships have been attributed to higher
137 photosynthetic capacity and a higher potential for a quick return on investment of resources in
138 fast-growing species, leading to a higher growth rate (Reich, 2014; Wright et al., 2004). Even
139 though linking functional traits and plant performance is important, the majority of the studies
140 have reported rather weak links between plant functional traits and plant performance. For
141 example, only 3.1% of variance in tree growth was explained by leaf traits at the global scale
142 in forests (Paine et al., 2015) and 4.8% of variance across functions by leaf and root traits
143 together in grasslands (van der Plas et al., 2020). The reasons for such weak links could be
144 due to the use of species-level mean trait data rather than individual-level trait data and/or
145 using single traits rather than multiple traits, thereby weakening the strength of the
146 relationships between plant functional traits and plant performance. The former might be
147 attributed to the fact that different individuals of the same species respond differently to
148 environmental variables (Siefert et al., 2015); for example, there is some evidence that
149 individual-level trait data improves the degree of trait-growth relationships (Liu et al., 2016;
150 Umaña et al., 2018). Fine roots serve a variety of functions, such as acquiring resources and
151 interacting with soil organisms, all of which influence plant performance (Bardgett et al.,
152 2014; Freschet, Roumet, et al., 2021; McCormack et al., 2015; Smith & Read, 2002).
153 However, our understanding of the relative importance of fine root traits for tree growth lags
154 behind that of leaf traits, partly due to the difficulty of sampling and/or measuring root traits
155 (Freschet, Roumet, et al., 2021). A few recent studies have examined the explanatory power
156 of root traits—in combination with leaf traits—on tree growth, in which for fine roots they
157 focused only on the first three root orders (Shen et al., 2022; Weemstra et al., 2021) or the
158 first two root orders (Da et al., 2023). Shen et al. (2022) showed that acquisitive leaf traits had
159 a higher explanatory power than fine root traits for relative growth rates for height across tree
160 species, even though SRL and RTD were significantly correlated with the relative growth
161 rates for height of individuals. By contrast, Da et al. (2023) found that the conservation
162 gradient of absorptive root traits explained forest aboveground carbon storage and woody
163 biomass productivity better than conservation gradients in leaves and absorptive root
164 collaboration gradients. Hence, the question is, why these previous studies found contrasting
165 relationships between fine root traits and tree growth. A possibility, that has so far been
166 unexplored, is that these contrasting relationships are driven by functional differences
167 between absorptive and transport roots, whereby trait coordination, as well as their effects on

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

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

186 **2. Materials and Methods**

187 **2.1. Study area and experimental design**

188 This study was carried out in the research arboretum ARBOfun located near Leipzig,
189 Germany (51°16'N, 12°30'E; 150 m a.s.l.). The arboretum was established between 2012 and
190 2014 and is designed for 100 tree species belonging to 39 families planted 5.8 m apart. The
191 2.5 ha of the arboretum is subdivided into five blocks, with each block containing one
192 individual of each species. The mean annual precipitation is approximately 534.3 mm, and the
193 mean annual temperature is 9.4 °C (Deutscher Wetterdienst (DWD), 2024). The soil type of
194 the arboretum, which was previously used as a managed arable field, is Luvisol, and it has a
195 pH of 5.7 (Ferlian et al., 2017).

196 **2.2. Root sampling and measurement**

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

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

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

222 For the measurement of anatomical root traits, root subsamples were cleaned similarly
223 as above, separated by root orders, and placed in scintillation vials containing fixing solution
224 Roti®-Histofix 4% formaldehyde. The samples were left at room temperature for two hours
225 and then refrigerated overnight. The next day, root samples were dehydrated with a series of
226 ethanol with steps of 10%, 30%, 50% and 70%, in which the root samples rested for one hour
227 each to gradually remove the water remained in the root tissue (Zadworny et al., 2016).
228 Samples were kept in the refrigerator in another 70% ethanol solution until further processing.
229 We used an automated tissue processing system (Donatello, Diapath) with (i) 45 min each at
230 38°C: twice 80% ethanol and twice 96% ethanol, (ii) 60 min each at 38°C and at 40°C xylol
231 and (iii) 80 min each at 62°C three times paraffin, followed by manual embedding of root
232 fragments using a paraffin embedding center (TES 99, Medite). Embedded samples were

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

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

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

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

270 **2.3. Leaf sampling and measurement**

271 13 fully expanded and intact sun-exposed leaves were randomly selected and collected from
272 each individual tree species between 2018 and 2022, following the standard protocol
273 (Cornelissen et al., 2003). Of the 13 leaves, five were scanned at 600 dpi with flatbed
274 Expression 11000XL, and the images were analysed using WinFolia (Regent Instrument,
275 Canada) to get the fresh leaf area. After scanning, the lamina and petiole were separated, blot-
276 dried, and weighed to get their fresh weights. Then the samples were oven-dried at 60°C for
277 five days and weighed. The leaf mass per area (LMA) was computed by dividing the dry mass
278 of the five leaves (including both lamina and petiole) by their total fresh area. The leaf dry
279 matter content (LDMC) was determined by dividing the mean leaf dry weight to the mean leaf
280 fresh lamina weight. We measured force to punch using a motorised vertical test stand along
281 with a Sauter FH50 with dynamometer combined with a flat-sided needle on three positions
282 of three leaves per species. Additionally, three leaves per species were manually crosscut
283 using a blade to obtain thin sections in the central area of the leaf. The resulting cross sections
284 were then placed in a drop of water on an object slide and examined under a microscope.
285 Then, the mean leaf thickness was determined using the Axiocam (Zeiss, Germany) and the
286 software ZEN 2 core. We then calculated the leaf toughness for each leaf by dividing force to
287 punch of the leaf by the leaf thickness and then computed the individual mean leaf toughness
288 (Westbrook et al., 2011).

289 **2.4. Quantification of tree growth**

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

$$296 \quad \text{Average basal area increment} = \ln \left(\frac{\sum_{j=1}^n \left(\frac{\pi}{4} * DBH_{j(2022)}^2 \right)}{\text{tree age since planting}} \right)$$

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

301 **2.5. Statistical analyses**

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

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

332 **3. Results**

333 **3.1. Covariation in absorptive and transport root traits**

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

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

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

374 Considering only leaf traits, the PCA showed that the first two axes together captured
375 88% of leaf trait variation (Figure S4a). PCA1 axis is negatively associated with LDMC, and
376 PCA2 was positively associated with LT while being negatively related to LMA (Figure S4a).

377 **3.2. The relationships between fine root and leaf traits and tree growth**

378 Our results of linear regressions between PCA1 and average basal tree area increment reveal
379 that absorptive root morphological traits were negatively associated with tree growth ($R^2 =$
380 0.13 , $P < 0.01$; Figure 2a), showing a higher growth for trees with thinner absorptive roots
381 (lower root diameter), while no relationship was found for morphological transport roots
382 (Figure 2d). Morphological combined with anatomical traits of absorptive roots showed an
383 even higher explanatory power for tree growth ($R^2 = 0.18$, $P < 0.001$; Figure 2b), where trees
384 with lower root diameter, and MCR showed higher growth rates (Figure 1; Table S2). In
385 contrast, there were no significant relationship between tree growth and morphological
386 combined with anatomical transport roots (Figure 2d). Finally, absorptive root and leaf traits
387 together explained even more variance in tree growth ($R^2 = 0.20$, $P < 0.001$; Figure 2c), where
388 trees with higher root diameter and MCR but with lower LDMC showed lower growth
389 (Figure 1; Table S2). The combination of transport root traits and leaf traits also revealed a
390 significant relationship with tree growth ($R^2 = 0.09$, $P < 0.05$; Figure 2f), where trees with
391 lower MCR but with higher LDMC and LMA showed higher growth (Figure 1; Table S2).
392 The explanatory power of absorptive root and leaf traits on tree growth was stronger (Figure
393 2c) than transport root and leaf traits (Figure 2f). Surprisingly, none of the PCA2 axes showed
394 a significant relationship with tree growth (Figure S3), despite their high loadings of 18% to
395 38%. In line with the PCA results on multiple traits, single root and leaf traits were also

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

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

405 **4. Discussion**

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

415 **4.1. Covariation in absorptive and transport root traits**

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

429 Against our expectation, there was no significant difference in mycorrhizal
430 colonization between absorptive and transport roots (Figure S1), which is contrary to the
431 generally acknowledged notion that higher root orders (or transport roots) are not or less
432 colonized by mycorrhizae (King et al., 2023; McCormack et al., 2015). Indeed, transport roots
433 possess lower potential for mycorrhizal colonization due to their thinner cortex (or presence
434 of periderm), providing smaller space for mycorrhizal colonization (Eissenstat et al., 2015;
435 Kong et al., 2017; McCormack et al., 2015). Our inconsistent results might be partly
436 attributed to topological root order classification, in which a higher proportion of thinner roots
437 (absorptive roots) are classified as having higher root orders (transport roots); therefore, the
438 percentage of transport roots is higher than in the morphometric root order classification
439 method (Freschet, Pagès, et al., 2021). Moreover, species-specific differences in mycorrhizal
440 dependence might affect the overall colonization of the roots with mycorrhizae (Zhou et al.,
441 2022). There is some evidence that, for example, *Fraxinus rhynchophylla* Hance. has
442 mycorrhizal colonization in fourth order roots and *Acacia auriculiformis* A.Cunn. ex Benth. is
443 colonized even in fifth order roots, meaning that some species are more colonized by
444 mycorrhizae than others even in higher root orders (Guo, Xia, et al., 2008; Long et al., 2013).
445 This is because plant species differ in the secondary growth development, and mycorrhizal
446 colonization in higher root orders also confirms a higher dependency of those species on
447 mycorrhizae for nutrient uptake (Zhou et al., 2022). This was the case in our mycorrhizal
448 colonization data. As such, order-based root mycorrhizal colonization data showed that for the
449 majority of species, mycorrhizal colonization was greater in the lower root orders or remained
450 on the same level in the higher root orders. Yet, in some species, like *Fraxinus excelsior* L.,
451 *Euonymus europaeus* L. and *Frangula alnus* L. mycorrhizal colonization slightly increased
452 with increasing root orders. Altogether, this might lessen the overall mycorrhizal colonization
453 rate differences between absorptive and transport roots.

454 Our results further corroborate previous studies that AM species are thought to have
455 thicker roots with a thicker cortex, supporting higher rates of mycorrhizal colonization
456 compared to EM species (Laliberté, 2017). In contrast, EM species possess thinner, higher
457 branching intensity and longer roots, allowing them to independently explore a larger volume
458 of below-ground resources without relying on the root cortex (Cheng et al., 2016; Yan et al.,
459 2022). Segregation of AM and EM species across trait coordination shows their strong
460 differences in root traits, distinctions in life-history strategy and distinct nutrient sources in
461 the root economics space (Averill et al., 2019; Yan et al., 2022).

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

468 **4.2. Absorptive root traits better explain tree growth than transport root traits**

469 Past attempts at exploring the contribution of fine root traits to plant performance have
470 considered fine roots as a homogenous pool without regard to their distinct functional roles
471 (Orwin et al., 2018; van der Plas et al., 2020). Thus far, our understanding of how fine roots
472 contribute to tree growth stems from studies testing either the first two or three root orders
473 (Da et al., 2023; Shen et al., 2022; Weemstra et al., 2021), but there is no study testing the
474 effects of functionally discrete fine roots on tree growth. By separating fine roots into
475 absorptive and transport roots, we found that absorptive fine root traits are highly correlated
476 with tree growth, consistent with our second hypothesis (H2). The greater contribution of
477 absorptive root traits to tree growth compared to transport root traits can be attributed to the
478 functioning role of absorptive roots within the plant system (Freschet & Roumet, 2017;
479 McCormack et al., 2015). Within the plant, absorptive roots are mainly involved in soil-based
480 resource acquisition (e.g., nutrients and water), which is directly linked to tree growth. More
481 specifically, the absorptive root traits loaded on the PCA1 (MCR, root diameter and C:S ratio)
482 were the key traits associated with tree growth, highlighting the importance of root anatomical
483 and mycorrhizal associations for tree growth (Lynch et al., 2021). Indeed, the positive
484 associations among mycorrhizal colonization, root diameter and cortex-to-stele ratio are
485 characteristic of absorptive roots (Smith & Read, 2002), and we observed that those traits
486 have stronger correlations in absorptive roots (Figure S2). More precisely, our results showed
487 that species with thicker roots that are more colonised by mycorrhizal fungi (Comas et al.,
488 2012; Eissenstat et al., 2015) were negatively correlated with tree growth. Indeed, plants with
489 thicker roots tend to have a longer lifespan and a smaller surface area, resulting in a smaller
490 volume of below-ground resources explored and thus a high dependence on mycorrhizal
491 colonization (McCormack & Iversen, 2019; Pregitzer et al., 2002). In contrast, SRL, as a part
492 of root collaboration gradient in root economic space, was positively correlated with tree
493 growth, meaning that species with the ability to independently explore soil for resources
494 efficiently produce higher growth. Similar results were obtained based on single-trait bivariate

495 relationships, where mycorrhizal colonization, root diameter, and cortex-to-stele ratio are
496 significantly and negatively correlated with tree growth, while SRL is marginally positively
497 correlated with tree growth (Figure S5). In addition, tree species in Leipzig are experiencing
498 drought from 2018 to 2020 (Schnabel et al., 2022), so it seems that thinner and smaller root
499 diameters, i.e., potentially reaching smaller pores of soil, are more beneficial, particularly
500 during dry years (Comas et al., 2013), thereby enabling the acquisition of higher nutrients and
501 water with low investment. A higher SRL and smaller root diameter are associated with
502 higher hydraulic conductivity, which reflects drought tolerance capacity (Comas et al., 2012,
503 2013; Hernández et al., 2010).

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

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

528 this was the case only for species with higher LDMC and LMA. More specifically, species
529 with a slow-growing strategy (higher LDMC and LMA) tend to have higher growth,
530 indicating a decoupled root and leaf trait strategy explaining tree growth. The opposite pattern
531 has been reported where species with high root diameter but a lower specific leaf area
532 enhanced tree growth (Weemstra et al., 2021). Taken together, these findings confirm that
533 traits more directly related to resource uptake above- and below-ground are important
534 indicators of tree growth (Weemstra et al., 2021; Weigelt et al., 2021). In addition,
535 incorporation of leaf traits to transport root traits significantly explained tree growth
536 estimation. Based on the trait loading on the PCA axes (Table S2), we believe that this
537 contribution arises from leaf traits rather than transport root traits, as LDMC and LMA are
538 primarily loaded on the first PCA axis, however mycorrhizal colonization rate was the only
539 absorptive root trait loaded on the first PCA axis (Figure 1f, Table S2). This is also supported
540 by the fact that leaf traits alone explain tree growth equally well as, if not better than, leaf and
541 transport roots together (Figure S4). This is not surprising and confirms that transport roots
542 are mainly involved in the transport and storage of resources and also play crucial roles in
543 protecting plants against pathogens and from dehydration (Enstone et al., 2002; Lynch et al.,
544 2021) rather than resource acquisitions that are directly related to growth (McCormack et al.,
545 2015).

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

556 **Acknowledgments**

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

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

563 **Conflict of Interest Statement**

564 The authors declare that they have no competing interests.

565 **Author Contributions**

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

571 **Data Availability Statement**

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

573 **References**

- 574 Averill, C., Bhatnagar, J. M., Dietze, M. C., Pearse, W. D., & Kivlin, S. N. (2019). Global
575 imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proceedings of the*
576 *National Academy of Sciences*, *116*(46), 23163–23168.
577 <https://doi.org/10.1073/pnas.1906655116>
- 578 Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: root traits as
579 drivers of ecosystem processes. *Trends in Ecology & Evolution*, *29*(12), 692–699.
580 <https://doi.org/https://doi.org/10.1016/j.tree.2014.10.006>
- 581 Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-
582 Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M.,
583 Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M.,
584 Sweeney, C. J., van Ruijven, J., York, L. M., & Mommer, L. (2020). The fungal
585 collaboration gradient dominates the root economics space in plants. *Science Advances*,
586 *6*(27), eaba3756. <https://doi.org/10.1126/sciadv.aba3756>
- 587 Boczoń, A., Hilszczańska, D., Wrzosek, M., Szczepkowski, A., & Sierota, Z. (2021). Drought
588 in the forest breaks plant–fungi interactions. *European Journal of Forest Research*,
589 *140*(6), 1301–1321. <https://doi.org/10.1007/s10342-021-01409-5>
- 590 Cheng, L., Chen, W., Adams, T. S., Wei, X., Li, L., McCormack, M. L., DeForest, J. L.,
591 Koide, R. T., & Eissenstat, D. M. (2016). Mycorrhizal fungi and roots are
592 complementary in foraging within nutrient patches. *Ecology*, *97*(10), 2815–2823.
593 <https://doi.org/https://doi.org/10.1002/ecy.1514>
- 594 Comas, L. H., Becker, S., Cruz, V. M., Byrne, P. F., & Dierig, D. A. (2013). Root traits
595 contributing to plant productivity under drought. *Frontiers in Plant Science*, *4*.
596 <https://www.frontiersin.org/articles/10.3389/fpls.2013.00442>

- 597 Comas, L. H., Mueller, K. E., Taylor, L. L., Midford, P. E., Callahan, H. S., & Beerling, D. J.
598 (2012). Evolutionary Patterns and Biogeochemical Significance of Angiosperm Root
599 Traits. *International Journal of Plant Sciences*, 173(6), 584–595.
600 <https://doi.org/10.1086/665823>
- 601 Cornelissen, J., Castro Diez, P., & Hunt, R. (1996). Seedling Growth, Allocation and Leaf
602 Attributes in a Wide Range of Woody Plant Species and Type. *Journal of Ecology*,
603 84(5), 755–766.
- 604 Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich,
605 P. B., Steege, H. ter, Morgan, H. D., Heijden, M. G. A. van der, Pausas, J. G., & Poorter,
606 H. (2003). A handbook of protocols for standardised and easy measurement of plant
607 functional traits worldwide. *Australian Journal of Botany*, 51(4), 335–380.
608 <https://doi.org/10.1071/BT02124>
- 609 Da, R., Fan, C., Zhang, C., Zhao, X., & von Gadow, K. (2023). Are absorptive root traits
610 good predictors of ecosystem functioning? A test in a natural temperate forest. *New*
611 *Phytologist*, 239(1), 75–86. <https://doi.org/https://doi.org/10.1111/nph.18915>
- 612 Deutscher Wetterdienst (DWD). (2024).
613 https://www.dwd.de/DE/wetter/wetterundklima_vorort/sachsen/leipzig/_node.html.
- 614 Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer,
615 M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H.,
616 Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D.
617 (2016). The global spectrum of plant form and function. *Nature*, 529(7585), 167–171.
618 <https://doi.org/10.1038/nature16489>
- 619 Dietrich, P., Ferlian, O., Huang, Y., Luo, S., Quosh, J., & Eisenhauer, N. (2023). Tree
620 diversity effects on productivity depend on mycorrhizae and life strategies in a temperate
621 forest experiment. *Ecology*, 104(2), e3896.
622 <https://doi.org/https://doi.org/10.1002/ecy.3896>
- 623 Eissenstat, D. M., Kucharski, J. M., Zadworny, M., Adams, T. S., & Koide, R. T. (2015).
624 Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate
625 forest. *New Phytologist*, 208(1), 114–124.
626 <https://doi.org/https://doi.org/10.1111/nph.13451>
- 627 Endo, I., Kobatake, M., Tanikawa, N., Nakaji, T., Ohashi, M., & Makita, N. (2021).
628 Anatomical patterns of condensed tannin in fine roots of tree species from a cool-
629 temperate forest. *Annals of Botany*, 128(1), 59–71. <https://doi.org/10.1093/aob/mcab022>
- 630 Enstone, D. E., Peterson, C. A., & Ma, F. (2002). Root Endodermis and Exodermis: Structure,
631 Function, and Responses to the Environment. *Journal of Plant Growth Regulation*,
632 21(4), 335–351. <https://doi.org/10.1007/s00344-003-0002-2>
- 633 Feild, T. S., & Arens, N. A. N. C. (2007). The ecophysiology of early angiosperms. *Plant,*
634 *Cell & Environment*, 30(3), 291–309. [https://doi.org/https://doi.org/10.1111/j.1365-](https://doi.org/https://doi.org/10.1111/j.1365-3040.2006.01625.x)
635 [3040.2006.01625.x](https://doi.org/https://doi.org/10.1111/j.1365-3040.2006.01625.x)

- 636 Ferlian, O., Wirth, C., & Eisenhauer, N. (2017). Leaf and root C-to-N ratios are poor
637 predictors of soil microbial biomass C and respiration across 32 tree species.
638 *Pedobiologia*, 65, 16–23. [https://doi.org/https://doi.org/10.1016/j.pedobi.2017.06.005](https://doi.org/10.1016/j.pedobi.2017.06.005)
- 639 Freschet, G. T., Pagès, L., Iversen, C. M., Comas, L. H., Rewald, B., Roumet, C., Klimešová,
640 J., Zadworny, M., Poorter, H., Postma, J. A., Adams, T. S., Bagniewska-Zadworna, A.,
641 Bengough, A. G., Blancaflor, E. B., Brunner, I., Cornelissen, J. H. C., Garnier, E.,
642 Gessler, A., Hobbie, S. E., ... McCormack, M. L. (2021). A starting guide to root
643 ecology: strengthening ecological concepts and standardising root classification,
644 sampling, processing and trait measurements. *New Phytologist*, 232(3), 973–1122.
645 [https://doi.org/https://doi.org/10.1111/nph.17572](https://doi.org/10.1111/nph.17572)
- 646 Freschet, G. T., & Roumet, C. (2017). Sampling roots to capture plant and soil functions.
647 *Functional Ecology*, 31(8), 1506–1518. [https://doi.org/https://doi.org/10.1111/1365-
648 2435.12883](https://doi.org/10.1111/1365-2435.12883)
- 649 Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B.,
650 Bardgett, R. D., De Deyn, G. B., Johnson, D., Klimešová, J., Lukac, M., McCormack,
651 M. L., Meier, I. C., Pagès, L., Poorter, H., Prieto, I., Wurzbürger, N., Zadworny, M.,
652 Bagniewska-Zadworna, A., ... Stokes, A. (2021). Root traits as drivers of plant and
653 ecosystem functioning: current understanding, pitfalls and future research needs. *New
654 Phytologist*, 232(3), 1123–1158. [https://doi.org/https://doi.org/10.1111/nph.17072](https://doi.org/10.1111/nph.17072)
- 655 Gambetta, G. A., Fei, J., Rost, T. L., Knipfer, T., Matthews, M. A., Shackel, K. A., Walker,
656 M. A., & McElrone, A. J. (2013). Water Uptake along the Length of Grapevine Fine
657 Roots: Developmental Anatomy, Tissue-Specific Aquaporin Expression, and Pathways
658 of Water Transport. *Plant Physiology*, 163(3), 1254–1265.
659 <https://doi.org/10.1104/pp.113.221283>
- 660 Gibert, A., Gray, E. F., Westoby, M., Wright, I. J., & Falster, D. S. (2016). On the link
661 between functional traits and growth rate: meta-analysis shows effects change with plant
662 size, as predicted. *Journal of Ecology*, 104(5), 1488–1503.
663 [https://doi.org/https://doi.org/10.1111/1365-2745.12594](https://doi.org/10.1111/1365-2745.12594)
- 664 Guo, D., Li, H., Mitchell, R. J., Han, W., Hendricks, J. J., Fahey, T. J., & Hendrick, R. L.
665 (2008). Fine root heterogeneity by branch order: exploring the discrepancy in root
666 turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist*,
667 177(2), 443–456. [https://doi.org/https://doi.org/10.1111/j.1469-8137.2007.02242.x](https://doi.org/10.1111/j.1469-8137.2007.02242.x)
- 668 Guo, D., Xia, M., Wei, X., Chang, W., Liu, Y., & Wang, Z. (2008). Anatomical traits
669 associated with absorption and mycorrhizal colonization are linked to root branch order
670 in twenty-three Chinese temperate tree species. *New Phytologist*, 180(3), 673–683.
671 [https://doi.org/https://doi.org/10.1111/j.1469-8137.2008.02573.x](https://doi.org/10.1111/j.1469-8137.2008.02573.x)
- 672 Hernández, E. I., Vilagrosa, A., Pausas, J. G., & Bellot, J. (2010). Morphological traits and
673 water use strategies in seedlings of Mediterranean coexisting species. *Plant Ecology*,
674 207(2), 233–244. <https://doi.org/10.1007/s11258-009-9668-2>
- 675 King, W. L., Yates, C. F., Cao, L., O'Rourke-Ibach, S., Fleishman, S. M., Richards, S. C.,
676 Centinari, M., Hafner, B. D., Goebel, M., Bauerle, T., Kim, Y.-M., Nicora, C. D.,
677 Anderton, C. R., Eissenstat, D. M., & Bell, T. H. (2023). Functionally discrete fine roots

- 678 differ in microbial assembly, microbial functional potential, and produced metabolites.
679 *Plant, Cell & Environment*, 46(12), 3919–3932.
680 <https://doi.org/https://doi.org/10.1111/pce.14705>
- 681 Kong, D. L., Wang, J. J., Kardol, P., Wu, H. F., Zeng, H., Deng, X. B., & Deng, Y. (2016).
682 Economic strategies of plant absorptive roots vary with root diameter. *Biogeosciences*,
683 13(2), 415–424. <https://doi.org/10.5194/bg-13-415-2016>
- 684 Kong, D., Wang, J., Zeng, H., Liu, M., Miao, Y., Wu, H., & Kardol, P. (2017). The nutrient
685 absorption–transportation hypothesis: optimizing structural traits in absorptive roots.
686 *New Phytologist*, 213(4), 1569–1572. <https://doi.org/https://doi.org/10.1111/nph.14344>
- 687 Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., &
688 Laughlin, D. C. (2016). Root traits are multidimensional: specific root length is
689 independent from root tissue density and the plant economic spectrum. *Journal of*
690 *Ecology*, 104(5), 1299–1310. <https://doi.org/https://doi.org/10.1111/1365-2745.12562>
- 691 Laliberté, E. (2017). Below-ground frontiers in trait-based plant ecology. *New Phytologist*,
692 213(4), 1597–1603. <https://doi.org/https://doi.org/10.1111/nph.14247>
- 693 Lavorel, S., & Grigulis, K. (2012). How fundamental plant functional trait relationships scale-
694 up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, 100(1), 128–
695 140. <https://doi.org/https://doi.org/10.1111/j.1365-2745.2011.01914.x>
- 696 Li, T., Ren, J., He, W., Wang, Y., Wen, X., Wang, X., Ye, M., Chen, G., Zhao, K., Hou, G.,
697 Li, X., & Fan, C. (2022). Anatomical structure interpretation of the effect of soil
698 environment on fine root function. *Frontiers in Plant Science*, 13.
699 <https://www.frontiersin.org/journals/plant-science/articles/10.3389/fpls.2022.993127>
- 700 Liu, J., Zhang, X., Song, F., Zhou, S., Cadotte, M. W., & Bradshaw, C. J. A. (2015).
701 Explaining maximum variation in productivity requires phylogenetic diversity and single
702 functional traits. *Ecology*, 96(1), 176–183. <https://doi.org/https://doi.org/10.1890/14-1034.1>
- 704 Liu, X., Swenson, N. G., Lin, D., Mi, X., Umaña, M. N., Schmid, B., & Ma, K. (2016).
705 Linking individual-level functional traits to tree growth in a subtropical forest. *Ecology*,
706 97(9), 2396–2405. <https://doi.org/https://doi.org/10.1002/ecy.1445>
- 707 Long, Y., Kong, D., Chen, Z., & Zeng, H. (2013). Variation of the Linkage of Root Function
708 with Root Branch Order. *PLOS ONE*, 8(2), e57153-
709 <https://doi.org/10.1371/journal.pone.0057153>
- 710 Lynch, J. P., Strock, C. F., Schneider, H. M., Sidhu, J. S., Ajmera, I., Galindo-Castañeda, T.,
711 Klein, S. P., & Hanlon, M. T. (2021). Root anatomy and soil resource capture. *Plant and*
712 *Soil*, 466(1), 21–63. <https://doi.org/10.1007/s11104-021-05010-y>
- 713 McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D.,
714 Helmisaari, H.-S., Hobbie, E. A., Iversen, C. M., Jackson, R. B., Leppälammil-Kujansuu,
715 J., Norby, R. J., Phillips, R. P., Pregitzer, K. S., Pritchard, S. G., Rewald, B., &
716 Zadworny, M. (2015). Redefining fine roots improves understanding of below-ground
717 contributions to terrestrial biosphere processes. *New Phytologist*, 207(3), 505–518.
718 <https://doi.org/https://doi.org/10.1111/nph.13363>

- 719 McCormack, M. L., & Iversen, C. M. (2019). Physical and Functional Constraints on Viable
720 Belowground Acquisition Strategies. *Frontiers in Plant Science*, *10*.
721 <https://www.frontiersin.org/articles/10.3389/fpls.2019.01215>
- 722 McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community
723 ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185.
724 <https://doi.org/https://doi.org/10.1016/j.tree.2006.02.002>
- 725 McGonigle, T. P., Miller, M. H., Evans, D. G., Fairchild, G. L., & Swan, J. A. (1990). A new
726 method which gives an objective measure of colonization of roots by vesicular—
727 arbuscular mycorrhizal fungi. *New Phytologist*, *115*(3), 495–501.
728 <https://doi.org/https://doi.org/10.1111/j.1469-8137.1990.tb00476.x>
- 729 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.
730 R., O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., &
731 Wagner, H. (2021). vegan: Community ecology package. [https://Cran.r-](https://Cran.r-Project.Org/Web/Packages/Vegan/Index.Html)
732 [Project.Org/Web/Packages/Vegan/Index.Html](https://Cran.r-Project.Org/Web/Packages/Vegan/Index.Html).
- 733 Orwin, K. H., Mason, N. W. H., Jordan, O. M., Lambie, S. M., Stevenson, B. A., & Mudge,
734 P. L. (2018). Season and dominant species effects on plant trait-ecosystem function
735 relationships in intensively grazed grassland. *Journal of Applied Ecology*, *55*(1), 236–
736 245. <https://doi.org/https://doi.org/10.1111/1365-2664.12939>
- 737 Ostonen, I., Püttsepp, Ü., Biel, C., Alberton, O., Bakker, M. R., Lõhmus, K., Majdi, H.,
738 Metcalfe, D., Olsthoorn, A. F. M., Pronk, A., Vanguelova, E., Weih, M., & Brunner, I.
739 (2007). Specific root length as an indicator of environmental change. *Plant Biosystems -*
740 *An International Journal Dealing with All Aspects of Plant Biology*, *141*(3), 426–442.
741 <https://doi.org/10.1080/11263500701626069>
- 742 Paine, C. E. T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide,
743 H., Dainou, K., de Gouvenain, R. C., Doucet, J.-L., Doust, S., Fine, P. V. A., Fortunel,
744 C., Haase, J., Holl, K. D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., ... Hector, A.
745 (2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do
746 not know why. *Journal of Ecology*, *103*(4), 978–989.
747 <https://doi.org/https://doi.org/10.1111/1365-2745.12401>
- 748 Pedersen, T. L. (2022). ggraph: An Implementation of Grammar of Graphics for Graphs and
749 Networks. <https://Cran.r-Project.Org/Web/Packages/Ggraph/Index.Html>.
- 750 Phillips, R. P., Brzostek, E., & Midgley, M. G. (2013). The mycorrhizal-associated nutrient
751 economy: a new framework for predicting carbon–nutrient couplings in temperate
752 forests. *New Phytologist*, *199*(1), 41–51.
753 <https://doi.org/https://doi.org/10.1111/nph.12221>
- 754 Poorter, L., & Bongers, F. (2006). Leaf traits are good predictors of plant performance across
755 53 rain forest species. *Ecology*, *87*(7), 1733–1743.
756 [https://doi.org/https://doi.org/10.1890/0012-9658\(2006\)87\[1733:LTAGPO\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[1733:LTAGPO]2.0.CO;2)
- 757 Pregitzer, K. S. (2002). Fine roots of trees – a new perspective. *New Phytologist*, *154*(2), 267–
758 270. https://doi.org/https://doi.org/10.1046/j.1469-8137.2002.00413_1.x

- 759 Pregitzer, K. S., DeForest, J. L., Burton, A. J., Allen, M. F., Ruess, R. W., & Hendrick, R. L.
760 (2002). Fine root architecture of nine north American trees. *Ecological Monographs*,
761 72(2), 293–309. [https://doi.org/https://doi.org/10.1890/0012-](https://doi.org/https://doi.org/10.1890/0012-9615(2002)072[0293:FRAONN]2.0.CO;2)
762 9615(2002)072[0293:FRAONN]2.0.CO;2
- 763 R Core Team. (2022). *R: A language and environment for statistical computing*. R
764 Foundation for Statistical Computing, Vienna, Austria. URL.
- 765 Reich, P. B. (2014). The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto.
766 *Journal of Ecology*, 102(2), 275–301. [https://doi.org/https://doi.org/10.1111/1365-](https://doi.org/https://doi.org/10.1111/1365-2745.12211)
767 2745.12211
- 768 Schnabel, F., Purrucker, S., Schmitt, L., Engelmann, R. A., Kahl, A., Richter, R., Seele-
769 Dilbat, C., Skiadaresis, G., & Wirth, C. (2022). Cumulative growth and stress responses
770 to the 2018–2019 drought in a European floodplain forest. *Global Change Biology*,
771 28(5), 1870–1883. <https://doi.org/https://doi.org/10.1111/gcb.16028>
- 772 Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of
773 image analysis. *Nature Methods*, 9(7), 671–675. <https://doi.org/10.1038/nmeth.2089>
- 774 Schulze, E.-D. (2006). Biological control of the terrestrial carbon sink. *Biogeosciences*, 3(2),
775 147–166. <https://doi.org/10.5194/bg-3-147-2006>
- 776 Seethepalli, A., Dhakal, K., Griffiths, M., Guo, H., Freschet, G. T., & York, L. M. (2021).
777 RhizoVision Explorer: open-source software for root image analysis and measurement
778 standardization. *AoB PLANTS*, 13(6), plab056. <https://doi.org/10.1093/aobpla/plab056>
- 779 Shen, Y., Natalia Umaña, M., Li, W., Fang, M., Chen, Y., Lu, H., & Yu, S. (2022). Linking
780 soil nutrients and traits to seedling growth: A test of the plant economics spectrum.
781 *Forest Ecology and Management*, 505, 119941.
782 <https://doi.org/https://doi.org/10.1016/j.foreco.2021.119941>
- 783 Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L.
784 W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V, de L. Dantas, V., de Bello, F.,
785 Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka,
786 K., Jackson, B., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of
787 intraspecific trait variation in plant communities. *Ecology Letters*, 18(12), 1406–1419.
788 <https://doi.org/https://doi.org/10.1111/ele.12508>
- 789 Smith, S. E., & Read, D. J. (2002). 1 - The symbionts forming VA mycorrhizas. In S. E.
790 Smith & D. J. Read (Eds.), *Mycorrhizal Symbiosis (Second Edition)* (pp. 11–I).
791 Academic Press. <https://doi.org/https://doi.org/10.1016/B978-012652840-4/50002-4>
- 792 Steidinger, B. S., Crowther, T. W., Liang, J., Van Nuland, M. E., Werner, G. D. A., Reich, P.
793 B., Nabuurs, G. J., de-Miguel, S., Zhou, M., Picard, N., Herault, B., Zhao, X., Zhang, C.,
794 Routh, D., Peay, K. G., Abegg, M., Adou Yao, C. Y., Alberti, G., Almeyda Zambrano,
795 A., ... consortium, G. (2019). Climatic controls of decomposition drive the global
796 biogeography of forest-tree symbioses. *Nature*, 569(7756), 404–408.
797 <https://doi.org/10.1038/s41586-019-1128-0>
- 798 Umaña, M. N., Zipkin, E. F., Zhang, C., Cao, M., Lin, L., & Swenson, N. G. (2018).
799 Individual-level trait variation and negative density dependence affect growth in tropical

- 800 tree seedlings. *Journal of Ecology*, 106(6), 2446–2455.
801 <https://doi.org/https://doi.org/10.1111/1365-2745.13001>
- 802 van der Plas, F., Schröder-Georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard,
803 R. L., Buchmann, N., de Kroon, H., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M.,
804 Gleixner, G., Hildebrandt, A., Koller-France, E., Leimer, S., Milcu, A., Mommer, L., ...
805 Wirth, C. (2020). Plant traits alone are poor predictors of ecosystem properties and long-
806 term ecosystem functioning. *Nature Ecology & Evolution*, 4(12), 1602–1611.
807 <https://doi.org/10.1038/s41559-020-01316-9>
- 808 Vierheilig, H., P, C. A., Urs, W., & Yves, P. (1998). Ink and Vinegar, a Simple Staining
809 Technique for Arbuscular-Mycorrhizal Fungi. *Applied and Environmental Microbiology*,
810 64(12), 5004–5007. <https://doi.org/10.1128/AEM.64.12.5004-5007.1998>
- 811 Weemstra, M., Zambrano, J., Allen, D., & Umaña, M. N. (2021). Tree growth increases
812 through opposing above-ground and below-ground resource strategies. *Journal of*
813 *Ecology*, 109(10), 3502–3512. <https://doi.org/https://doi.org/10.1111/1365-2745.13729>
- 814 Weigelt, A., Mommer, L., Andraczek, K., Iversen, C. M., Bergmann, J., Bruelheide, H., Fan,
815 Y., Freschet, G. T., Guerrero-Ramírez, N. R., Kattge, J., Kuyper, T. W., Laughlin, D. C.,
816 Meier, I. C., van der Plas, F., Poorter, H., Roumet, C., van Ruijven, J., Sabatini, F. M.,
817 Semchenko, M., ... McCormack, M. L. (2021). An integrated framework of plant form
818 and function: the belowground perspective. *New Phytologist*, 232(1), 42–59.
819 <https://doi.org/https://doi.org/10.1111/nph.17590>
- 820 Weigelt, A., Mommer, L., Andraczek, K., Iversen, C. M., Bergmann, J., Bruelheide, H.,
821 Freschet, G. T., Guerrero-Ramírez, N. R., Kattge, J., Kuyper, T. W., Laughlin, D. C.,
822 Meier, I. C., van der Plas, F., Poorter, H., Roumet, C., van Ruijven, J., Sabatini, F. M.,
823 Semchenko, M., Sweeney, C. J., ... McCormack, M. L. (2023). The importance of trait
824 selection in ecology. *Nature*, 618(7967), E29–E30. [https://doi.org/10.1038/s41586-023-](https://doi.org/10.1038/s41586-023-06148-8)
825 [06148-8](https://doi.org/10.1038/s41586-023-06148-8)
- 826 Westbrook, J. W., Kitajima, K., Burleigh, J. G., Kress, W. J., Erickson, D. L., & Wright, S. J.
827 (2011). What Makes a Leaf Tough? Patterns of Correlated Evolution between Leaf
828 Toughness Traits and Demographic Rates among 197 Shade-Tolerant Woody Species in
829 a Neotropical Forest. *The American Naturalist*, 177(6), 800–811.
830 <https://doi.org/10.1086/659963>
- 831 Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits.
832 *Trends in Ecology & Evolution*, 21(5), 261–268.
833 <https://doi.org/https://doi.org/10.1016/j.tree.2006.02.004>
- 834 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-
835 Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom,
836 P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R.
837 (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827.
838 <https://doi.org/10.1038/nature02403>
- 839 Xia, M., Guo, D., & Pregitzer, K. S. (2010). Ephemeral root modules in *Fraxinus*
840 *mandshurica*. *New Phytologist*, 188(4), 1065–1074.
841 <https://doi.org/https://doi.org/10.1111/j.1469-8137.2010.03423.x>

- 842 Yan, H., Freschet, G. T., Wang, H., Hogan, J. A., Li, S., Valverde-Barrantes, O. J., Fu, X.,
843 Wang, R., Dai, X., Jiang, L., Meng, S., Yang, F., Zhang, M., & Kou, L. (2022).
844 Mycorrhizal symbiosis pathway and edaphic fertility frame root economics space among
845 tree species. *New Phytologist*, 234(5), 1639–1653.
846 <https://doi.org/https://doi.org/10.1111/nph.18066>
- 847 Zadworny, M., McCormack, M. L., Mucha, J., Reich, P. B., & Oleksyn, J. (2016). Scots pine
848 fine roots adjust along a 2000-km latitudinal climatic gradient. *New Phytologist*, 212(2),
849 389–399. <https://doi.org/https://doi.org/10.1111/nph.14048>
- 850 Zhou, M., Guo, Y., Sheng, J., Yuan, Y., Zhang, W.-H., & Bai, W. (2022). Using anatomical
851 traits to understand root functions across root orders of herbaceous species in a temperate
852 steppe. *New Phytologist*, 234(2), 422–434.
853 <https://doi.org/https://doi.org/10.1111/nph.17978>
- 854
- 855
- 856
- 857
- 858
- 859
- 860
- 861
- 862
- 863
- 864
- 865
- 866
- 867
- 868
- 869
- 870
- 871
- 872
- 873
- 874
- 875

876 **Figure captions**

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

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

890

891

892

893

894

895

896

897

898

899

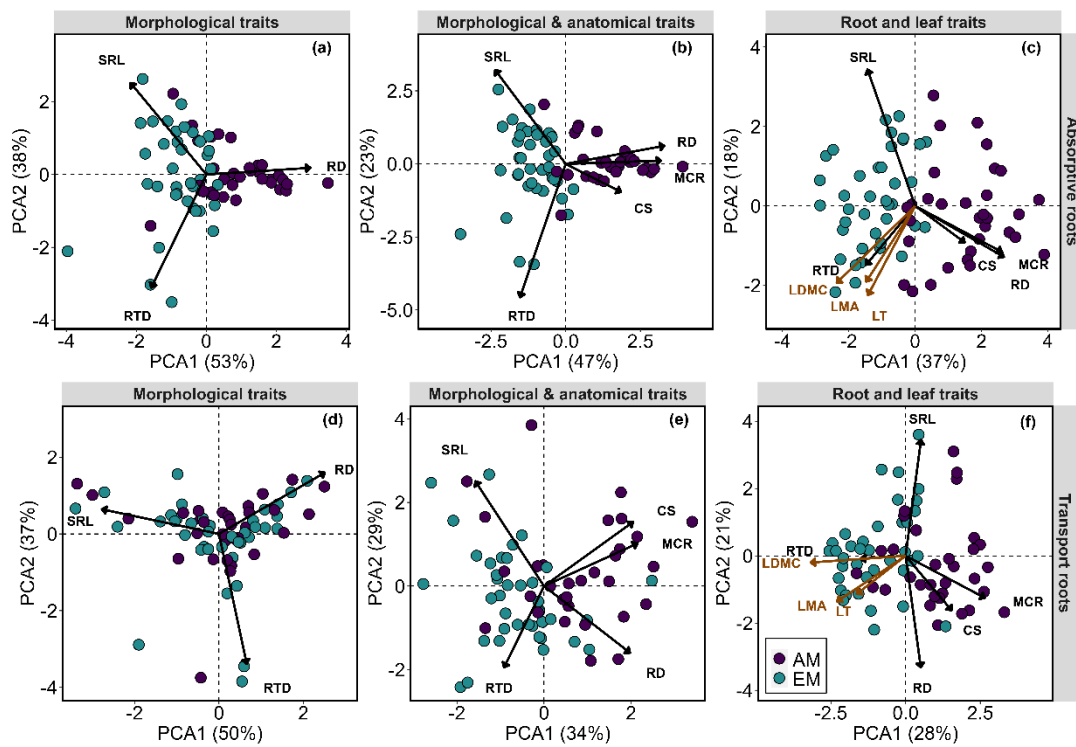
900

901

902

903

904 **Figure 1.**



905

906

907

908

909

910

911

912

913

914

915

916

917

918

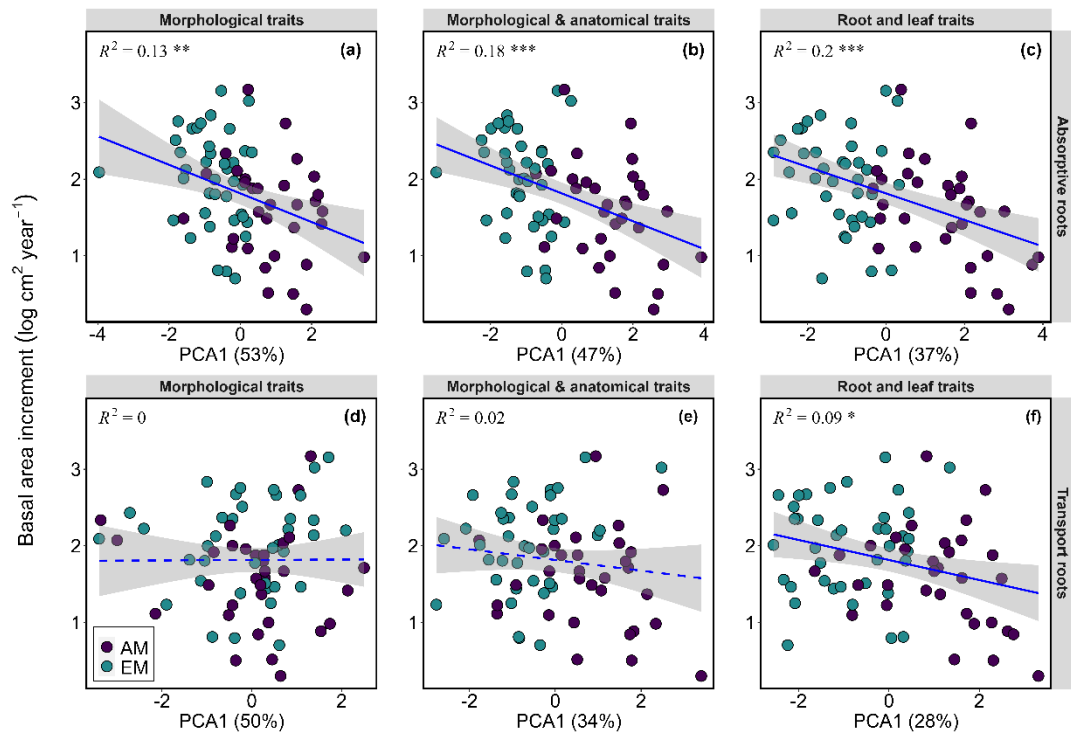
919

920

921

922

923 **Figure 2.**



924

925

926

927

928

929

930

931

932

933

934

935

936

937

938

939

940

941