

1 **The worldwide allometric relationship in anatomical structures for plant roots**

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18 **Abstract**

19 The anatomical structures, i.e., the cortex and stele, are fundamental for the absorptive
20 function of plant roots. Unraveling how the allometric structures are assembled in
21 absorptive roots is essential for our understanding the plant ecology, physiology and
22 responses to global environmental changes. In this review study, we first compile a
23 globally largest dataset on key root structural traits, i.e., root diameter, cortex
24 thickness and stele radius across 512 species. Using this largest dataset, we confirm
25 an allometric relationship of absorptive root structures in a previous study using a
26 much smaller species pool, i.e., the cortex thickness increased much faster than the
27 stele radius with increasing root diameter. The allometric relationship is further
28 validated within and across different plant growth forms (woody, grass, and liana
29 species), mycorrhiza types (arbuscular mycorrhiza, ectomycorrhiza, and orchid
30 mycorrhizas), phylogenetic gradients (from ferns to Orchidaceae of primitive
31 angiosperms), and environmental change scenarios (e.g., the elevation of atmospheric
32 CO₂ concentration and nitrogen fertilization), supporting the universal allometric
33 relationship in plant roots. We then summarized recent proceedings as well as possible
34 issues on mechanisms underlying the root allometric relationship. The ecological and
35 evolutionary implications for this allometric relationship in roots are also discussed.
36 Finally, we propose several directions that should be stressed in future studies
37 regarding the allometric relationship in plant roots.

38

39 **Key words:** allometric relationship, root diameter, cortex thickness, stele radius

40 **1. Introduction**

41 Plant roots play a crucial role in plant growth, vegetation dynamics, ecosystem
42 functioning like productivity formation, nutrient cycle and their responses to
43 environmental changes (Carmona et al., 2021; Laughlin et al., 2021; Chandregowda et
44 al., 2022; Encinas-Valero et al., 2022; Hong et al., 2022). Compared to studies on plant
45 above-ground organs such as leaves and stems that have undergone enormous
46 proceedings (Wright et al., 2004; Diaz et al., 2016; Joswig et al., 2022), our
47 understanding of plant roots remains in its infancy. The core function of plant roots is
48 to absorb soil water and nutrients, which is undertaken by a few terminal root branch
49 orders, i.e., absorptive roots, mainly bearing primary root tissues (Guo et al., 2008b).
50 Generally, the absorptive function is depicted by a range of traits in root morphology,
51 physiology, anatomy, chemistry, mechanics and microbial symbiosis (McCormack et
52 al., 2017; Wambsganss et al., 2021; Wen et al., 2022; Yan et al., 2022). Among these
53 root traits, root diameter seems like the most important one given that it is closely
54 associated with a suite of other root traits as well as mycorrhizal fungi apart from its
55 well-known feature of easily measured and great inter-specific variation (Eissenstat et
56 al., 2015; Li et al., 2018; Bergmann et al., 2020; Wen et al., 2022). Furthermore, root
57 diameter is the phylogenetically most conservative root trait, suggesting that the great
58 inter-specific variation could largely be an evolutionarily imprint from the geological
59 environmental change such as atmospheric CO₂ decline since the Cretaceous (Comas
60 et al., 2012; Chen et al., 2013; Pineiro et al., 2020; Lugli et al., 2021).

61 The absorption function of plant roots is essentially determined by root anatomical

62 structures. Generally, absorptive roots are composed of two cylindrical components,
63 i.e., cortex and stele. The cortex directly takes part in the absorption of water and
64 nutrients and indirectly acquire these resources by associations with mycorrhizal fungi
65 (Brundrett, 2002; Ma et al., 2018; Rich et al., 2021). The stele is responsible for
66 transporting water and nutrients upward to stems and leaves, and the stele supply energy
67 demanding of the roots with leaf photosynthate. Theoretically, the change in root
68 diameter is mainly derived from the size variations of the cortex and stele, while how
69 the cortex and stele are coordinated with the shifts of root diameter has not been
70 uncovered until 2014 when two research groups independently found an allometric
71 relationship between the cortex and stele (Gu et al., 2014; Kong et al., 2014), i.e., the
72 cortex thickness increased linearly and much faster than the stele radius with increasing
73 root diameter. Later, this allometric relationship was reported in many studies, and was
74 synthesized by Kong et al. (2019) who reported a global existence of the allometric
75 relationship in root cortex and stele across 204 plant species.

76 Uncovering of the allometry relationship paves a new way for our understanding
77 of the form-function relationship in roots and plant evolution and adaptation to
78 environmental changes (McCormack et al., 2017; Kong et al., 2019; Bergmann et al.,
79 2020; Zhou et al., 2022). Since the global recognition of the allometric relationship
80 between root cortex and stele in 2019, mounting studies have focused on root
81 anatomical traits for one hand, and for the other hand we also note that some early
82 studies on Orchidaceae and vine root anatomy were neglected in Kong et al. (2019).
83 Further, despite the worldwide mycorrhizal associations in terrestrial plants, we know

84 little about whether and how the allometric relationship in absorptive roots varies
85 among mycorrhizal types with contrasting mycorrhizal structures and functioning
86 (e.g., arbuscular mycorrhiza (AM) vs. ectomycorrhiza (EM)) (Brundrett, 2002; Martin
87 et al., 2017) Additionally, no studies to date have explored how the environmental
88 changes affect the above allometric relationship in roots. Therefore, it is necessary to
89 further test the generality of the root allometric relationship using a much larger
90 species pool than that in Kong et al. (2019).

91 To fulfill this purpose, in this review paper, we made a thorough screening of the
92 data on the cortex thickness and the stele radius of absorptive roots in Web of Science,
93 Google Scholar, FRED 3.0 and CNKI (China's national knowledge infrastructure)
94 using keywords included “cortex”, “stele”, “anatomic structure”, “allometric
95 relationship”, “root diameter”. Our searching yielded 3,676,679 papers and reports.
96 We then refined these results according to additional criteria: (1) the study must be an
97 empirical rather than a review or perspective; (2) the data on root diameter and stele
98 radius were accessible. We also included some unpublished data (supplementary data
99 2) on root anatomical traits which were measured at the same sites and following the
100 same procedures as our previous study (Kong et al., 2014). Finally, our dataset
101 included 32 empirical studies (supplementary data 1) with a total of 698 observations
102 of 512 species at 41 sites (Fig. 1). Specifically, the dataset included 271 woody
103 species and 241 non-woody species (78 grass, 92 herb, 37 fern and 28 Orchidaceae
104 species). In addition, 13 liana species were included in the dataset. For the same
105 species appearing in different studies, we used the average value of the root traits

106 across species as the trait value of this species. For some studies with only the data of
107 the stele radius and root diameter, we use the difference between the root diameter
108 and stele radius (equal to the thickness of tissues outside the stele including the
109 epidermis, exodermis and cortex, i.e., tToS, as a proxy approximate to the cortex
110 thickness (Kong et al., 2019). For the studies with root trait data displayed in figures
111 or only photos on root anatomical structures presented, we digitalized the root trait
112 data using the software “SigmaScan Pro software (V5.0, SPSS Inc., Chicago, USA)”
113 and the software “IMAGE J (NIH Image, Bethesda, MD, USA)”, respectively.

114 Overall, in this review we aim to: (1) test the generality of the allometric
115 relationship between root cortex and stele within and across different plant growth
116 forms, mycorrhizal types and environmental treatments; (2) summarize mechanisms
117 and implications for such allometric relationship; (3) propose important directions for
118 future studies regarding the root allometric relationship.

119 **2. Generality of the allometric relationship in absorptive roots**

120 The allometric relationship between the cortex and the stele still held across the 698
121 observations and 512 species of root anatomical structures (Table 1; Fig. 2a, 2b). For
122 the 26 studies with root anatomical structures examined in at least three species, the
123 allometric relationship in absorptive roots existed in most of the studies, while only
124 four studies seemed exceptional (Table 2; Fig. 3; Supplementary data 1).

125 The allometric relationship in absorptive roots also occurred in different plant
126 growth forms. For example, the thickness of tToS in woody species increases 7.6-fold
127 faster than the stele radius with increasing root diameter, and the slope difference

128 (3.3-fold) is much lower in non-woody species (Table 1; Fig. 4), This allometric
129 relationship is very similar to that reported by Kong et al. (2019) using less than half
130 of the species number as in our study Within the non-woody species, the allometric
131 relationship was found in each of the fern grass, herb, and Orchidaceae (Fig. 5).
132 Interestingly, we observed a 5.1-fold difference of the slope in the root allometric
133 relationship in Orchidaceae species while the slope difference is much lower in other
134 three non-woody groups (Table 1). Finally, for the vine species, both the woody and
135 non-woody ones, followed the allometric manner in building their absorptive roots
136 (Supplementary Table 1; Supplementary Fig. 2a, 2b, 2c).

137 Among the dominant mycorrhizal types, the allometric relationship between root
138 cortex and stele was observed in AM (Fig. 6a), regardless of being woody or non-
139 woody of the plants (Fig. 7a, 7b), and the dual mycorrhizas of AM & EM plants but
140 not in EM plants (Table 1; Fig. 6b, 6c). While we do note a significant allometric
141 relationship in broadleaf EM trees but not in coniferous EM trees (Table 2; Fig. 8).
142 Therefore, it is likely that the inclusion of such coniferous EM trees could lead to the
143 overall no root allometric relationship across the EM plants. Considering only six
144 coniferous EM plant species included in our dataset, we can not rule out the
145 possibility of the root allometric relationship in other coniferous EM trees.
146 Nevertheless, the contrasting root allometric relationships between broadleaf and
147 coniferous EM trees may reflect the interior difference of the two types of EM plants
148 in root structures and functioning (Guo et al., 2008b; Chen et al., 2016). the
149 coniferous EM trees usually have vascular conduits (tracheid and sieve cells) with

150 much lower matter (water and photosynthates) transport efficiency relative to the
151 more efficient conduits (vessels and sieve tubes) in broadleaf EM plants (Guo et al.,
152 2008b). It is likely that with the shift of root diameter across coniferous EM trees,
153 some unknown strategies could be adopted rather than only change the size of the
154 stele to increase matter transport efficiency; this, as such, results in no root allometric
155 relationship in the coniferous EM plants. Finally, we show for the first time that the
156 root allometric relationship still exists in another important mycorrhizal type, i.e., the
157 Orchid mycorrhiza (OM) plants (Table 2; Fig. 5d), usually bearing much thicker
158 absorptive roots (up to 4.6mm) (Zhu et al., 2016) than most of the AM and EM plants.

159 Root anatomical structures have also been measured sparsely under different
160 environmental change scenarios (e.g., soil nitrogen or phosphorus fertilization,
161 increase of atmospheric CO₂ concentration and seasonality in rainfall) (Table 1; Fig.
162 9), which provides an opportunity to test the consistency of the root allometric
163 relationship. Although the root allometric relationship in some scenarios does not hold
164 statistically (Fig. 9), this is apparently due to the inclusion of a few species with
165 “exceptionally” large or small size of root cortex and stele or the inclusion of some
166 species with “exceptional” responses to the environmental changes (e. g., Fig. 9a₂, a₃,
167 b₂, b₃, d₂, d₃). Overall, our results suggested a relative insensitiveness of the root
168 allometric relationship to the environmental changes. Interestingly, we note that the
169 cortex thickness increases slower and the stele radius increases faster with increasing
170 root diameter in the rainy season compared with that in the dry season, consequently
171 causing an equal rather than allometric increase rate of the cortex thickness and stele

172 radius in the rainy season (Fig. 9d₂, d₃). It is worthwhile to test the generality of such
173 impact on the root allometric relationship by rainfall seasonality and uncover the
174 underlying mechanisms in future studies.

175 Together, the wide existence of the allometric relationship between root cortex
176 and stele across different climatic zones (tropical, sub-tropical and temperate),
177 ecosystem types (forests, grasslands, deserts and mangroves), mycorrhizal types (AM,
178 some EM, AM&EM, OM), phylogenetic gradients (from ferns to Orchidaceae), and
179 environmental change scenarios support the universal rule of the allometric
180 relationship by which the root anatomical structures are assembled.

181 **3. Mechanisms of the root allometric relationship**

182 Currently, two theories have been proposed in explaining why the allometric
183 relationship between the cortex and stele is formed. One is the nutrient absorption-
184 transportation balance theory (Kong et al., 2017) and the other is the carbon supply-
185 consumption balance theory (Kong et al., 2021; Colombi et al., 2022) (Fig. 10). Both
186 theories run according to the principle of functional balance of the matter (nutrients,
187 photosynthates) transport within root tissues as well as the physical law of fluid
188 transport in the conduits, namely the “Hagen-Poiseuille law” (Jensen et al., 2016). Here,
189 we only outline the two theories and readers can refer to the original papers for details
190 of the theories.

191 There are two parallel vascular systems in root steles, i.e., vessels responsible for
192 transporting water and nutrients upward to stems and leaves and sieves responsible for
193 meeting the carbon demanding of the root. According to the Hagen-Poiseuille law, both

194 volumetric flow rates in the conduits (i.e., water and nutrient transportation via vessels
195 and photosynthate transportation via sieves) scale to the fourth power of the root radius;
196 while even the maximum nutrient absorption (via mycorrhizal fungi in the cortex) and
197 carbon consumption (via the cortex) scale less than the twice power of root radius. In
198 this case, only a much faster increase of the cortex thickness than the stele radius with
199 increasing root diameter (i.e., the allometric relationship) can lead to a *balance between*
200 *the nutrient absorption* (via mycorrhizal fungi in the cortex) *and the nutrient*
201 *transportation* (via vessels in the stele) *and a balance between the carbon supply* (via
202 sieves in the stele) *and carbon consumption* (via the cortex).

203 Nevertheless, we should also keep in mind of some important limitations of the
204 above two theories. Firstly, the *nutrient absorption-transportation balance* theory holds
205 on a prerequisite of a universal association of plant roots with mycorrhizal fungi, while
206 there are still a lot of species with no mycorrhizal associations (Vander et al., 2015;
207 Brundrett and Tedersoo, 2018; Correia et al., 2018). Secondly, the two theories seem
208 running independently although they are based on two interconnected vascular
209 conducts, i.e., vessels and sieves. It is also interesting to learn about how the above two
210 theories are linked with leaves, the important sink of nutrients and the source of carbon.
211 Thirdly, empirical evidence is urgently needed to test the prediction of the above
212 functional balance that underlies the root allometric relationship.

213

214 **4. Implication of the root allometric relationship**

215 **4.1 Relationship with the "root economics spectrum"**

216 Traditionally, root economic spectrum is considered to be the core trait dimension in
217 roots which conveys a trade-off between nutrient uptake and conservation (Freschet et
218 al., 2010; Reich, 2014; Kramer-Walter et al., 2016). It has been widely recognized that
219 a positive correlation between root diameter and root life span (i.e., conservation of
220 nutrient) (Guo et al., 2008a; Gu et al., 2017; Liese et al., 2019) and a negative
221 correlation between root nutrient uptake and root tissue density (RTD) (Zadworny et
222 al., 2017; Stock et al., 2021). If the trade-off exists between root nutrient uptake and
223 conservation, there should be a positive correlation between RTD and root diameter.
224 However, besides such a prediction, many studies also found a negative or no
225 relationship between RTD and root diameter (Weemstra et al., 2016; Kong et al.,
226 2019; Han and Zhu, 2021). Based on the universal allometric relationship between
227 root cortex and stele, we predict a negative and non-linear relationship between RTD
228 and root diameter, and this prediction has been verified using a global root trait
229 dataset (Kong et al., 2019). Therefore, the formation of the root allometric
230 relationship may not support the existence of the widely acknowledged root economic
231 spectrum.

232

233 **4.2 Plant evolution and adaptation to environment**

234 The evolution of angiosperms is closely related to the decline of atmospheric CO₂
235 concentration since the mid-Cretaceous (Beerling and Berner, 2005; Gerhart and
236 Ward, 2010). For example, the reduction of atmospheric CO₂ concentration often
237 lowers leaf photosynthesis, consequently causing “carbon starvation” to plants. To

238 survive in this carbon limitation condition, plants tend to increase stomatal
239 conductance to compensatively improve leaf CO₂ fixation (Zhou et al., 2013; Holttä et
240 al., 2017). However, large stomatal conductance will enhance the transpiration water
241 loss, as such causing physiological drought to plants (Khan et al., 2007; Wang et al.,
242 2018). The surge of leaf vein density in angiosperms since the mid-Cretaceous, hence
243 resulting more efficient water supply to the mesophyll cell for photosynthesis, can be
244 considered as evidence for plant adaptation to the physiological drought (Baraloto et
245 al., 2010; Feild et al., 2011; Baird et al., 2021; Yan et al., 2022).

246 Coordinated with the evolutionary change in leaves, thinning of the absorptive
247 roots is regarded as an adaptation to the physiological drought caused by the decline
248 of atmospheric CO₂ concentration (Fig. 11a) (Comas et al., 2012; Chen et al., 2013;
249 Ma et al., 2018). Alongside the thinning of the absorptive roots, the much faster
250 decrease of the cortex thickness than the stele radius means effectively reducing the
251 resistance of water and nutrients entering the root tissues for one hand and for the
252 other hand effectively reducing the carbon consumption by root cortex (Fig. 11b).
253 Therefore, the allometrically structured roots are much beneficial for plants to survive
254 under the carbon and water limited environment. From this point of view, the
255 allometric relationship in absorptive roots is insightful for our understanding of how
256 the roots, whole plants and even the ecosystems respond and adapt to the geological
257 and the on-going environmental changes.

258

259 **5. Future directions**

260 **5.1 Differences of the root allometric relationship among studies**

261 Studies to date always concentrate on the general pattern of the root allometric
262 relationship, i.e., a much larger slope of the cortex thickness *vs.* root diameter
263 regression than the slope of the stele radius *vs.* root diameter regression, while ignore
264 the great difference of the above allometry, that is, the slope difference ranging from
265 the minimum 1.2-fold to the maximum 15.7-fold across studies (Table 2). We are still
266 unclear about mechanisms accounting for such huge difference in the root allometric
267 relationship. This is a fascinating question that could stimulate far-reaching outcomes
268 in this field.

269 **5.2 Examining root anatomical structures in more species**

270 The global establishment of the allometric relationship between root cortex and stele
271 relies on about 500 plant species, much smaller than the total vascular plant species
272 number (about 390,000) on the earth (Cantwell-Jones et al., 2022). Even in the global
273 root trait dataset, such as FRED 3.0 (Iversen et al., 2021), the measurements of root
274 anatomical traits are far less than the measurements of other root traits such as root
275 diameter and root tissue density. Therefore, it is necessary to measure root anatomical
276 structures in more plant species, especially the families with a large number of species
277 like Orchidaceae with over 20, 000 species.

278 **5.3 Effects of environmental changes on the root allometric relationship**

279 By far, only four studies are available for our evaluation on how environmental changes
280 alter the allometric relationship in absorptive roots. Moreover, only a few
281 environmental change scenarios are considered and no interactions among these factors

282 have been examined in these studies. Apart from the studies under controlled
283 environments, we need to pay more attention to plants growing in naturally stressful
284 conditions such as alpine forests, deserts, and coast environments in high salinity.
285 Comparison of the root allometric relationship under the controlled and the natural
286 conditions could be instructive for our understanding and prediction of vegetation
287 dynamics under global climate change.

288

289 **5.4 Linking the root allometric relationship with plant above-ground organs**

290 Plant growth and evolution depends on the functional coordination between plant
291 above- and below-ground organs (Aritsara et al., 2022; Weigelt et al., 2021; Zhou et
292 al., 2022). In the framework of the root allometric relationship, the faster increase of
293 the cortex thickness than stele radius could be accompanied with a faster supply of
294 leaf photosynthate to the roots. We know little about how plants with thick absorptive
295 roots assign their leaf traits to meet functional balance of water, nutrients and carbon
296 between roots and leaves. Another interesting question is how the root allometric
297 relationship can be coordinated with plant reproductive organs like flowers, fruits and
298 seeds given that the reproductive organs usually compete with roots for
299 photosynthates and with leaves for water and nutrients. Therefore, linking the root
300 allometric relationship with plant above-ground organs could pave a new way for our
301 understanding of the co-evolution within plants and between plants and animals for
302 pollination or seed dispersal.

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304

305 **Author Contributions**

306 Y.Z. and D.K. conceived the ideas of this review paper, D.K. and Y.Z. performed the
307 data analysis, Y.Z. wrote the first draft of this manuscript and Y.Z., D.K., J.C., Q.Y.,
308 M.W., and Y.Z. all contributed to the editing and revision of the final version of the
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310

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317

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Table 1. The relationships between root diameter (RD) and the cortex thickness (CT) and the stele radius (SR) for different plant forms and different environmental treatments. *Slope* _(RD-CT): the slope for the regression of the cortex thickness with root diameter; *Slope* _(RD-SR) the slope for the regression of the stele radius with root diameter; *Slope* _(RD-CT) / *Slope* _(RD-SR): ratio of the *Slope* _(RD-CT) to the *Slope* _(RD-SR); Slope comparison: the statistical test of the difference between the above two slopes using standardized major axis method.

Species class		The number of species	<i>Slope</i> _(RD-CT)	<i>Slope</i> _(RD-SR)	<i>Slope</i> _(RD-CT) / <i>Slope</i> _(RD-SR)	Slope comparison
	Measurement	698	0.44***	0.15***	2.93	***
Species level	All species	512	0.40***	0.12***	3.33	***
	Woody	271	0.53***	0.07***	7.57	***
	Non-woody					
	Fern + grass + herb +Orchidaceae	241	0.39***	0.12***	3.25	***
	Fern	37	0.31***	0.17***	1.82	***
	Grass	78	0.39***	0.19***	2.05	***
	Herb	92	0.38***	0.11***	3.45	***
	Orchidaceae	28	0.41***	0.08***	5.12	***
Mycorrhiza type	AM					
	Woody + non-woody	217	0.53***	0.07***	7.57	***
	Woody	197	0.53***	0.07***	7.57	***
	Non-woody	212	0.35***	0.18***	1.94	***
	EM					
	Coniferous +broadleaf	20	0.19ns	0.21***	-	-
	Coniferous	6	0.11ns	0.22ns	-	-
	Broadleaf	14	0.58***	0.10***	5.80	***
	AM&EM	13	0.33**	0.13**	2.54	**
	OM	28	0.41***	0.08***	5.13	***
Different treatment	Control +CO ₂ increase	17	0.27***	0.18***	1.50	**
	Control	17	0.26***	0.18***	1.44	-

ts	CO ₂ increase	17	0.28***	0.18***	1.56	*
	Control + N increase	14	0.46***	0.11***	4.18	***
	Control	14	0.52*	0.09ns	-	-
	N increase	14	0.43***	0.11***	3.91	***
	Control + P increase	14	0.53***	0.08**	6.63	***
	Control	14	0.52***	0.09ns	-	-
	P increase	14	0.54***	0.07ns	-	-
	Dry + rainy season	8	0.25***	0.20***	1.25	-
	Dry season	8	0.42***	0.12*	3.50	*
	Rainy season	8	0.24***	0.21*	1.14	-

457 ***, ** and * indicate significant levels at $p < 0.001$, $p < 0.01$, and $p < 0.05$, and ns indicates no significance ($p > 0.05$).
 458 The $Slope_{(RD-CT)} / Slope_{(RD-SR)}$ and the Slope comparison are denoted by “-” when either of the above slopes is statistically different.

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461 **Table 2.** The allometric relationships between root diameter (RD) and the cortex thickness (CT) and the stele radius (SR) in each of the 26 studies with more than 3
 462 plant species examined. See supplementary data 1 for the details of these studies. *Slope* _(RD-CT): the slope for the regression of the cortex thickness with root diameter;
 463 *Slope* _(RD-SR): the slope for the regression of the stele radius with root diameter; *Slope* _(RD-CT)/*Slope* _(RD-SR): ratio of the *Slope* _(RD-CT) to the *Slope* _(RD-SR); Slope
 464 comparison: the statistical test of the difference between the above two slopes using standardized major axis method.

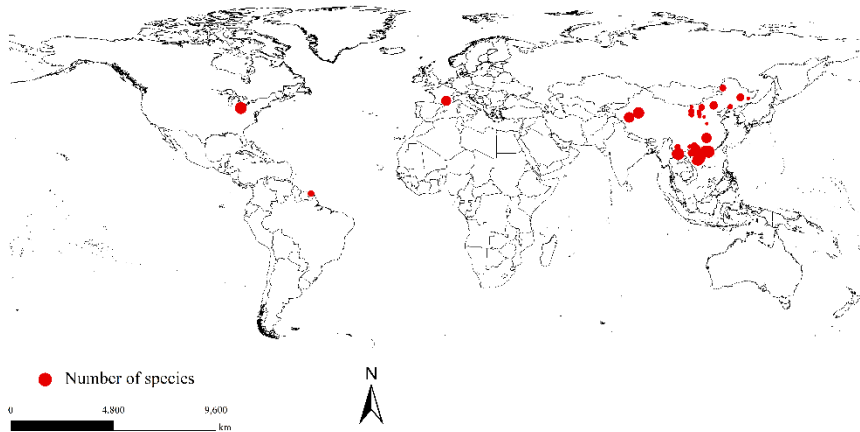
Study	The number of species	<i>Slope</i> _(RD-CT)	<i>Slope</i> _(RD-SR)	<i>Slope</i> _(RD-CT) / <i>Slope</i> _(RD-SR)	Slope comparison
1	19	0.27***	0.23***	1.17	-
2	14	0.37***	0.13*	2.85	*
3	20	0.39***	0.12***	3.25	***
4	23	0.37***	0.14***	2.64	**
5	27	0.40***	0.10***	4.00	***
6	5	0.39**	0.07*	5.57	**
7	96	0.75***	0.10***	7.50	***
8	9	0.47***	0.03ns	-	-
9	12	0.39***	0.11***	3.55	***
10	7	0.32***	0.08**	4.00	**
11	34	0.47***	0.03***	15.67	***
12	6	0.40***	0.13*	3.08	**
13	12	0.06ns	0.25***	-	-
14	15	0.70***	0.004ns	-	-
15	16	0.89***	0.08*	11.13	***
16	91	0.35***	0.11***	3.18	***
17	34	0.27***	0.18***	1.50	**
18	3	0.52ns	0.14ns	-	-
19	18	0.37***	0.13***	2.85	***
20	42	0.48***	0.10***	4.80	***
21	32	0.39***	0.04***	9.75	***

22	8	0.09ns	0.05ns	-	-
23	26	0.33***	0.15***	2.20	**
24	16	0.25***	0.20***	1.25	-
25	10	0.39***	0.11***	3.55	***
26	17	0.42***	0.08***	5.25	***

465 ***, ** and * indicate significant levels at $p < 0.001$, $p < 0.01$, and $p < 0.05$, and ns indicates no significance ($p > 0.05$). The $Slope_{(RD-CT)} / Slope_{(RD-SR)}$ and the Slope
466 comparison are denoted by “-” when either of the above slopes is statistically different.

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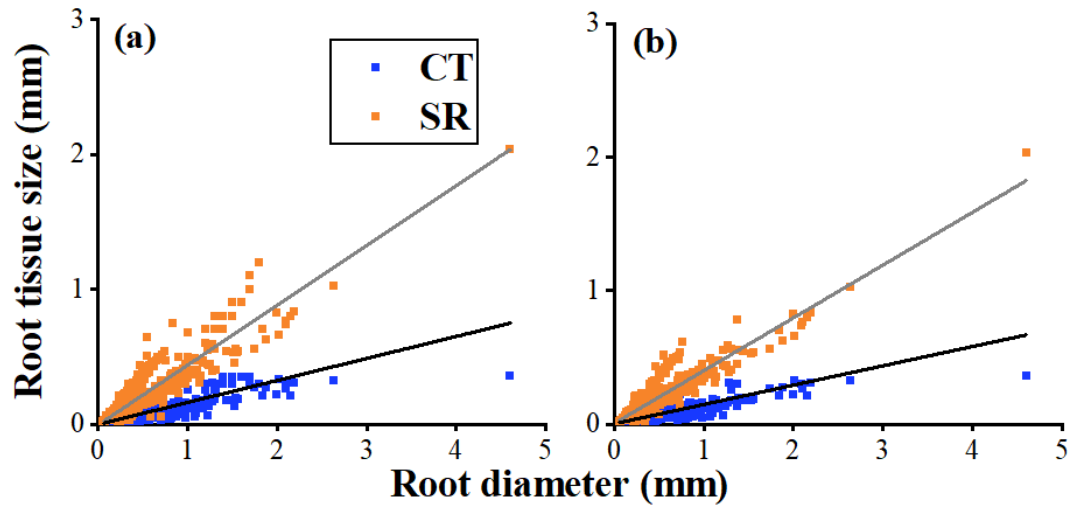


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470 **Fig. 1** A global map of 32 studies reporting data of the cortex and the stele in absorptive roots.

471 Each study is represented by a red circle, and the size of the circle is proportional to the species

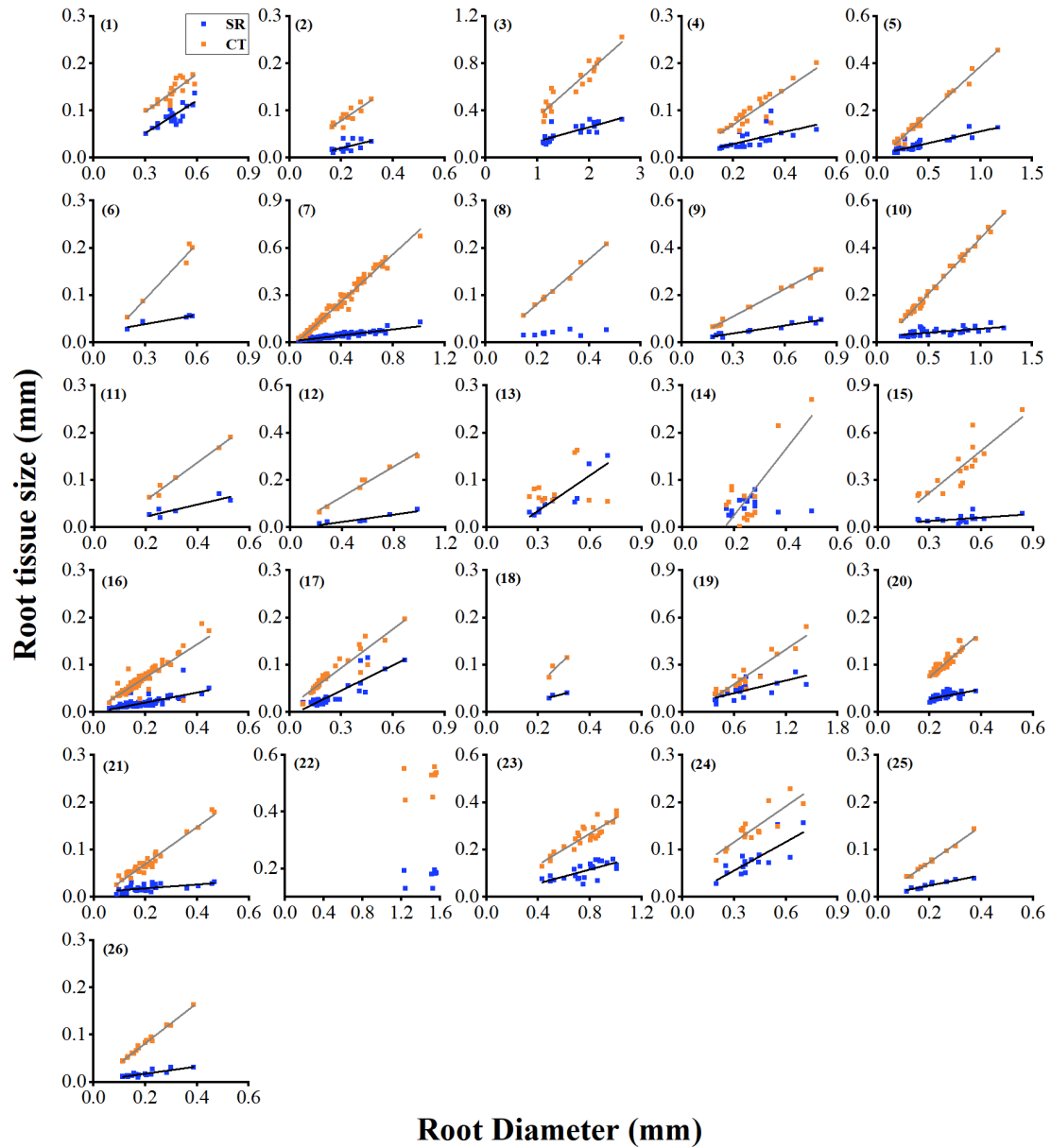
472 number included in the studies.



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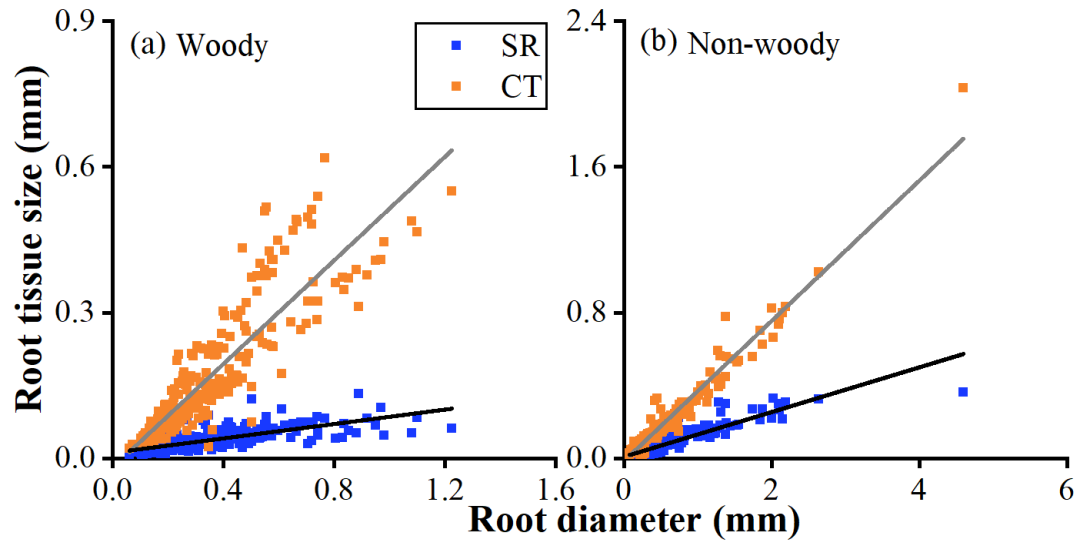
474 **Fig. 2** The Allometric relationship between the root cortex and the stele across 698 observation (a)

475 and 512 species (b), CT: cortex thickness; SR: stele radius.



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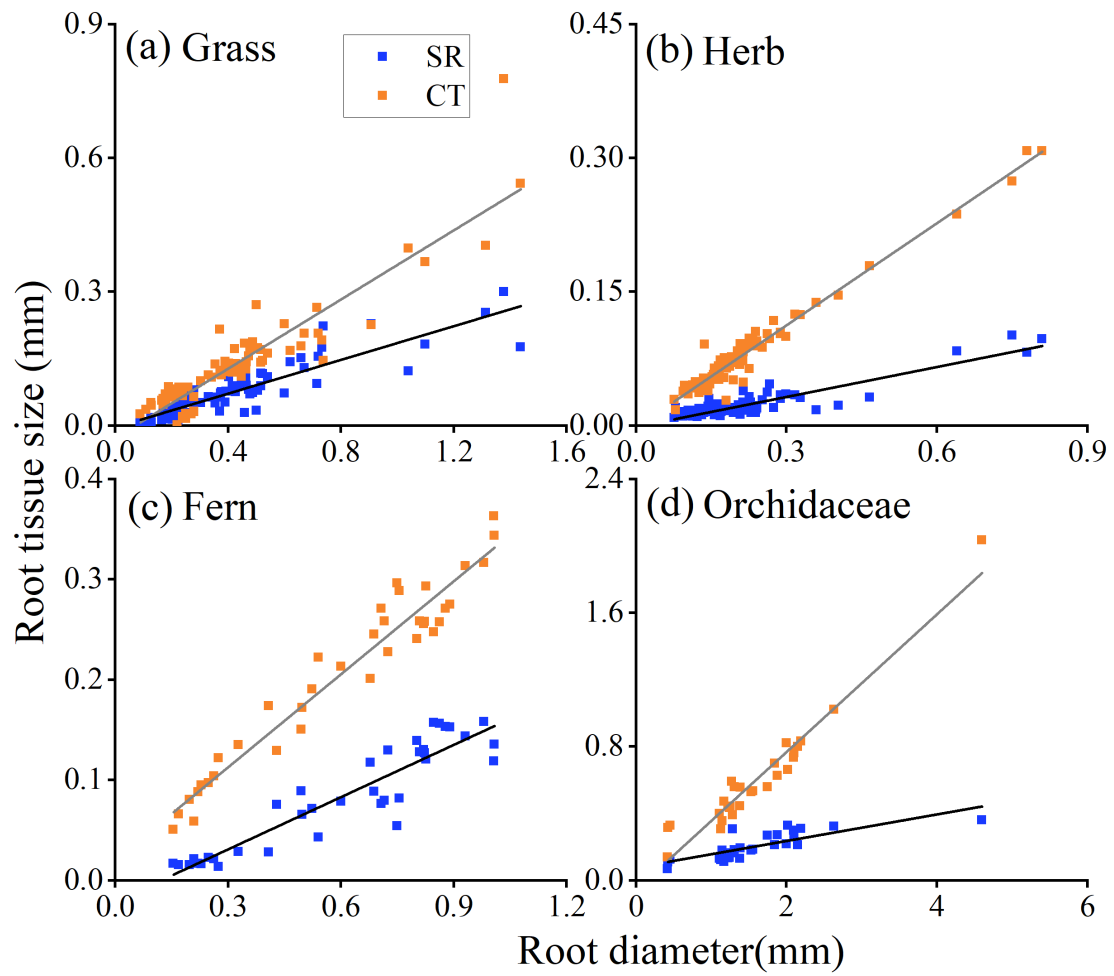
477 **Fig. 3** The Allometric relationship between the root cortex and the stele in 26 studies with more
478 than three plant species examined. See supplementary data 1 and 2 for detailed information of these
479 studies. CT: cortex thickness; SR: stele radius.



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481 **Fig. 4** The Allometric relationship between the root cortex and the stele in woody (a) and non-
482 woody (b) species. CT: cortex thickness; SR: stele radius.

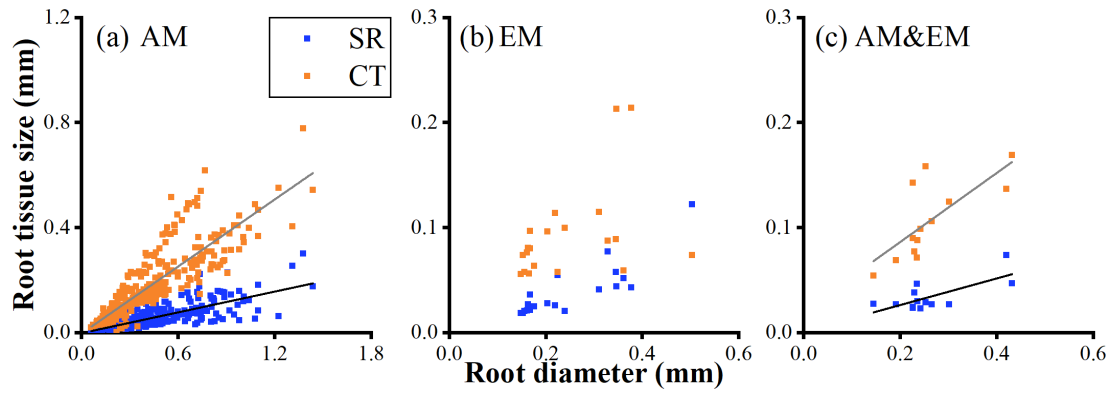
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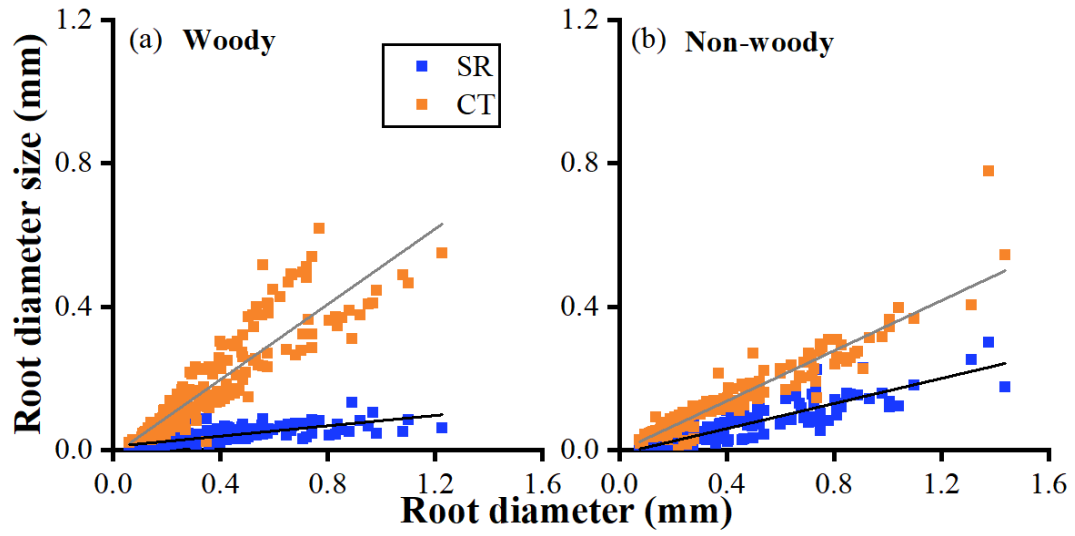
485 **Fig. 5** The allometric relationship between the root cortex and stele in grass (a), herb (b), fern (c)
486 and Orchidaceae (d). CT: cortex thickness, SR: stele radius.

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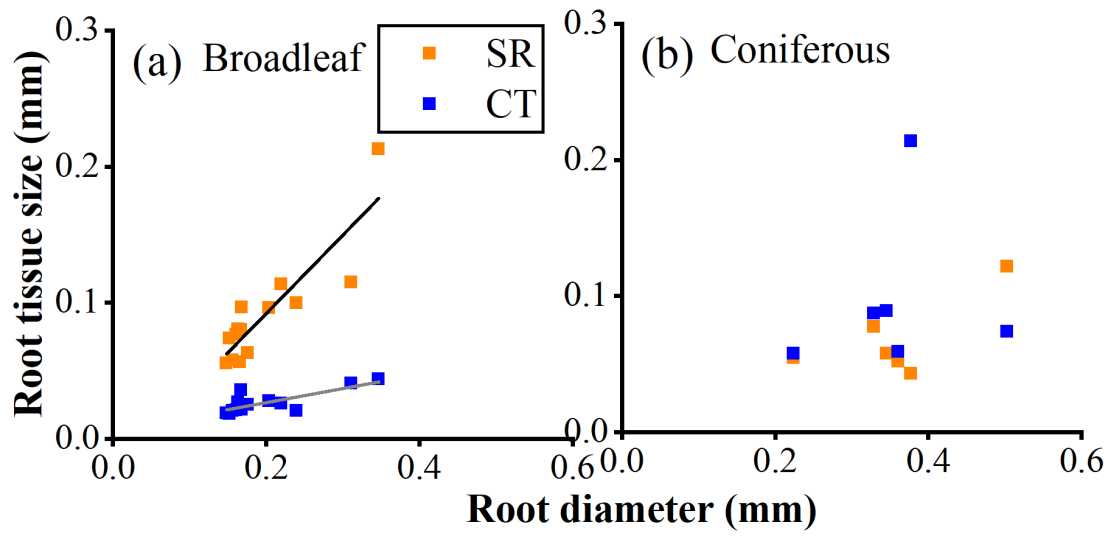
489 **Fig. 6** The allometric relationship between the root cortex and the stele in different mycorrhizal
490 plants. AM: Mycorrhizae (a); EM: Ectomycorrhizae (b); AM&EM: dual mycorrhizas of AM
491 and EM (c); CT: cortex thickness, SR: stele radius.



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493 **Fig. 7** The allometric relationship between the root cortex and the stele in woody AM plants (a)
494 and non-woody AM plants (b). CT: cortex thickness, SR: stele radius.

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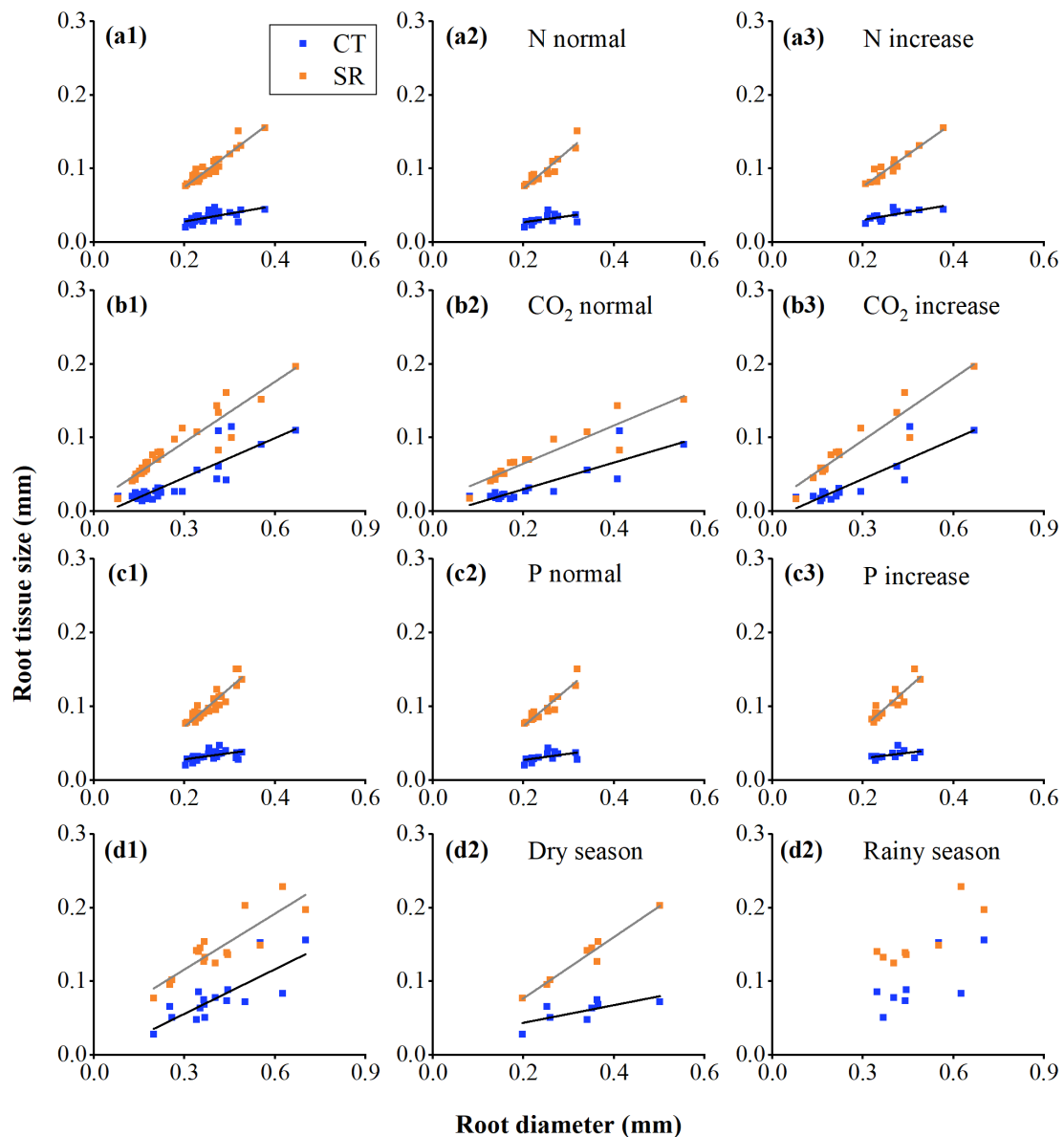
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Fig. 8 The allometric relationship between the root cortex and the stele in broadleaf EM plants (a) and coniferous EM plants (b). CT: cortex thickness, SR: stele radius.

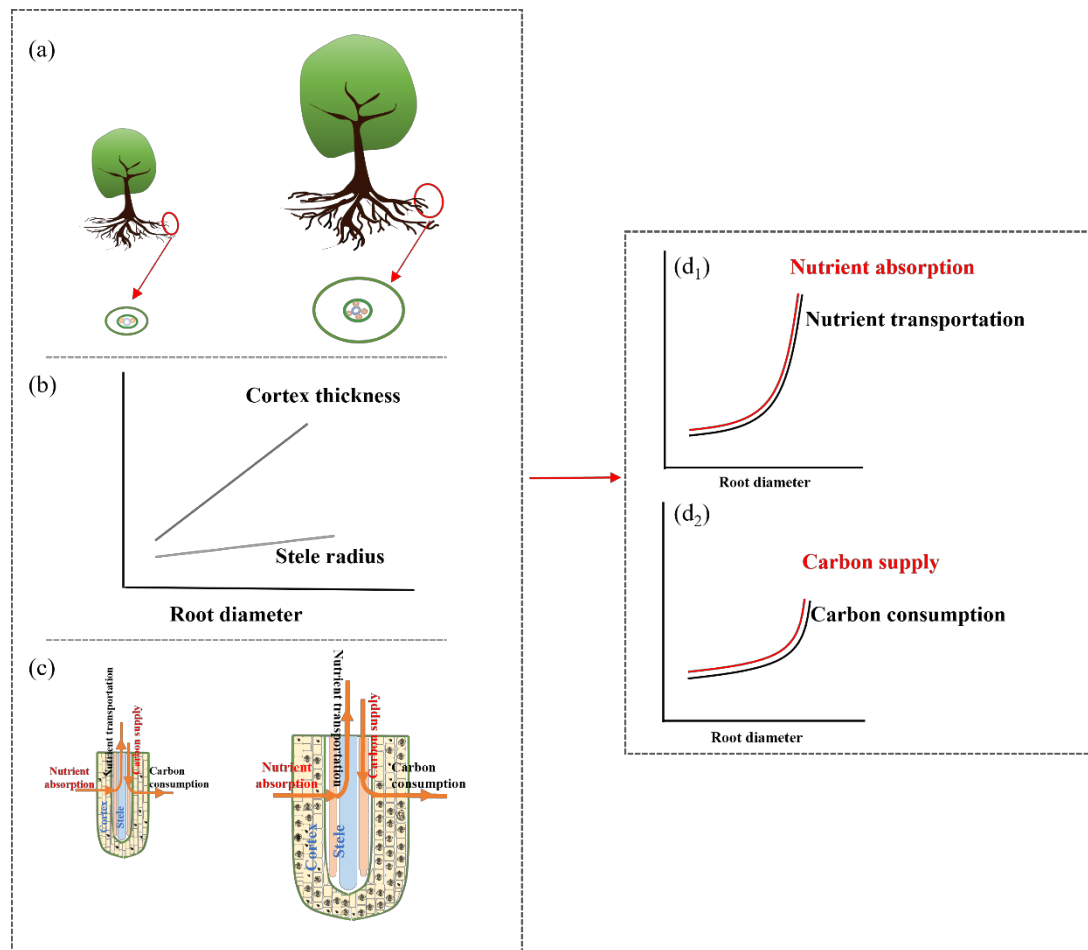
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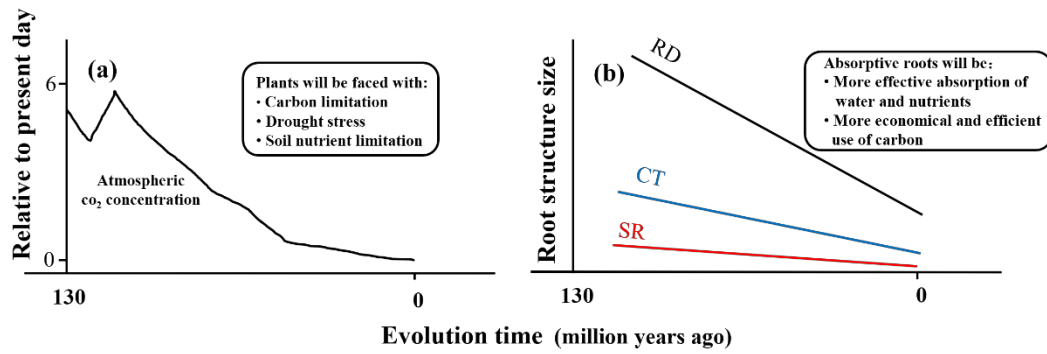
501 **Fig. 9** The allometric relationship between the root cortex and the stele under different
502 environmental treatments. Nitrogen (N) deposition: control + N deposition (a₁), control (a₂) and N
503 increase (a₃); elevation of atmospheric CO₂ concentration: control + CO₂ increase (b₁), control
504 (b₂), CO₂ increase (b₃); phosphorus (P) fertilization: control + P increase (c₁), control
505 (c₁), P increase (c₁); seasonality: dry season + rain season (d₁), dry season (d₂), rain season (d₃). CT:
506 cortex thickness, SR: stele radius.

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509 **Fig. 10** Mechanisms for the allometric relationship between the cortex and the stele in
510 absorptive roots. For simplicity, we presented two plant species with a thin and a thick
511 absorptive root, respectively, followed by the cross-sectional area of the roots (a). The
512 cortex section is indicated by the area between the two green circles; the inner green
513 circle, the stele; blue circles, the vessels; orange circles, the sieves. Different functions
514 of the root anatomical structures are shown in the longitudinal section model of the
515 roots (b) The change in the size of the cortex and stele with the shift of root diameter
516 across species is shown in (c): cortex, sites for the symbiosis with mycorrhizal fungi
517 (i.e., the intermingled lines in the cortical cells) and carbon consumption; vessels,
518 transport for the water and nutrients; sieves, transport for carbohydrates. The
519 allometric relationship between the root cortex and stele is considered to meet the
520 balance between nutrient absorption (via mycorrhizal fungi in the cortex) and nutrient
521 transportation (via the stele) (d₁) and between carbon supply (via the stele) and carbon
522 consumption (via the cortex) (d₂). The conceptual models in (d₁) and (d₂) are redrawn
523 from Kong et al. (2017) and Kong et al. (2021).



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Fig. 11 The co-variation of atmospheric CO₂ concentration (a) and anatomical structures in absorptive roots (b) since the Cretaceous. The pattern for the change of atmospheric CO₂ concentration is redrawn from the study by Beerling et al. (2010). The resulting environmental changes and the adaptive responses of the roots are presented as insets in this figure. RD: absorptive root diameter; CT: cortex thickness, SR: stele radius.