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1 **Intra- and inter-specific variation in root mechanical traits for twelve herbaceous**
2 **plants and their link with the root economics space**

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6

7 **Abstract**

8 Root mechanical traits, including tensile strength (T_r), tensile strain (ϵ_r), modulus of
9 elasticity (E_r) and tensile toughness (W_r), play a key role in plant functioning (e.g.,
10 anchorage and stem stability). Yet, their variability and their relationships with other root
11 traits are poorly known. Here, we characterize T_r , ϵ_r , E_r and W_r at both intra- and
12 interspecific levels and examine how they covary with other root traits related to root
13 economics space (RES). We used twelve herbaceous species from contrasting
14 taxonomical families grown in controlled plein-air conditions. For each species, we
15 excavated root systems and measured morphological and chemical traits and mechanical
16 traits at two locations (*proximal* versus *distal*) for two root types (*absorptive* versus
17 *transport* roots). Transport roots tended to show higher mechanical trait values than
18 absorptive roots, especially for ϵ_r , while the location where the root was sampled showed
19 a limited effect on root mechanics. The five monocots (Poaceae species) had higher
20 mechanical traits than the seven dicots (including five Fabaceae species) except for E_r .
21 Root mechanical traits covaried positively and were strongly positively correlated with
22 specific root length, i.e., a trait related to soil exploration strategy, and negatively with
23 root diameter and root tissue density, i.e. a trait related to root life span. We demonstrate
24 the important role of species category and root type in governing mechanical trait
25 variation at both intra- and inter-specific levels. Our results can be regarded as the first
26 evidence of the link between root mechanical robustness and the RES through a strong
27 association with the ‘do-it-yourself’ soil exploration strategy.

28 **Key words:** mechanical traits, tensile strength, modulus of elasticity, tensile strain, toughness,
29 economics spectrum, root economics space.

30

31 1 INTRODUCTION

32 Mechanical properties differ throughout plant organs and impact growth, defence, survival and
33 reproduction (Wright and Westoby 2002; Read and Stokes 2006). For example, mechanical
34 traits of roots strongly influence anchorage and the capacity of a root of root to penetrate soil
35 during resource scavenging (Chimungu et al. 2015; Loades et al. 2015; Niklas et al. 2002;
36 Stokes et al. 2009). However, root mechanical traits have been studied little, especially in
37 herbaceous species, and our knowledge of the underlying mechanisms impacting the resistance
38 of roots to loading forces, both within and across species, remains scarce.

39 Roots of herbaceous species need to avoid uprooting from e.g. animal grazers and soil
40 displacement (Stokes et al. 2009). Resistance to uprooting depends on the shape of the root
41 system and root mechanical properties. As a root is exposed to various forces during uprooting,
42 it will stretch, then either slip through the soil or break (Waldron and Dakessian 1981). Four
43 representative mechanical traits can be cited to describe the mechanical quality of root tissue as
44 a material in a uprooting processes (Table 1): (i) tensile strength (T_r) is the maximum force
45 required, per cross-sectional area of the root, to cause failure in tension. Failure can occur
46 through either breakage or permanent deformation. T_r is the mechanical trait most frequently
47 measured on individual roots (Freschet et al. 2021) and a higher value of T_r means root tissue
48 (not an individual root) is stronger. (ii) Longitudinal modulus of elasticity (E_r) is the resistance
49 to being deformed elastically in tension, but without failure occurring. E_r measures tensile
50 stiffness of root tissue. A higher value of E_r means that root tissue is more elastic or stiffer, and
51 has a better capacity to withstand tension without undergoing permanent deformation,
52 improving plant anchorage. (iii) Tensile strain (ε_r) is the relative longitudinal extension when
53 failure occurs. During uprooting, root tissue with a high strain value can better help a root
54 remain anchored in soil, even after soil failure has occurred, holding vegetation in place and
55 reducing soil movement. (iv) Tensile toughness (W_r) is the energy (or work) required per unit

56 root volume to cause failure in tension. Toughness helps protect against disturbance and so
57 enhances organ lifespan (Read and Stokes 2006). As well as describing how roots are anchored
58 in soil, and how they fail during loading, these traits are also key parameters in root
59 reinforcement and slope stability models that assess the contribution of vegetation for protecting
60 against shallow landslides (Mao 2022).

61 At the intraspecific level, root mechanical traits are highly variable and are usually
62 characterized as a function of root diameter (de Baets et al. 2008; Burylo et al. 2011; Ghestem
63 et al. 2014; Ji et al. 2020). For example, many studies have shown that a negative power law
64 relationship occurs between root strength and diameter (Genet et al. 2005; Fan and Su 2008;
65 Mao et al. 2012; Ghestem et al. 2014; Ji et al. 2020; Meijer 2021), suggesting that finer roots
66 are stronger as a material than coarser roots. This phenomenon has been attributed to differences
67 in root structure, with thinner roots possessing more cellulose per dry mass than coarser roots
68 (Zhang et al. 2014; Zhu et al. 2020). Also, differences in root anatomy occur, with thinner roots
69 often possessing a higher proportion of lignified stele (Kong et al. 2014) and a lower proportion
70 of mechanically weak cortex (Mao et al. 2018). However, a number of recent studies revealed
71 that root diameter is not an ideal predictor of mechanical traits. For example, according to
72 species, the relationship between strength and diameter is either positive, null or negative
73 (Boldrin et al. 2017; 2018; Mao et al. 2018). Root age or root location (e.g. sampling distance
74 from root tip; Dumlao et al. 2015; Loades et al. 2015; Boldrin et al. 2021), water status (Boldrin
75 et al. 2018; Ekeoma et al. 2021), type (nodal, seminal or lateral; Loades et al. 2015), anatomy
76 (Chimungu et al. 2015; Mao et al. 2018) and topological order (Mao et al. 2018) have all been
77 found to better explain mechanical trait variation than diameter alone. Roots of most plant
78 species can be classed into (i) *absorptive* roots, which represent the most distal roots dedicated
79 to the acquisition and uptake of resources, and (ii) *transport* roots, that occur at higher
80 branching orders and have mainly transport and mechanical functions (McCormack et al. 2015).

81 [Mao et al. \(2018\)](#) examined the intraspecific variation of mechanical traits as a function of
82 topological order for four tropical tree species and showed that lower-order *absorptive* roots
83 were weaker and less stiff, but could extend further before failure, compared to higher-order
84 *transport* roots. Therefore, root mechanical quality contributes to the shift from acquisition to
85 transport functions .In addition,, the effect of root location (*proximal* vs *distal*) within
86 *absorptive* and *transport* roots on mechanical properties ([Fig. 1](#)) is poorly known, even though
87 it may impact anchorage capacity.

88 Mechanicals traits of individual roots have mostly been studied in an attempt to find species
89 with strong roots that can resist uprooting and substrate mass movement ([Ghestem et al. 2014](#);
90 [Boldrin et al. 2017](#)). However, the drivers of interspecific variability are poorly understood
91 ([Freschet et al. 2021](#)) and can result from inherent structural and anatomical design , as well as
92 differences in chemical make-up of cell tissue. Compared to studies on traits aboveground, there
93 is a lack of comparative studies investigating the relationships between root mechanical traits
94 and other morphological and chemical traits ([Freschet et al. 2021](#)). For example, a global pattern
95 of interspecific mechanical trait variation in leaves has showed that leaf strength (work to shear
96 failure) was strongly and positively correlated with leaf mass area, thickness, tissue density and
97 life span ([Wright and Westoby 2002](#); [Onoda et al. 2011](#); [Méndez-Alonzo et al. 2013](#)). These
98 relationships show that leaf strength is part of the leaf economics spectrum highlighting a trade-
99 off between carbon and nutrient acquisition and conservation ([Wright et al. 2004](#)). To our best
100 knowledge, whether such patterns also occur in root system has not been investigated. Based
101 on a database of more than 1800 species worldwide, [Bergmann et al. \(2020\)](#) demonstrated that
102 fine roots traits (classed as ≤ 2.0 mm) covaried in a two-dimensional space, namely the root
103 economics space (RES). One axis, the conservation gradient, represents a trade-off between
104 high metabolic activity, with high root nitrogen concentration (RNC) and an investment in long
105 lived structural tissues, i.e., high root tissue density (RTD). The other axis is called the

106 collaboration gradient, and relates to soil exploration strategies. This axis represents a trade-off
107 between (i) a “do-it-yourself” strategy, where soil exploration and exploitation is achieved by
108 roots with high specific root length (SRL) and (ii) an “outsourcing” strategy, where resource
109 acquisition is delegated to mycorrhizal fungi hosted in thick roots, i.e. high mean root diameter
110 (RD). This framework considered morphological and chemical, traits, but did not integrated
111 mechanical traits for the simple reason that these traits are not available in root trait databases
112 (Iversen et al. 2017; Guerrero-Ramírez et al. 2021). Nevertheless, as for global patterns of leaf
113 mechanical properties (Onoda et al. 2011), fine root strength and other mechanical traits are
114 expected to be an integral part of the RES. The few studies examining relationships among
115 mechanical, morphological and chemical traits suggest that mechanical traits are associated
116 with the conservation axis, because tensile strength and/or stiffness are positively associated
117 with RTD (Yang et al. 2016; Boldrin et al. 2018), cellulose concentration (Genet et al. 2005),
118 lignin concentration (Zhang et al. 2014; Zhu et al. 2020; Hathaway and Penny 1975) and/or
119 lignin to cellulose ratio (Hathaway and Penny 1975; Zhang et al. 2014) and are negatively
120 correlated with soluble sugar concentration (Genet et al. 2011). However, these studies mostly
121 focused on woody species and measured on different root types (with diameters ranging from
122 0.1 to 10.0 mm). It remains unclear whether such patterns (i) are consistent within *absorptive*
123 and *transport* fine roots, (ii) are consistent for mechanical traits other than tensile strength and
124 stiffness (e.g., toughness and strain) and (iii) can be extrapolated to herbaceous species
125 belonging to different species categories (monocots versus dicots).

126 Monocot root systems differ from dicots in terms of architecture (Pagès 2016) and generally
127 have a fibrous root system with many root axes lacking secondary xylem in the stele. Dicots
128 often have a well-anchored taproot and roots possessing secondary tissues. Monocot roots were
129 usually thinner with low tissue density, RNC and cellulose concentration, but higher SRL and
130 C:N ratio than dicots (Roumet et al. 2016; Freschet et al. 2017; Rossi et al. 2020). In addition,

131 monocot leaves are generally more resistant to tearing than dicot leaves (Onoda et al. 2011).
132 Altogether, this suggest that roots of monocot roots are stronger and tougher than dicot roots,
133 but a comparative study of plant species grown in the same conditions has not been performed.
134 In this study, using twelve herbaceous species from contrasting taxonomical families and
135 species categories (monocots versus dicots), we aim at characterizing the intra- and interspecific
136 variations of four root mechanical traits, including tensile strength (T_r); tensile strain (ϵ_r);
137 modulus of elasticity (E_r) and tensile toughness (W_r), and examine how these mechanical traits
138 covary with root morphological and chemical traits related to root economics. For each species,
139 we measured mechanical traits at two locations (*proximal* versus *distal*) for two root types
140 (*absorptive* versus *transport*), using a standardized protocol. We hypothesize that: (H1) at the
141 intraspecific level, root diameter, type (*absorptive* versus *transport* roots) and location
142 (*proximal* versus *distal*) contribute to explain variations in mechanical traits; (H2) at the
143 interspecific scale, root mechanical traits are part of the root economics space. In particular, we
144 expect that species with thinner roots and high SRL and/or with more recalcitrant tissues (i.e.,
145 low RNC, but high RTD and C:N ratio) have stronger, stiffer and tougher root tissues that are
146 capable of being deformed before failure. Finally, we hypothesize that: (H3) monocots with
147 high SRL and thinner roots have higher mechanical quality than dicots.

148 2 MATERIALS AND METHODS

149 *2.1 Species and experimental setup*

150 The experiment was conducted on twelve perennial herbaceous species, including five
151 monocots and seven dicots belonging to four botanical families (Table 2). These species were
152 grown at the CEFÉ experimental garden (Montpellier, France; 43° 38' 20" N, 3° 51' 51" E). The
153 climate is Mediterranean subhumid (Daget 1977) with high sunshine hours, warm and dry
154 summer (with mean daily maximum temperature in July; 24 °C) and cool to cold winters (with

155 mean daily minimum temperature in January; 7 °C). During the experiment, from October 2016
156 (seed-sowing) to July 2017 (plant harvesting), a weather station in the experimental garden
157 measured the maximum, mean and minimum air temperatures, which were 30 °C, 13 °C and -
158 0.4 °C, respectively, and the cumulative precipitation, which was 349 mm (Rossi et al. 2020).

159 This study was part of a larger program on the revegetation of embankments in southern France
160 (Rossi et al., 2020). Therefore, the twelve herbaceous plant species were grown as monocultures
161 in three replicate steel boxes (0.7 m in length × 0.7 m width × 0.3 m depth) and positioned at a
162 slight inclined angle (20° relative to horizon) for mimicking a road embankment, where these
163 species are commonly found. Each species was sown in October 2016 in lines, with both intra-
164 row and inter-row spaces between two plants fixed to 75 mm, resulting in a plant density of 155
165 plants per m². The soil used for the cultivation was excavated at Villefort, France (44° 26' 25"
166 N, 3°55' 58" E) and was a sandy loam with 63% sand, 26% silt and 11 % clay, respectively.
167 The concentrations of total organic C, total N, and Olsen P were 16.90 g kg⁻¹, 1.36 g kg⁻¹ and
168 0.069 g kg⁻¹, respectively. The pH was 7.06 and cation-exchange capacity was 7.98 cmol kg⁻¹.
169 All the treatments, from soil sieving, box filling and *Rhizobium* inoculation for soil, to daily
170 irrigation with programmed sprinklers, weeding (manually, every week) and mowing (every
171 four months) for plants, were identically applied to all the boxes (Rossi et al. 2020).

172 ***2.2 Root sampling and measurement for root morphological and chemical traits***

173 For each box (i.e., three replicates per species), a cylinder soil core (75 mm diameter, 200 mm
174 depth), centered on one individual plant per species was collected in July 2017. Roots were
175 washed under water and sorted into two root types: *absorptive* roots, typically the first, second
176 and third root orders (defined as the most distal root orders), and *transport* roots, that were
177 higher order roots (all orders above third order roots, following McCormack et al. (2015)). By

178 default, root topological orders in this study refer to those counted by the morphometric root
179 classification method, see [Freschet et al. \(2021\)](#).

180 For each species, two subsamples of absorptive and of transport roots were used for
181 measurements of root morphology and chemical composition. For morphological traits, roots
182 were stained in methyl violet solution (0.5 g L^{-1}), scanned at 800 dpi (Epson Expression 1680,
183 Canada), oven dried at $60 \text{ }^\circ\text{C}$ for 3 days and weighed to obtain dry root mass. The scanned
184 images were analyzed via the software Winrhizo Pro (Regent Instruments, Quebec, Canada) to
185 obtain the root length, root volume in different diameter classes (from 0 to 2 mm diameter with
186 a 0.1 mm interval) and mean root diameter (RD, in mm) was calculated for absorptive and
187 transport roots as the weighted average of the median of each diameter class by the length of
188 the roots in each class. Specific root length (SRL, in m g^{-1}) was calculated as the ratio between
189 root length and dry root mass. Root tissue density (RTD, in g cm^{-3}) was calculated as the ratio
190 between root dry mass and root volume. For each root type, root carbon (C) and nitrogen (N)
191 concentrations were measured with another subsample of roots using an elemental analyser
192 (CHN model EA 1108; Carlo Erba Instruments, Milan, Italy) so that root carbon to nitrogen
193 ratio (i.e., C:N ratio) could be estimated. Mean values of the above traits for are summarized in
194 [Table S1](#).

195 ***2.3 Root sampling for root mechanical traits***

196 Unlike the above root morphological and chemical traits, root mechanical traits were measured
197 per root individual rather than on a sample of several roots. Because of the destructive nature
198 of the sampling procedure that would affect other root trait or soil feature measurements, for
199 each species, we randomly selected one of the three replicate boxes for sampling roots (one box
200 per species). For each selected box, a soil monolith (18 cm (length) \times 18 cm (width) \times 30 cm
201 (depth)) was excavated in the middle of the box so that multiple (≥ 5) plant individuals were

202 sampled. Each soil monolith was then transferred into a container filled with water. Using a
203 shower nozzle, soil was removed without damaging roots. Then, we placed the mass of roots in
204 a tray filled with clean water and carefully selected five entire root branches (i.e., five replicates)
205 in a random manner. Root branch selection at the same location of the plants was avoided. Each
206 selected root branch started from either a root connected to a taproot (for dicots; i.e., the 1st
207 order lateral of a basal root according to the developmental root classification approach
208 (Freschet et al. 2021) or a root from the base of a culm (for monocots) (Fig. 1). This method
209 ensured that the lateral root branches of different species followed the same selection criterion
210 and so facilitated interspecific comparison. For each species, each of the five root branches was
211 carefully removed from the rest of root system, using a knife. In each root branch, we defined
212 four categories of root segments (Fig. 1): (i) a segment at the proximal part of the root
213 originating from the taproot (in dicots) or the base of a culm (in monocots) (*Transport –*
214 *Proximal*); (ii) a segment from the distal part of the same root (*Transport – Distal*); (iii) a
215 proximal segment from a daughter root (*Absorptive – Proximal*) and (iv) a distal segment from
216 the lower part of the same root (*Absorptive – Distal*). We carried out a visual check and used
217 Fitter (1982)'s morphometric root classification method (Freschet et al., 2021) for assessing
218 topological order, counting from the distal segments to ensure that samples (1) and (2) were
219 *transport* roots with root orders >3 and whose main function is supposed to be transport and
220 anchorage, and samples (3) and (4) were *absorptive* roots with root orders ≤ 3 whose main
221 function is supposed to be the absorption of water and nutrients. Based on an anatomical
222 approaches over 34 herbaceous species, Zhou et al. (2022) found that root function shifted from
223 absorption to transport with increase root order for both monocots and dicots, although the
224 proportion between cortex and stele differed between the two species categories. In this paper,
225 we need to apply the same criteria when comparing roots of different species. That is why the

226 categorization between 1–3rd and 4–5th was applied for all the species regardless of category
227 (monocot versus dicot).

228 **2.4 Root mechanical test and trait estimation**

229 Procedures of root mechanical test and trait estimation generally followed the protocol used in
230 [Mao et al. \(2018\)](#). Each of the selected root segments ($N = 20$ per species: 2 root types \times 2
231 positions \times 5 replicate branches) was carefully cut for the measurement of diameter using a
232 microscope. We took three high resolution images at three different locations: in the middle
233 and near each end of the root segment. For each image, root diameter was measured twice at
234 two randomly selected locations along the root segment. Consequently, we obtained six
235 measurements of root diameter per sample. We used the mean of the six diameters (d , in mm)
236 in the calculation of T_r , E_r and W_r .

237 An In-Spec 2200 BT (Instron© Corporation) tensile testing machine was used for mechanical
238 tests. A force transducer with a maximum capacity of 125 N was used and each root segment
239 was placed into vertically aligned rubber-lined jaws that were manually tightened. Roots with
240 diameter > 1.0 mm were fixed using strips of sandpaper and cyanoacrylate adhesive to prevent
241 slippage ([Giadrossich et al. 2017](#)). Roots that slipped during a test were discarded and all tests
242 where roots broke in between the jaws were considered as successful (the success rate
243 was $>80\%$; [Table 2](#)).

244 For each root segment tested, the initial gauge length (i.e. distance between the two grips, L_0 ,
245 in mm) was measured using Vernier callipers and ensured to be at least 20 times the diameter
246 of the root. The crosshead speed was fixed at 5.0 mm min^{-1} . After a test started, the time-
247 dependant tensile load, or force (F , in N) and stress (σ , defined as the standardized tensile load
248 by root cross-sectional area, in MPa), displacement (L , defined as the absolute root deformation,
249 in mm) and strain (ϵ , defined as the relative deformation to the initial length L_0 , in %) were

250 measured automatically until the occurrence of root failure. For each root segment, the curve
251 of F against L can be converted to the curve of σ against ε which shares the same shape to the
252 former (Table 1). Based on both curves, five parameters were estimated (Table 1), including
253 tensile load required to cause root failure (F_r ; in N), root tensile strength (T_r ; in MPa), root
254 tensile strain (ε_r ; in %), root modulus of elasticity in the longitudinal direction (E_r , *idem.* to
255 MoEL in Freschet et al. (2021); in MPa) and root tensile toughness (W_r ; in MJ m⁻³).

256 Mathematically, E_r and W_r could be retrieved by performing a derivative and an integral over a
257 polynomial equation fitted curve of σ against ε between the start of the test and the failure of
258 the root segment, respectively. F_r is closely dependent on root diameter (Table S2), as a thicker
259 sample of the same material requires a higher force for rupture (Mao et al. 2018). We observed
260 strong and positive increases in F_r with increasing diameter and their relationships were well
261 fitted by a power law function (with adjusted R² = 0.16–0.99; Fig. S1; see also Section 2.5).
262 Unlike F_r , all the other metrics (T_r , ε_r , E_r and W_r) are standardized by root size either root cross-
263 sectional area ($0.25\pi d^2$) or initial length (L_0) or both and reflect the intrinsic quality of root
264 material (Table 1). Hereafter, root mechanical traits only refer to T_r , ε_r , E_r and W_r in the Results
265 and Discussion sections. It is to be noted that W_r of this study slightly differs from that in Ji et
266 al. (2021) that did not standardize the energy-based metric by root initial length (L_0).

267 **2.5 Statistical analyses**

268 At the intraspecific level, we performed power law regression fits to explore the relationships
269 between root mechanical parameter and root diameter for each species (Cohen et al. 2011;
270 Meijer 2021):

$$271 Y_r = Ad^B \quad (\text{Eq. 1})$$

272 Where, Y_r denotes a root mechanical parameter (e.g., F_r , T_r , ε_r , E_r or W_r); d denotes root diameter
273 of a single root (mm); A (multiplier) and B (exponent) are the two parameters to calibrate. The
274 power law regression is negative when $B < 0$ and positive when $B > 0$, i.e. roots of larger
275 diameters have respectively a lower ($B < 0$) or larger mechanical traits ($B > 0$). When B is not
276 significant from zero, it signifies that mechanical traits varies little as a function of diameter.
277 Then, for each species, we performed the Student's t-test to examine the effect of root type
278 (*transport* roots versus *absorptive* roots) and root position (*proximal* versus *distal*).

279 At the interspecific level, we first performed the Student's t-tests to check the effect of species
280 category (monocot versus dicot). The tests were applied to data of all species and for each of
281 the combinations of root type (*transport* versus *absorptive*) and location (*proximal* versus
282 *distal*). We additionally performed analyses of variance (ANOVA) and Post-hoc tests (i.e.,
283 Tukey Honestly Significant Difference (HSD) tests) to discriminate between root mechanical
284 traits among species for each root type and location.

285 We performed two principal component analyses (PCA) to explore multiple-trait relationships
286 for absorptive and transport roots, respectively. We used averaged traits of the four structural
287 traits (SRL, RNC, RTD and RD) and the four mechanical traits (T_r , ε_r , E_r and W_r) per root type.
288 Before a PCA, traits were standardized using the zero-mean approach. Facilitating visual data
289 interpretation, we used the convex hull polygon algorithm to describe the occupation of the data
290 points belonging to a category (monocots versus dicots). Besides PCA, we used scatter plots to
291 illustrate the relationships between the four mechanical traits (T_r , ε_r , E_r and W_r) and the four
292 structural traits (SRL, RNC, RTD and RD) as a function of root type and species category, for
293 which linear regressions were performed.

294 We also used Pearson's correlation for bivariate correlations and before the test, traits were log-
295 transformed to minimize the effect of nonlinearity. Besides the trait-value based correlation, we

296 also performed Pearson's correlation using phylogenetic-independent contrasts (PICs) that take
297 into account the phylogenetic nonindependence of the species during the evolutionary history
298 ([Felsenstein 1985](#)). We performed a Mantel test between trait-based and PIC-based correlation
299 matrices to examine whether correlation patterns differ when including PICs.

300 All statistical analyses were performed using R 4.1.0 ([R Core Team, 2021](#)). PCA was performed
301 with the R package "vegan" ([Oksanen et al., 2020](#)). Tukey HSD test was performed with the
302 help of the R package "multcompView" ([Graves et al., 2015](#)). Pearson's correlation was
303 performed with the R package "Hmisc" ([Harrell Jr, 2019](#)). PICs were calculated using the R
304 package "APE" ([Paradis et al. 2004](#)) based on the species' phylogenic relationship generated
305 by the R package "V.PhyloMaker" ([Jin and Qian 2019](#)).

306 3 RESULTS

307 3.1 Intraspecific variation in root mechanical traits

308 Relationships between any mechanical trait and root diameter were poorly captured by the
309 power law function that is usually used to describe such relationships (Meijer 2021) (Figs. 2, 3,
310 4 and 5). The best fit was found for tensile strain (ε_r) (with adjusted $R^2 = 0.14$ – 0.65 Fig. 3),
311 whereas both tensile strength (T_r) and modulus of elasticity (E_r) showed either positive,
312 negative or non-significant relationships with root diameter depending on species (Figs. 2 and
313 4). For most species, the exponent parameter (B) was not significantly different from zero (11
314 out of 12 species for T_r and 9 out of 12 species for E_r) (Figs. 2 and 4), but an opposite pattern
315 was found for ε_r (10 out of 12 species having B significantly higher than zero) (Fig. 3).
316 Toughness (W_r) showed either no relationship (i.e. B not significantly different from zero for 9
317 out of 12 species) or a slightly positive relationship (i.e. B significantly different from zero for
318 3 out of 12 species) with increasing root diameter (Fig. 5).

319 For 10 out of the 12 species ε_r was significantly higher in *transport* roots than in *absorptive*
320 roots (Table 3; Fig. 3). More than half the species did not show any differences in T_r , E_r and W_r
321 between *transport* and *absorptive* roots, although a tendency toward higher values in *transport*
322 roots was observed (Table 3; Figs. 2, 4 and 5).

323 Compared to root type (*transport* versus *absorptive*), root location (*proximal* versus *distal*) did
324 not strongly impact mechanical traits, except in certain species (Table 3). This result is
325 especially true for *absorptive* roots of *M. sativa* and for *transport* roots of *P. lanceolata* and *L.*
326 *corniculatus* which were the only species showing significant differences in mechanical traits
327 between *proximal* and *distal* roots (Table 3).

328 3.2 Interspecific variation in root mechanical traits

329 For any mechanical trait of either *transport* or *absorptive* roots, the effect of species was always
330 significant (ANOVA; Table 3). The first two species that possessed the highest values were
331 always from the Poaceae family, whereas mechanical traits of the remaining 10 species were
332 not significantly different regardless of root type or location (Table 3).

333 Significant effects of species category (monocots versus dicots) on mechanical traits were found
334 for most combinations of root type and location (Student's t-tests; Fig. 6). For both *absorptive*
335 and *transport* roots, the seven dicots had significantly lower T_r , ε_r and W_r compared to the five
336 monocots, whereas E_r did not differ between monocots and dicots (Fig. 6).

337 ***3.3 Relationships among mechanical, morphological and chemical traits for absorptive*** 338 ***and transport roots***

339 The Mantel r of 0.905 with $P < 0.001^{***}$ showed that there was strong positive correlation
340 between the trait-based and PIC-based matrices, indicating the generally constant tendencies of
341 trait-trait relationships between the trait-based and PIC-based matrices. Considering or not the
342 effect of phylogeny changed little the correlations among root mechanical traits, but did affect
343 correlations between root economics-related morphological and chemical traits and between
344 mechanical traits and economics-related traits (Table 4). Hereafter, results of trait-based
345 Pearson' correlation are referred to by default. For both *transport* and *absorptive* roots, in
346 general, the four mechanical traits covaried positively and they were all positively correlated
347 with SRL and negatively correlated with RD (Table 4). RNC was not correlated with T_r and E_r ,
348 but was negatively correlated with ε_r and weakly and negatively correlated with W_r (only for
349 *transport* roots) (Table 4). The correlation between RTD and ε_r was negative for *transport* roots,
350 but not significant for *absorptive* roots (Table 4). The correlation between RTD and T_r and E_r
351 was not significant for *transport* roots but was negative for *absorptive* roots (Table 4). Results

352 from Pearson's correlations were in good accordance with those from linear regressions (Fig.
353 S3), despite some disparities of significance due to different methods.

354 In both PCAs, the first two axes explained >75% and >80% of the variation among all traits for
355 *transport* roots and *absorptive* roots, respectively (Fig. 7). In particular, both of the first axes
356 explained more than 65% of the variation. Trait coordination of *transport* and *absorptive* roots
357 showed some consistency along their first axes, despite pronounced differences along the
358 second axes. For both root categories, the first PCA axis was driven by RD toward the positive
359 direction, and by SRL toward the negative direction (Fig. 7). For *absorptive* roots, the second
360 axis was associated with RNC at one end and with RTD at the other end. In contrast, for
361 *transport* roots, RTD and RNC were strongly associated with RD along the first axis.

362 For both root types, all mechanical traits tended to be associated with the first axis toward the
363 negative direction (i.e., in the same direction as SRL but opposite to RD). The second axis
364 slightly distinguished ϵ_r (toward the positive direction) from T_r , E_r and W_r for *transport* roots
365 (Fig. 7b) and distinguished E_r (toward the negative direction) from ϵ_r for *absorptive* roots (Fig.
366 7a). The quasi-non-overlapped convex hull polygons in both PCAs indicated that the five
367 monocots were strongly discriminated from the seven dicots (Fig. 7). The monocots were
368 mainly associated with higher SRL, C:N ratio and higher T_r , ϵ_r , E_r and W_r , but lower RD, RNC
369 and RTD (Table S1; Fig. 7). Scatter plots with linear regressions between mechanical and
370 economics-related traits showed that data points were more segregated by root type (*absorptive*
371 versus *transport*) rather than species category (monocot versus dicot; Fig. S3).

372

373 4 DISCUSSION

374 We found that along with root diameter, root type (*transport* versus *absorptive*), but not root
375 location (*proximal* versus *distal*), could best explain the variation in mechanical traits at
376 intraspecific levels, thus partially rejecting our hypothesis H1. In line with our H2, we showed
377 that a strong coordination existed between mechanical traits and several economics-related
378 morphological and chemical traits. As expected, in both *absorptive* and *transport* roots, thin
379 roots with high SRL were stronger and tougher, but surprisingly, also had lower RTD. Then, in
380 line with our H3, we showed that species category (monocots versus dicots), significantly
381 affected mechanical traits: monocots had stronger (i.e., higher T_r), tougher roots (i.e., higher W_r)
382 roots that deformed more under loading (i.e., higher ϵ_r) than dicots, but stiffness (E_r) was not
383 altered.

384 ***4.1 Intraspecific variation in mechanical traits is driven by root type, not by root*** 385 ***location (H1)***

386 At the intraspecific level for most species (nine out of twelve), we showed that strength (T_r),
387 stiffness (E_r) and toughness (W_r) did not vary significantly with root diameter and only in a few
388 species (two to six) were *transport* roots stronger, stiffer and tougher than the thinner *absorptive*
389 roots. These results contrast with most previous studies showing that T_r and E_r of roots decrease
390 with increasing diameter, not only in herbaceous species, but also in shrubs and trees (Fan and
391 Su 2008; Mao et al. 2012; Loades et al. 2015). The absence of a relationship between T_r and
392 diameter is however not so surprising given the number of factors other than root diameter
393 controlling root strength, such as root age (Boldrin et al. 2021), water content (Ekeoma et al.
394 2021), topological order and anatomy (Mao et al. 2018). In order to avoid all these confounding
395 effects we normalized root sampling: (i) roots were sampled according to root type and location
396 within the root system, (ii) >99 % of roots had a diameter of <2 mm (iii) roots were fully

397 hydrated to avoid drying that influence root diameter and mechanical properties and (iv) in each
398 sampling population, equal or quasi-equal numbers of replicates were ensured (Table 2). This
399 procedure avoided a major pitfall in many previous studies, where root samples are arbitrarily
400 picked along a given diameter span, resulting in an over-sampling of the more abundant very
401 fine roots, or sampling of mixtures of *transport* and *absorptive* roots. Root strength and stiffness
402 are highly variable in very fine roots, often displaying extreme values (Mao et al. 2018), and
403 biasing mean results. Additionally, including thicker (2 – 8 mm) and highly lignified roots (see
404 Genet et al. 2005 and de Baets et al. 2008) may also bias results, as root mechanical integrity
405 can be compromised due to the presence of material defects in cell wall microstructure. Material
406 defects can non-linearly deteriorate the mechanical quality of a material (Timoshenko 1956)
407 and are the result of anomalies in cell wall differentiation, imperfections in cell adhesion or
408 damage caused as, for example, a root grows through soil with its multitude of diverse physical
409 properties and root herbivores (Schumacher et al., 2021; Williamson and Gleason, 2003).

410 Root tensile strain significantly increased with increasing root diameter for ten out of the twelve
411 species, but it was the only trait calculated using root length measurements before and after the
412 mechanical test (Table 1), therefore the influence of mechanical defects will have a smaller
413 effect on results compared to root thickness.

414 *Transport* roots were thicker and able to deform further (i.e., higher ϵ_r) than *absorptive* roots
415 and this result was consistent for ten out of twelve species (Table 3; Fig. 3). Differences between
416 *transport* and *absorptive* roots likely result from internal anatomical design. Compared to
417 *transport* roots, *absorptive* roots (i.e. the lower root orders) have a higher cortex:stele surface
418 area ratio and little or no secondary thickening (i.e., low suberisation and lignification)
419 (McCormack et al. 2015). Compared to the lignified stele, cortex is usually much weaker
420 mechanically due to its higher content of large, water-filled and thin-walled parenchyma cells
421 (Ekeoma et al. 2021). In addition, *absorptive* roots are generally ephemeral and so may not

422 require a major investment in mechanical quality, whereas *transport* roots possess both
423 structural and transport functions and so their high mechanical resistance to failure as shown in
424 this study shall help enhance persistence and life span in soil.

425

426 ***4.2 Interspecific variation of mechanical traits: strong coordination with*** 427 ***morphological traits (H2)***

428 At the interspecific level, as expected but in contrast to results found at the intraspecific level,
429 mechanical traits (except for stiffness) were negatively correlated with root diameter. The best
430 predictor of mechanical traits was SRL, for both *absorptive* and *transport* roots.

431 In *absorptive* roots, the PCA performed with the four mechanical traits and the four core root
432 traits of the root economics space (RES) (SRL, RD, RTD and RNC; [Bergmann et al. 2021](#))
433 supports the RES framework and demonstrates that mechanical traits are an integral part of the
434 RES. The four fundamental traits of the RES covaried along two axes ([Fig. 5a](#)). The first axis
435 opposed SRL and RD and represents the collaboration gradient related to the species' soil
436 exploration strategy varying from a “do-it-yourself” acquisition strategy by roots that are
437 efficient for soil exploration, to an “outsourcing” acquisition strategy via the investment of
438 carbon in a mycorrhizal fungal partner for the return of limiting resources (Bergmann et al.,
439 2020). The second axis is defined by RNC and RTD; it represents the conservation gradient
440 opposing traits associated with high metabolic activity and traits associated with resource
441 conservation in dense and long-living tissues. All mechanical traits increased with increasing
442 SRL and decreasing root diameter. Such a result can be explained by the disparity of soil
443 exploration strategy among species. Species adopting the “do-it-yourself” strategy may develop
444 stronger and tougher roots to e.g. improve anchorage against grazing herbivores and facilitate
445 soil penetration in compacted soils. On the other side of the axis, species adopting the

446 “outsourcing strategy” rely more on symbiotic partners to explore soil and acquire resources,
447 therefore a large investment in mechanical quality is less important for survival. This strategy
448 is especially true for species in the Fabaceae family that “collaborate” with both rhizobia and
449 arbuscular mycorrhizal fungi. For these species, roots are not solely responsible for the
450 exploration of soil volume, and nutrients are acquired by a large and complex fungi network.
451 Our results reinforce this hypothesis, as roots from species in the Fabaceae family were
452 mechanically weaker and less tough than those from individuals in the Poaceae family.

453 Surprisingly and in contrast with our expectations, the strength, stiffness and toughness of
454 *absorptive* roots generally decreased with increasing RTD. This result contrasts with those from
455 studies performed on roots of woody species (Ghestem et al. 2014; Yang et al. 2016; Boldin et
456 al. 2018). For herbaceous species, which have lower RTD than in roots from woody species
457 (Ma et al. 2018), our results suggest that mechanical properties are more driven by SRL and
458 RD than by RTD. In contrast to results for *absorptive* roots, we found that in *transport* roots,
459 the four fundamental traits of the RES covaried along a single axis of variation with SRL at one
460 end, and RD, RNC and RTD at the other end (Fig. 5b). The covariation of *transport* root traits
461 has, to our knowledge, never been studied, but it is not surprising that they did not follow the
462 RES found for *absorptive* roots since they have different functions. *Transport* roots are
463 composed of the highest root orders, and possess a high proportion of stele, indicating reduced
464 absorptive functionality but strong transportation capacity (McCormack et al. 2015). This
465 investment of biomass in structural dense tissue was also indicated by the positive relationship
466 between RD and RTD.

467 ***4.3 Interspecific variation of mechanical traits: and strong differences between monocots***
468 ***and dicots (H3)***

469 For both *absorptive* and *transport* roots, the first PCA axis strongly discriminated monocots
470 and dicots. Monocots with higher SRL (i.e., with the “do-it-yourself” strategy), had stronger,
471 tougher roots that deformed less under loading than dicot roots, with greater flexibility (ϵ_r) and
472 a higher load/work to failure for the same cross-sectional area (T_r and W_r) (Figs. 2, 3 and 5),
473 while dicots displaying higher RD, RNC and RTD (i.e., the outsourcing strategy) had weaker
474 root mechanical quality. Only modulus of elasticity (E_r) was similar between monocot and dicot
475 roots (Figs. 4, 6e and 6f). These results are not surprising, since monocots and dicots generally
476 exhibit contrasting root development pattern, anatomy, morphology and chemical compositions.
477 First, roots of monocots have higher SRL but lower diameter, tissue density and N concentration
478 than dicots (Freschet et al. 2017). These differences are consistent with the absence of
479 secondary growth in monocots, whereas in dicots the increase of secondary vascular tissue and
480 the loss of cortex with increasing root orders cause an increase in diameter and root tissue
481 density. The higher mechanical properties of monocots might thus result from: (i) their thinner
482 diameter since we demonstrated that at the interspecific level mechanical traits (except E_r) are
483 negatively correlated with RD and positively with SRL, (ii) their anatomy; despite roots of
484 monocots lack secondary growth, their endoderm undergo a secondary cell wall thickening
485 consisting in the development of suberin lamella and lignified cell-walls (Enstone et al., 2002;
486 Ma and Peterson, 2003; Lux et al. 2004; Zhou et al. 2020) that might increase mechanical
487 quality; (iii) their chemical composition; indeed in the same experiment, roots of monocots
488 tended to possess higher (non-significant) cellulose and lignin concentrations than dicot roots
489 (Rossi et al., 2020). As the two most important components of root cell walls, cellulose is a
490 polysaccharide comprising a linear chain of glucose units, and lignin is a polymer made by
491 cross-linking phenolic precursors (Genet et al. 2005; Zhang et al. 2014). Cellulose shapes the
492 structured microfibrils in root cell walls, while lignin fills the spaces between the microfibrils
493 and reinforces the cell wall, increasing root strength (Genet et al. 2005; Zhang et al. 2014).

494 However, results on the relationships between root cellulose, lignin and mechanical traits lack
495 a consensus in literature. For example, greater cellulose concentration was associated with
496 stronger ([Genet et al. 2005](#)), or weaker ([Zhang et al. 2014](#); [Zhu et al. 2020](#)) roots, or had no
497 influence on strength ([Hathaway and Penny 1975](#)). [Hathaway and Penny \(1975\)](#) and [Zhang et](#)
498 [al. \(2014\)](#) found that lignin concentration was a better predictor of strength than cellulose
499 concentration. However, all these studies focused on woody species rather than herbaceous
500 plants and examined intraspecific patterns rather than interspecific patterns. The differences
501 between monocots and dicots revealed in this study need however to be investigated further
502 with more species since our results are possibly biased by the dicots selected that are mostly
503 dinitrogen-fixing, comprising species with roots that have a low tissue density and are rich in
504 nitrogen ([Weigelt et al. 2021](#)).

505

506 5 CONCLUSIONS

507 Using twelve herbaceous species from contrasting taxonomical families cultivated in a
508 experimental garden, we found strong intra- and inter- specific variation of mechanical traits in
509 *absorptive* and *transport* roots, and revealed their relationships with morphological and
510 chemical traits related to root economics. Transport roots were usually stronger and tougher
511 and deformed more than absorptive roots that are ephemeral in nature, and so shall require less
512 investment for mechanical build-up than longer-lived *transport* roots. Mechanical traits were
513 not or only weakly related to root locations. Monocot roots were stronger and tougher than dicot
514 roots and had a greater capacity to withstand permanent deformation. As a pioneer study
515 exploring the relationships between mechanical traits and other functional traits related to root
516 economics, our study demonstrated that mechanical traits are a fundamental part of the root
517 economics spectrum through a strong association with the ‘do-it-yourself’ soil exploration
518 strategy. Species adopting the “do-it-yourself” acquisition strategy (i.e., thin roots with high
519 SRL for efficient soil exploration), had stronger and tougher roots that would also improve
520 anchorage and facilitate soil penetration. On the other side of the axis, species with an
521 “outsourcing” acquisition strategy (i.e., with a greater investment of carbon in a mycorrhizal
522 fungal partner for the return of limiting resources), invested less in mechanical quality. Given
523 the importance of root mechanical integrity in plant anchorage, our results provide new
524 evidence on the trade-off and synergy among organ multifunctionality, thus contributing to the
525 mechanistic understanding of plant functioning.

526 It is worthwhile to mention that the investigated mechanical traits are related to a plant’ ability
527 of providing the ecosystem service of soil reinforcement and slope stabilization against natural
528 hazards (Stokes et al. 2009; Ghestem et al. 2014). Our results are therefore useful for identifying
529 candidate herbaceous plant species in ecological restoration.

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664

665 **TABLE AND FIGURE CAPTIONS**

666 **Table 1** Root mechanical traits and intermediate metrics included in the study and their function
667 and significance.

668 **Table 2** Species, family and number of root samples used in mechanical tests.

669 **Table 3** Intra- and interspecific variation of root mechanical traits for each species as a function
670 of root type (*Transport* versus *Absorptive*) and root position (*Transport-Proximal* versus
671 *Transport-Distal* and *Absorptive-Proximal* versus *Absorptive-Distal*).

672 **Table 4** Pearson's correlation coefficients among root traits of all species for *absorptive* roots
673 (a) and *transport* roots (b). Trait-based correlations are presented below the diagonal line, while
674 phylogenetic-independent contrast (PIC)-based correlations are presented above the central
675 diagonal. Significant correlations are in bold in coloured cells ($***P < 0.001$; $**P < 0.01$; $*P$
676 < 0.05): green – significantly positive correlation; orange – significantly negative correlation.

677 **Figure 1** Illustration of the root types and sampling locations in the root systems of dicots and
678 monocots.

679 **Figure 2** Root tensile strength (T_r) as a function of diameter (d). Symbols: coloured symbols
680 represent data for the species under consideration (small purple symbols for *absorptive* roots;
681 large green symbols for *transport* roots) and grey symbols in the background (for better viewing)
682 represent data values for the remaining species. Text: blue – Poaceae species; brown –
683 Plantaginaceae species; orange – Rosaceae species; red – Fabaceae species; grey – all species
684 together. Curves: in each subplot, two curves of power law function are illustrated: the coloured
685 curve represents the fit for the concerned species using all root samples; the grey curve
686 represents the fit for all the species together; A (multiplier) and B (exponent) are the two
687 parameters of the power law. NS – the value of the parameter not significant from zero
688 ($***P < 0.001$; $**P < 0.01$; $*P < 0.05$). Note that R^2 are adjusted R^2 which could be
689 mathematically negative. See [Table 2](#) for the number of replicates.

690 **Figure 3** Root tensile strain (ϵ_r) as a function of diameter (d). Symbols: coloured symbols
691 represent data for the species under consideration (small purple symbols for *absorptive* roots;
692 large green symbols for *transport* roots) and grey symbols in the background (for better viewing)
693 represent data values for the remaining species. Text: blue – Poaceae species; brown –
694 Plantaginaceae species; orange – Rosaceae species; red – Fabaceae species; grey – all species
695 together. Curves: in each subplot, two curves of power law function are illustrated: the coloured
696 curve represents the fit for the concerned species using all the root samples; the grey curve
697 represents the fit for all the species together; A (multiplier) and B (exponent) are the two
698 parameters of the power law. NS – the value of the parameter not significant from zero
699 ($***P < 0.001$; $**P < 0.01$; $*P < 0.05$). Note that R^2 are adjusted R^2 which could be
700 mathematically negative. See [Table 2](#) for the number of replicates.

701 **Figure 4** Root modulus of elasticity (E_r) as a function of diameter (d). Symbols: coloured
702 symbols represent data for the species under consideration (small purple symbols for *absorptive*
703 roots; large green symbols for *transport* roots) and grey symbols in the background (for better
704 viewing) represent data values for the remaining species. Text: blue – Poaceae species; brown
705 – Plantaginaceae species; orange – Rosaceae species; red – Fabaceae species; grey – all species
706 together. Curves: in each subplot, two curves of power law function are illustrated: the coloured
707 curve represents the fit for the concerned species using all the root samples; the grey curve
708 represents the fit for all the species together; A (multiplier) and B (exponent) are the two
709 parameters of the power law. NS – the value of the parameter not significant from zero
710 ($***P < 0.001$; $**P < 0.01$; $*P < 0.05$). Note that R^2 are adjusted R^2 which could be
711 mathematically negative. See [Table 2](#) for the number of replicates.

712 **Figure 5** Root toughness (W_r) as a function of diameter (d). Symbols: coloured symbols
713 represent data for the species under consideration (small purple symbols for *absorptive* roots;
714 large green symbols for *transport* roots) and grey symbols in the background (for better viewing)
715 represent data values for the remaining species. Text: blue – Poaceae species; brown –
716 Plantaginaceae species; orange – Rosaceae species; red – Fabaceae species; grey – all species
717 together. Curves: in each subplot, two curves of power law function are illustrated: the coloured
718 curve represents the fit for the concerned species using all the root samples; the grey curve
719 represents the fit for all the species together; A (multiplier) and B (exponent) are the two
720 parameters of the power law. NS – the value of the parameter not significant from zero
721 (** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$). Note that R^2 are adjusted R^2 which could be
722 mathematically negative. See [Table 2](#) for the number of replicates.

723 **Figure 6** Effect of species category (monocots versus dicots) on root mechanical traits for each
724 combination of root functional type and sampling location for the 12 species. Error bars
725 represent standard errors. Numbers beside the bars represent numbers of observations. Pairs of
726 treatments: *Proximal* – monocot versus *Proximal* – dicot and *Distal* – monocot versus *Distal* –
727 dicot. For each pair, letters represent the Student's t-test results at $P < 0.05$ between the dicots
728 and the monocots; in case of significance, “a” represents the larger value, while “b” represents
729 the smaller value.

730 **Figure 7** Relationships between all root traits using principal component analysis for *absorptive*
731 (a) and *transport* roots (b). Colours of convex hull polygons: light red – dicots; light blue –
732 monocots. Colours of arrows: deep red – root mechanical traits; black – root morphological or
733 chemical traits. Each point represents a species, the colour of which is family-dependent: blue
734 – Poaceae species; brown – Plantaginaceae species; orange – Rosaceae species; red – Fabaceae
735 species names: Be – *Bromus erectus*; Dg – *Dactylis glomerata*; Fr – *Festuca rubra*; Lp
736 – *Lolium perenne*; Pp – *Poa pratensis*; Lc – *Lotus corniculatus*; Ms – *Medicago sativa*; Ov –
737 *Onobrychis viciifolia*; Tp – *Trifolium pratense*; Tr – *Trifolium repens*; Pl – *Plantago lanceolata*;
738 Sm – *Sanguisorba minor*. Symbols and acronyms of traits: T_r – tensile strength; ϵ_r – tensile
739 strain; E_r – modulus of elasticity; W_r – tensile toughness; RNC – root nitrogen concentration;
740 RTD – root tissue density; SRL – specific root length; RD – mean root diameter.

741

742 SUPPLEMENTARY TABLE AND FIGURE CAPTIONS

743 **Table S1** Intra- and inter-specific variation of root morphological and chemical traits for each
744 species as a function of root type (*Transport* versus *Absorptive*).

745 **Table S2** Intra- and inter-specific variation of tensile load required to cause root failure (F_r , in
746 N) for each species as a function of root type (*Transport* versus *Absorptive*) and root position
747 (*Transport–Proximal* versus *Transport–Distal* and *Absorptive–Proximal* versus *Absorptive–*
748 *Distal*).

749 **Figure S1** The tensile load (F_r) required to cause root failure as a function of diameter (d).
750 Symbols: coloured symbols represent data for the species under consideration (small purple
751 symbols for *absorptive* roots; large green symbols for *transport* roots) and grey symbols in the
752 background (for better viewing) represent data values for the remaining species. Text: blue –
753 Poaceae species; brown – Plantaginaceae species; orange – Rosaceae species; red – Fabaceae
754 species; grey – all species together. Curves: in each subplot, two curves of power law function
755 are illustrated: the coloured curve represents the fit for the concerned species using all the root
756 samples; the grey curve represents the fit for all the species together; A (multiplier) and B

757 (exponent) are the two parameters of the power law. NS – the value of the parameter not
758 significant from zero (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

759 **Figure S2** Interspecific variation of root mechanical traits for each species as a function of root
760 functional type (*transport* versus *absorptive*). T_r – root tensile strength (in MPa); ϵ_r – root tensile
761 strain (in %); E_r – root modulus of elasticity (in MPa); W_r – tensile toughness (in MJ m⁻³). For
762 x -axis (Species), species are ranged in family, in a descending order of mean T_r . Colours are
763 blue – Poaceae species; red – Fabaceae species; brown – Plantaginaceae species; orange –
764 Rosaceae species; species names: Be – *Bromus erectus*; Dg – *Dactylis glomerata*; Fr – *Festuca*
765 *rubra*; Lp – *Lolium perenne*; Pp – *Poa pratensis*; Lc – *Lotus corniculatus*; Ms – *Medicago*
766 *sativa*; Ov – *Onobrychis viciifolia*; Tp – *Trifolium pratense*; Tr – *Trifolium repens*; Pl –
767 *Plantago lanceolata*; Sm – *Sanguisorba minor*. In each subplot, the capital letters represent the
768 Tukey HSD test results at $P < 0.05$.

769 **Figure S3** Linear regressions between the four mechanical traits and the four morphological
770 and chemical traits at interspecific level. Before regressions, all the traits were in log-
771 transformed with base 10. y -axis: T_r – root tensile strength (in MPa); ϵ_r – root tensile strain
772 (in %); E_r – root modulus of elasticity (in MPa); W_r – root tensile toughness (in MJ m⁻³); x -axis:
773 RD – mean root diameter (mm); SRL – specific root length (m g⁻¹); RTD – root tissue density
774 (g cm⁻³); RNC – root nitrogen concentration (mg g⁻¹). In each subplot, a linear function was fit
775 for each root type (*absorptive* versus *transport*). For each root type, all the monocots (square
776 symbols) and dicots (triangle symbols) were used in the same regression. A solid line represents
777 that the slope is significantly different from zero. When it is not the case, a dashed line is used.
778 Levels of significance for intercept and slope: NS – the value of the parameter not significant
779 from zero; *** – $P < 0.001$; ** – $P < 0.01$; * – $P < 0.05$.
780

TABLES

Table 1

Intermediate metrics	Definition and calculation	Schemas
Load to a root (F , N) (Schemas A)	Time-dependent longitudinal load continuously and progressively applied to a root. F is measured by the datalogger of the test machine. The curve of F versus displacement (L) is noted as: $F = f(L)$	<p>(A)</p> <p>Load (F, N)</p> <p>Displacement (L, mm) ΔL (mm)</p> <p>$F = f(L)$ $L = f^{-1}(F)$</p> <p>(b)</p> <p>Stress (σ, Mpa)</p> <p>Strain (ϵ, %)</p> <p>T_r (MPa)</p> <p>W_r (MJ m⁻³)</p> <p>E_r (MPa)</p> <p>$d\sigma$</p> <p>$d\epsilon$</p> <p>ϵ_r (%)</p>
Root displacement (L , mm) (Schemas A)	Time-dependent absolute root deformation during a test. L is measured by the datalogger of the test machine. The curve of L versus load (F) is noted as: $L = f^{-1}(F)$	
Tensile load required to cause root failure (F_r , N) (Schemas A)	Maximum F , usually occurring at the root failure: $F_r = \max(F)$	
Ultimate root displacement (ΔL , mm) (Schemas A)	Root displacement when the maximum F occurs: $\Delta L = f^{-1}(F_r)$	
Root tensile stress (σ ; MPa) (Schemas B)	Time-dependent tensile load per unit root cross sectional area: $\sigma = 4F/(\pi d^2)$ Where d is mean diameter of the root (mm). The curve of σ versus deformation (ϵ) is noted as: $\sigma = g(\epsilon)$	
Root deformation/strain (ϵ , %) (Schemas B)	Relative longitudinal extension of a root during a test: $\epsilon = \Delta L/L_0$ Where L_0 is initial length of the root sample (mm). The curve of ϵ versus tensile stress (σ) is noted as: $\epsilon = g^{-1}(\sigma)$	
Traits	Definition and calculation	Function and significance
Root tensile strength (T_r , MPa) (Schemas B)	Maximum tensile load required per root cross-sectional area to cause failure of the root, either through breakage or nonreversible deformation: $T_r = \max(\sigma) = 4F_r/(\pi d^2)$	T_r represents root material's intrinsic ability of resistance to external forcing in tension. The higher T_r value that a root possesses, the stronger the root tissue is. A stronger root is able to mobilise higher strength when it is stretched out of soil, it thus improves plant anchorage and soil shear strength.

Root tensile strain (ε_r , %) (Schemas B)	Root deformation when the maximum T_r occurs: $\varepsilon_r = g^{-1}(T_r)$	ε_r reflects root material's intrinsic ability of deformation when being subject to external forcing. The higher ε_r value that a root possesses, the higher deformation the root tissue can reach before failure. Under perturbation, a root of higher ε_r may be more flexible against failure, but may also delay the root's efficacy to exert mechanical resistance.
Modulus of elasticity (E_r , MPa) (Schemas B)	Maximum slope of the quasi-linear part (elastic zone) of the relationship between σ and ε : $E_r = \max\left(\frac{d\sigma}{d\varepsilon}\right)$	E_r reflects the root material's tensile elasticity or stiffness (Cohen et al. 2009; Ekeoma et al. 2021). The higher E_r value that a root possesses, the more elastic or stiffer the root tissue is. Generally, a stiffer root is able to withstand a higher load to elastically deform it under a given displacement, thus improving plant anchorage and provide greater soil reinforcement (Mao et al. 2014). Roots with large E_r can remain anchored in soil, even after soil failure has occurred, thus holding vegetation in place and retarding or preventing mass substrate failure (Freschet et al. 2021).
Root tensile toughness (W_r , MJ m ⁻³) (Schemas B)	Amount of energy per unit volume that a root can absorb before its fracture. W_r is calculated as the surface area of the curve of σ against ε : $W_r = \int_0^{\varepsilon_r} f(\varepsilon)d\varepsilon$	W_r , also called deformation energy, represents the ability of a root to absorb energy without fracture and is an intrinsic mechanical quality of root tissue as a material by jointly considering strength and deformation (Ji et al. 2021). The higher W_r value that a root possesses, the tougher the root tissue is.

Note: In the schemas, the curve of σ against ε (in grey) is extracted from the mechanical test for one root sample (species: *Trifolium repens*, root type: *transport*; root location: *distal*; replicate no.: 3). Variables in red correspond to the traits used in plots and analyses, while variables in blue are intermediary metrics used to calculate the traits in red.

Table 2

Category	Family	Species	Abbreviation	Number of successful mechanical tests for root samples				Total
				<i>Absorptive roots</i>		<i>Transport roots</i>		
				<i>Proximal</i>	<i>Distal</i>	<i>Proximal</i>	<i>Distal</i>	
Monocot	Poaceae	<i>Bromus erectus</i>	Be	5	5	5	5	20
Monocot	Poaceae	<i>Dactylis glomerata</i>	Dg	3	4	5	4	16
Monocot	Poaceae	<i>Festuca rubra</i>	Fr	5	5	5	5	20
Monocot	Poaceae	<i>Lolium perenne</i>	Lp	5	5	5	5	20
Monocot	Poaceae	<i>Poa pratensis</i>	Pp	5	5	5	5	20
Dicot	Fabaceae	<i>Lotus corniculatus</i>	Lc	5	5	5	5	20
Dicot	Fabaceae	<i>Medicago sativa</i>	Ms	5	4	5	5	19
Dicot	Fabaceae	<i>Onobrychis viciifolia</i>	Ov	5	5	5	5	20
Dicot	Fabaceae	<i>Trifolium pratense</i>	Tp	5	3	4	5	17
Dicot	Fabaceae	<i>Trifolium repens</i>	Tr	5	5	5	5	20
Dicot	Plantaginaceae	<i>Plantago lanceolata</i>	Pl	5	4	5	5	19
Dicot	Rosaceae	<i>Sanguisorba minor</i>	Sm	5	5	5	5	20

Table 3

Trait	Species	Absorptive	Transport	Absorptive-Proximal	Absorptive-Distal	Transport-Proximal	Transport-Distal
T_r	Pp	AC 25.32 ± 4.15 b	B 57.05 ± 12.67 a	B 29.15 ± 6.81 a	A 21.49 ± 4.90 a	B 44.98 ± 6.54 a	B 69.11 ± 24.64 a
	Dg	A 26.93 ± 4.70 a	AB 44.74 ± 9.06 a	AB 23.94 ± 8.31 a	A 29.18 ± 6.23 a	AB 51.11 ± 11.17 a	AB 36.78 ± 15.70 a
	Lp	ABC 12.36 ± 3.72 a	AC 21.51 ± 11.68 a	AC 8.69 ± 2.77 a	A 16.04 ± 6.93 a	ABC 30.79 ± 22.32 a	A 12.23 ± 8.53 a
	Tr	BC 14.94 ± 2.15 a	AC 15.82 ± 1.40 a	C 13.41 ± 3.33 a	A 16.47 ± 2.94 a	ABC 15.23 ± 0.73 a	A 16.41 ± 2.85 a
	Fr	B 14.54 ± 3.45 a	C 15.27 ± 2.03 a	C 9.87 ± 2.56 a	A 19.22 ± 6.02 a	AC 17.30 ± 3.41 a	A 13.24 ± 2.20 a
	Tp	B 6.82 ± 2.73 a	C 12.50 ± 1.77 a	C 4.98 ± 1.40 a	A 11.39 ± 10.37 a	ABC 12.35 ± 2.01 a	A 12.62 ± 2.98 a
	Pl	B 3.48 ± 0.35 b	C 10.61 ± 2.24 a	C 3.54 ± 0.55 a	A 3.40 ± 0.46 a	AC 15.20 ± 2.95 a	A 6.03 ± 1.85 b
	Ms	B 7.81 ± 1.46 a	C 5.29 ± 0.50 a	C 5.03 ± 1.35 b	A 11.29 ± 1.60 a	C 5.33 ± 0.53 a	A 5.25 ± 0.92 a
	Ov	B 3.49 ± 0.53 b	C 7.79 ± 0.61 a	C 2.62 ± 0.70 a	A 4.35 ± 0.64 a	C 8.85 ± 0.65 a	A 6.74 ± 0.84 a
	Sm	B 3.92 ± 0.72 a	C 4.72 ± 1.27 a	C 3.62 ± 1.23 a	A 4.21 ± 0.89 a	C 5.97 ± 1.68 a	A 3.48 ± 1.90 a
	Be	B 2.13 ± 0.28 b	C 5.57 ± 1.32 a	C 2.65 ± 0.27 a	A 1.61 ± 0.39 a	C 8.11 ± 2.07 a	A 3.03 ± 0.62 a
	Lc	B 3.51 ± 1.04 a	C 3.47 ± 0.54 a	C 4.49 ± 1.99 a	A 2.54 ± 0.63 a	C 4.54 ± 0.64 a	A 2.39 ± 0.58 b
	All	10.18 ± 1.02 b	16.83 ± 2.17 a	8.83 ± 1.33 a	11.61 ± 1.54 a	18.41 ± 2.83 a	15.25 ± 3.30 a
ϵ_r	Fr	AC 23.74 ± 4.21 b	B 40.18 ± 3.25 a	B 21.42 ± 6.56 a	A 26.06 ± 5.83 a	B 43.20 ± 3.28 a	B 37.16 ± 5.68 a
	Pp	A 20.90 ± 3.10 b	AB 37.89 ± 2.24 a	AB 24.33 ± 4.42 a	A 17.47 ± 4.23 a	AB 38.13 ± 4.29 a	AB 37.65 ± 2.03 a
	Dg	ABC 24.70 ± 4.17 a	AC 31.58 ± 1.37 a	AC 27.72 ± 3.00 a	A 22.44 ± 7.24 a	ABC 30.45 ± 1.34 a	A 32.99 ± 2.67 a
	Lp	BC 19.81 ± 3.52 b	AC 33.50 ± 2.12 a	C 21.86 ± 5.44 a	A 17.77 ± 4.91 a	ABC 36.61 ± 1.54 a	A 30.40 ± 3.61 a
	Pl	B 12.14 ± 1.57 b	C 25.10 ± 2.63 a	C 13.76 ± 2.13 a	A 10.10 ± 2.17 a	AC 31.03 ± 1.89 a	A 19.18 ± 3.17 b
	Be	B 10.32 ± 1.36 b	C 26.41 ± 5.00 a	C 12.51 ± 1.86 a	A 8.14 ± 1.57 a	ABC 31.52 ± 8.88 a	A 21.31 ± 4.56 a
	Lc	B 10.26 ± 2.26 b	C 18.26 ± 2.55 a	C 14.25 ± 3.53 a	A 6.27 ± 1.61 a	AC 21.61 ± 2.37 a	A 14.91 ± 4.25 a
	Ov	B 11.05 ± 1.25 b	C 16.55 ± 1.98 a	C 9.60 ± 1.69 a	A 12.51 ± 1.77 a	C 19.86 ± 2.11 a	A 13.24 ± 2.78 a
	Tr	B 8.60 ± 1.70 b	C 18.70 ± 1.86 a	C 11.12 ± 2.31 a	A 6.07 ± 2.11 a	C 22.15 ± 0.97 a	A 15.24 ± 2.93 a
	Tp	B 10.01 ± 2.45 a	C 16.20 ± 2.11 a	C 9.54 ± 2.53 a	A 11.20 ± 7.72 a	C 16.11 ± 1.99 a	A 16.27 ± 3.70 a
	Ms	B 9.44 ± 1.09 a	C 13.19 ± 1.75 a	C 7.59 ± 1.21 b	A 11.76 ± 1.22 a	C 12.94 ± 1.67 a	A 13.44 ± 3.31 a
	Sm	B 7.76 ± 1.46 b	C 13.92 ± 2.19 a	C 8.26 ± 2.35 a	A 7.26 ± 1.97 a	C 15.56 ± 2.46 a	A 12.29 ± 3.76 a
	All	13.85 ± 0.89 b	24.30 ± 1.11 a	14.73 ± 1.23 a	12.93 ± 1.29 a	26.78 ± 1.53 a	21.82 ± 1.55 b

E_r	Dg	AC 251.23 ± 41.76 a	B 535.16 ± 164.65 a	B 226.53 ± 85.06 a	A 269.75 ± 47.12 a	B 660.21 ± 231.32 a	B 378.85 ± 242.54 a
	Pp	A 303.92 ± 46.24 a	AB 442.96 ± 126.51 a	AB 319.99 ± 62.44 a	A 287.86 ± 74.79 a	AB 313.74 ± 57.42 a	AB 572.18 ± 245.72 a
	Tr	ABC 362.14 ± 61.04 a	AC 322.25 ± 24.69 a	AC 273.69 ± 89.11 a	A 450.59 ± 70.10 a	ABC 299.51 ± 17.09 a	A 344.98 ± 46.82 a
	Lp	BC 246.65 ± 101.14 a	AC 218.00 ± 124.40 a	C 125.73 ± 65.22 a	A 367.56 ± 185.65 a	ABC 291.15 ± 231.60 a	A 144.86 ± 115.42 a
	Tp	B 138.10 ± 48.56 a	C 217.39 ± 26.54 a	C 136.12 ± 60.34 a	A 143.06 ± 114.38 a	AC 235.47 ± 36.12 a	A 202.92 ± 40.43 a
	Fr	B 163.84 ± 62.30 a	C 122.79 ± 17.64 a	C 98.04 ± 28.78 a	A 229.63 ± 120.29 a	ABC 131.83 ± 29.47 a	A 113.76 ± 22.15 a
	Ms	B 145.20 ± 33.32 a	C 118.29 ± 15.67 a	C 101.54 ± 40.00 a	A 199.78 ± 46.97 a	AC 130.74 ± 21.31 a	A 105.84 ± 23.95 a
	Sm	B 154.95 ± 38.96 a	C 52.40 ± 12.18 b	C 181.14 ± 79.33 a	A 128.76 ± 13.92 a	C 62.04 ± 18.75 a	A 42.76 ± 16.43 a
	Ov	B 58.79 ± 11.52 b	C 144.98 ± 13.66 a	C 45.44 ± 10.52 a	A 72.14 ± 19.94 a	C 165.18 ± 18.81 a	A 124.79 ± 16.80 a
	Pl	B 58.98 ± 15.06 a	C 109.87 ± 20.05 a	C 41.87 ± 11.47 a	A 80.36 ± 29.44 a	C 152.71 ± 19.38 a	A 67.02 ± 22.69 b
	Lc	B 84.18 ± 20.72 a	C 51.02 ± 6.84 a	C 75.39 ± 18.91 a	A 92.96 ± 39.18 a	C 67.53 ± 7.28 a	A 34.50 ± 4.61 b
	Be	B 38.69 ± 5.28 a	C 57.38 ± 7.40 a	C 45.10 ± 7.35 a	A 32.27 ± 7.13 a	C 68.25 ± 9.59 a	A 46.51 ± 9.77 a
	All	168.16 ± 16.45 a	196.38 ± 23.54 a	136.21 ± 18.10 b	201.86 ± 27.33 a	214.51 ± 33.42 a	178.24 ± 33.28 a
	W_r	Pp	AC 3.19 ± 0.81 b	B 13.43 ± 3.49 a	B 4.38 ± 1.35 a	A 2.01 ± 0.67 a	B 10.49 ± 2.47 a
Dg		A 4.01 ± 1.35 b	AB 8.49 ± 1.57 a	AB 3.62 ± 0.86 a	A 4.30 ± 2.45 a	AB 9.87 ± 2.09 a	AB 6.76 ± 2.39 a
Fr		ABC 2.12 ± 0.85 a	AC 3.74 ± 0.69 a	AC 1.05 ± 0.37 a	A 3.19 ± 1.58 a	ABC 4.47 ± 1.00 a	A 3.00 ± 0.92 a
Lp		BC 1.35 ± 0.58 a	AC 4.19 ± 2.31 a	C 1.02 ± 0.24 a	A 1.67 ± 1.19 a	ABC 6.27 ± 4.44 a	A 2.12 ± 1.44 a
Tr		B 0.64 ± 0.18 b	C 2.02 ± 0.30 a	C 0.71 ± 0.25 a	A 0.57 ± 0.28 a	AC 2.30 ± 0.15 a	A 1.74 ± 0.60 a
Pl		B 0.18 ± 0.03 b	C 1.88 ± 0.49 a	C 0.22 ± 0.05 a	A 0.14 ± 0.03 a	ABC 2.97 ± 0.62 a	A 0.78 ± 0.32 b
Tp		B 0.52 ± 0.32 a	C 1.36 ± 0.27 a	C 0.27 ± 0.16 a	A 1.16 ± 1.15 a	AC 1.37 ± 0.39 a	A 1.35 ± 0.41 a
Be		B 0.11 ± 0.03 a	C 1.07 ± 0.44 a	C 0.16 ± 0.03 a	A 0.07 ± 0.03 a	C 1.70 ± 0.80 a	A 0.45 ± 0.13 a
Ov		B 0.17 ± 0.03 b	C 0.87 ± 0.15 a	C 0.12 ± 0.03 a	A 0.23 ± 0.02 a	C 1.17 ± 0.13 a	A 0.58 ± 0.19 b
Ms		B 0.38 ± 0.10 a	C 0.49 ± 0.10 a	C 0.15 ± 0.03 b	A 0.67 ± 0.11 a	C 0.49 ± 0.09 a	A 0.49 ± 0.20 a
Lc		B 0.27 ± 0.16 a	C 0.43 ± 0.09 a	C 0.47 ± 0.32 a	A 0.07 ± 0.03 a	C 0.60 ± 0.10 a	A 0.26 ± 0.10 b
Sm		B 0.13 ± 0.04 a	C 0.54 ± 0.20 a	C 0.11 ± 0.04 a	A 0.16 ± 0.08 a	C 0.65 ± 0.21 a	A 0.44 ± 0.37 a
All		1.03 ± 0.18 b	3.18 ± 0.51 a	0.93 ± 0.21 a	1.14 ± 0.29 a	3.57 ± 0.62 a	2.79 ± 0.80 a

Note: In the column “Trait”: T_r – root tensile strength (in MPa); ϵ_r – root tensile strain (in %); E_r – root modulus of elasticity (in MPa); W_r – root tensile work (in MPa). In the column “Species,” for each trait, species are ranged in a descendent order according to the average of all the tested roots of the concerned trait (not shown); colours: blue – Poaceae species; red – Fabaceae species; brown – Plantaginaceae species; orange – Rosaceae species; species names: Be – *Bromus erectus*; Dg – *Dactylis glomerata*; Fr – *Festuca rubra*; Lp – *Lolium perenne*; Pp – *Poa pratensis*; Lc – *Lotus corniculatus*; Ms – *Medicago sativa*; Ov – *Onobrychis viciifolia*; Tp – *Trifolium pratense*; Tr – *Trifolium repens*; Pl – *Plantago lanceolata*; Sm – *Sanguisorba minor*. Data are mean \pm standard error. Statistical results for intraspecific variation: data in bold and in grey background highlight the significant cases according to the Student's t-test, each of which was performed for a pair of data (*Transport* versus *Absorptive*, *Transport–proximal* versus *Transport–Distal* and *Absorptive–proximal* versus *Absorptive–Distal*) for each species; the lower case letters after the values represent the Student's t-test results at $p < 0.05$; in case of significance, “a” represents the larger value, while “b” represents the smaller value. Statistical results for interspecific variation: the capital letters before the values represent the Tukey HSD test results at $p < 0.05$ across species for each of the six types of roots.

Table 4

(a) Absorptive roots

Trait category	Trait	T_r	ε_r	E_r	W_r	RD	SRL	RTD	RNC	C:N
Mechanical traits	Tensile strength	T_r	0.63*	0.78**	0.93***	-0.46	0.86***	-0.65*	0.14	0.05
	Tensile strain	ε_r	0.68*	0.22	0.80**	-0.08	0.51	-0.34	-0.33	0.51
	Modulus of elasticity	E_r	0.89***	0.36	0.80**	-0.08	0.51	-0.34	-0.33	0.51
	Tensile work	W_r	0.96***	0.84***	0.76**	-0.33	0.72*	-0.52	-0.00	0.19
Morphological and chemical traits	Mean root diameter	RD	-0.61*	-0.58*	-0.55	-0.62*	-0.69*	0.64*	-0.15	-0.18
	Specific root length	SRL	0.74**	0.61*	0.69*	0.74**	-0.97***	-0.83**	0.12	0.15
	Root tissue density	RTD	-0.80**	-0.42	-0.81**	-0.78**	0.42	-0.64*	-0.53	0.19
	Root nitrogen concentration	RNC	-0.12	-0.60*	0.05	-0.24	0.67*	-0.49	-0.25	-0.88***
	Carbon to nitrogen ratio	C:N	0.16	0.62*	0.00	0.28	-0.71*	0.54	0.19	-1.00***

(b) Transport roots

Trait category	Trait	T_r	ε_r	E_r	W_r	RD	SRL	RTD	RNC	C:N
Mechanical traits	Tensile strength	T_r	0.37	0.91***	0.98***	-0.05	0.24	-0.05	-0.25	0.54
	Tensile strain	ε_r	0.71**	0.12	0.48	-0.20	0.88***	-0.09	-0.22	0.70*
	Modulus of elasticity	E_r	0.91***	0.42	0.82**	-0.17	-0.05	-0.23	-0.33	0.44
	Tensile work	W_r	0.97***	0.85***	0.81**	-0.01	0.40	0.03	-0.24	0.58
Morphological and chemical traits	Mean root diameter	RD	-0.50	-0.70*	-0.35	-0.59*	-0.27	0.88***	0.59	-0.09
	Specific root length	SRL	0.64*	0.95***	0.35	0.79**	-0.79**	-0.05	-0.34	0.51
	Root tissue density	RTD	-0.45	-0.81**	-0.22	-0.59*	0.77**	-0.89***	0.39	0.02
	Root nitrogen concentration	RNC	-0.57	-0.76**	-0.24	-0.69*	0.54	-0.80**	0.58*	-0.58
	Carbon to nitrogen ratio	C:N	0.57	0.77**	0.25	0.70*	-0.54	0.81**	-0.59*	-1.00***

Notes: Colours: green – positive and significant correlation ; orange – negative and significant correlation. Significance code: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

FIGURES

Root type	Root segment	Root location
<p><i>Transport</i> root (order >3) From the same root, but differ-ing in distance to the tip.</p>	<p>1 (<i>Transport – Proximal</i>)</p> <p>2 (<i>Transport – Distal</i>)</p>	<p><i>Proximal</i> They are closer to stem.</p>
<p><i>Absorptive</i> root (order ≤3) From different roots branching from different locations of the same root.</p>	<p>3 (<i>Absorptive – Proximal</i>)</p> <p>4 (<i>Absorptive – Distal</i>)</p>	<p><i>Distal</i> They are closer to root tips.</p>

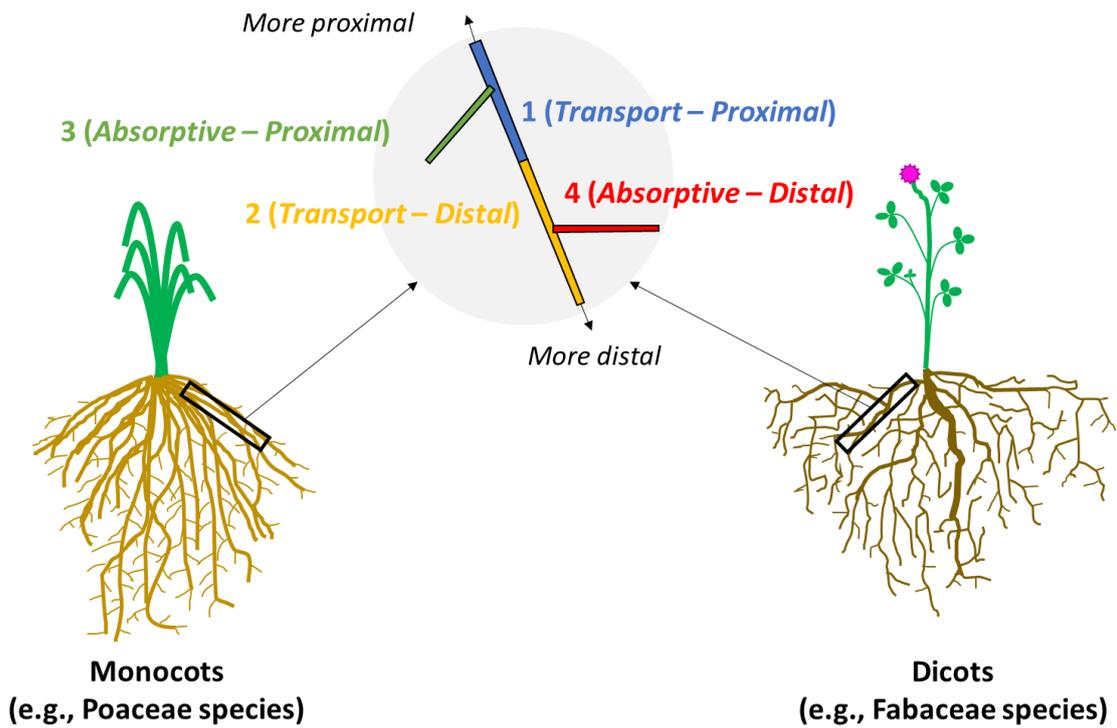


Figure 1

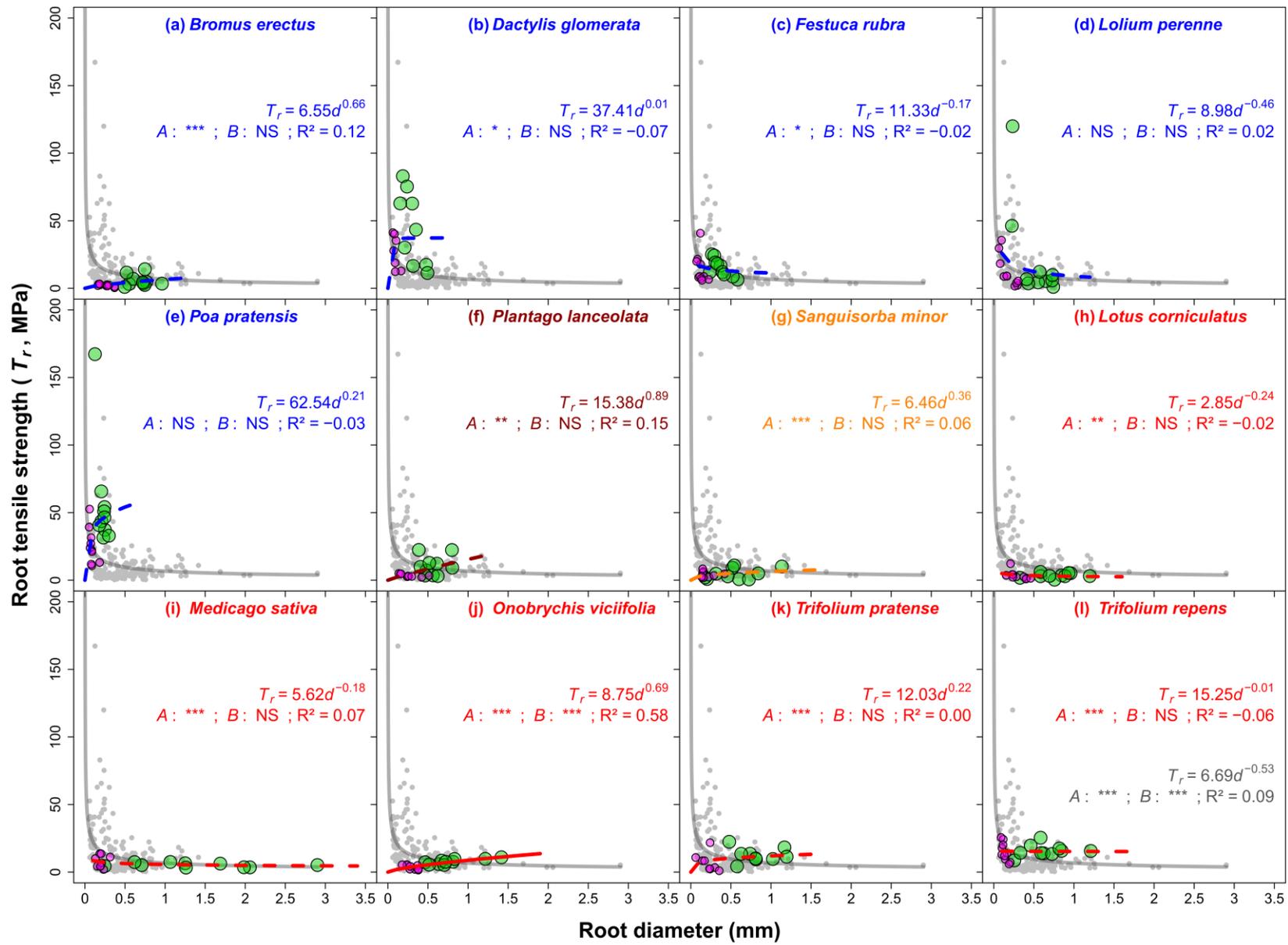


Figure 2

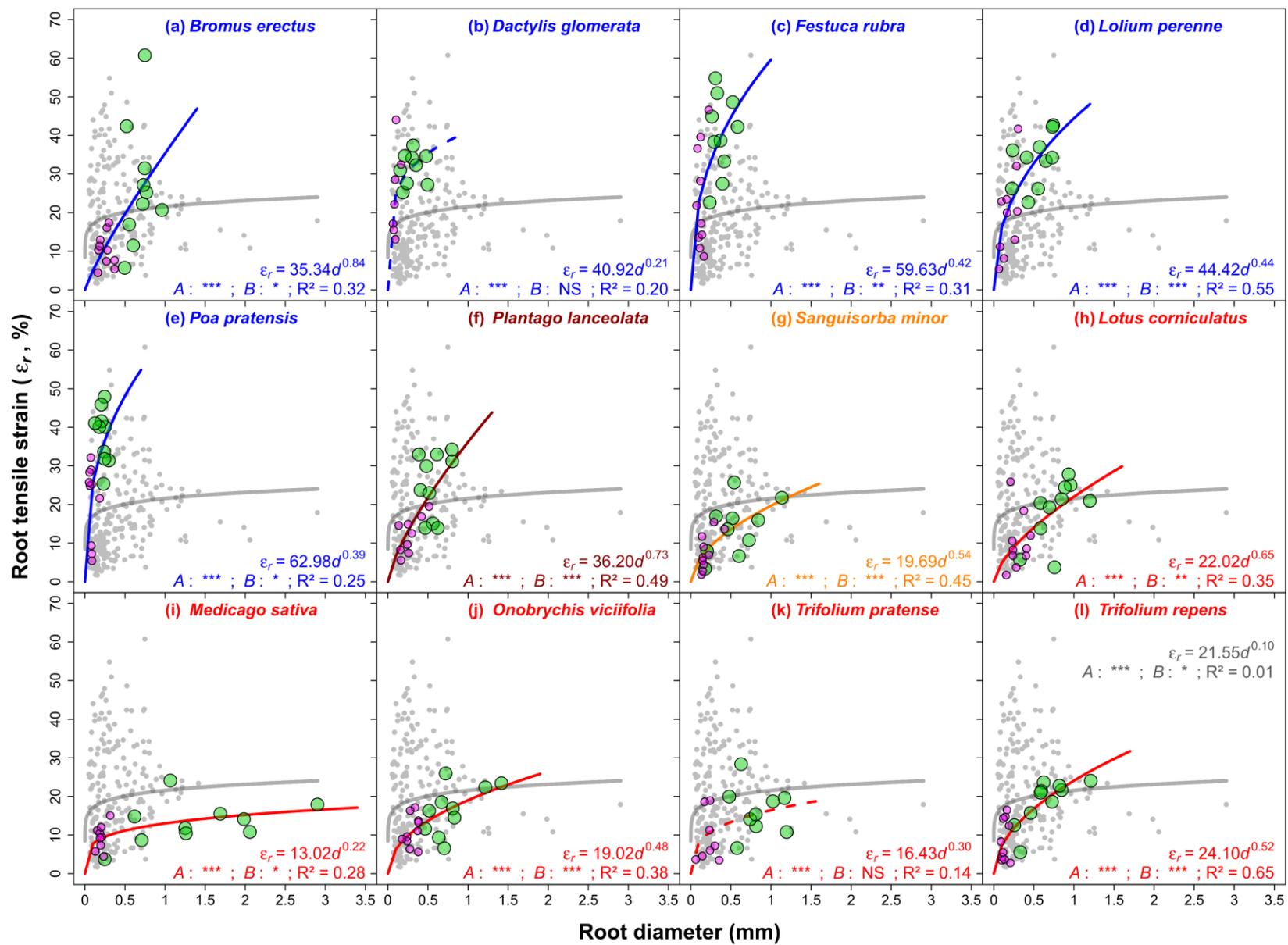


Figure 3

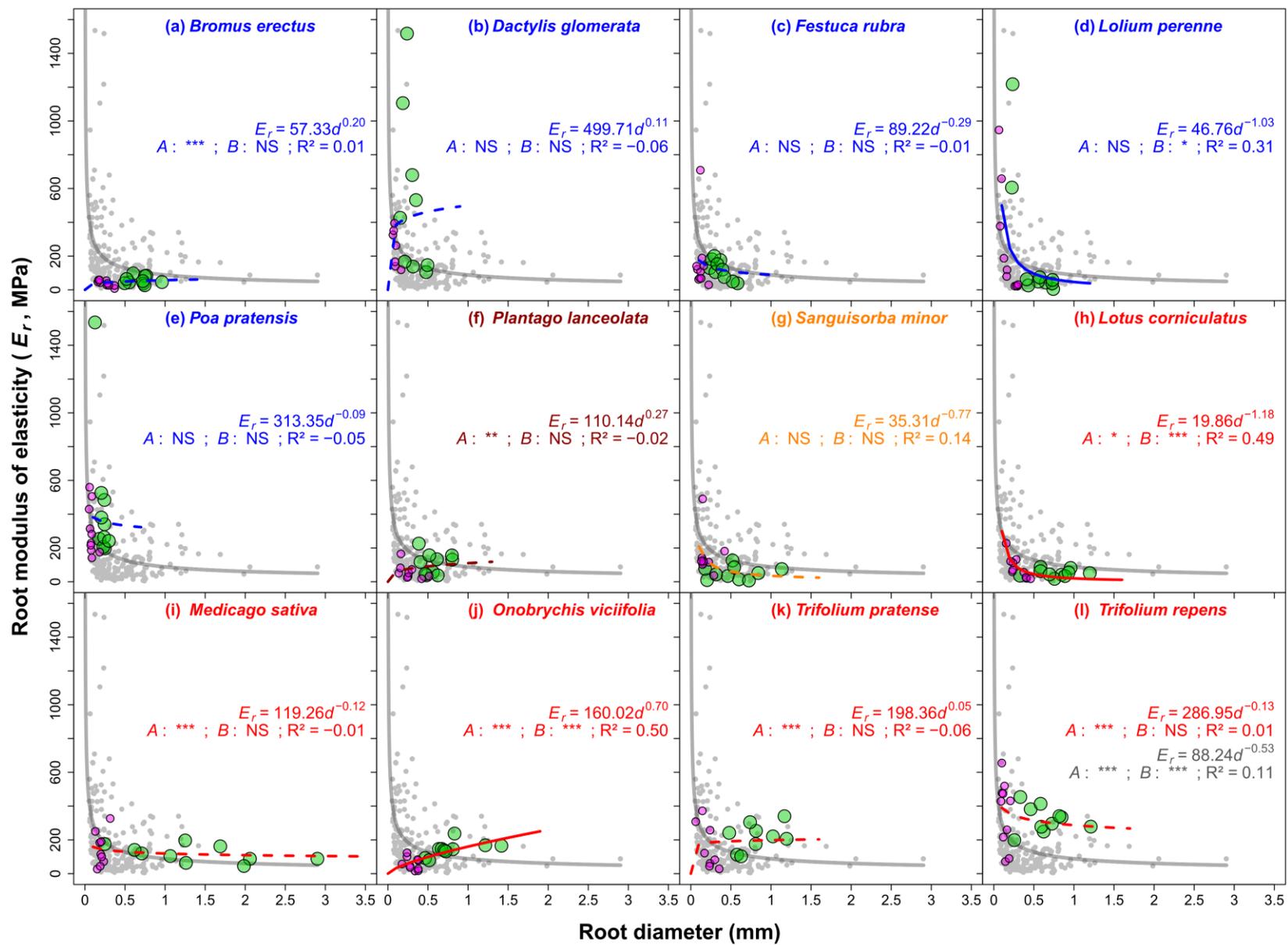


Figure 4

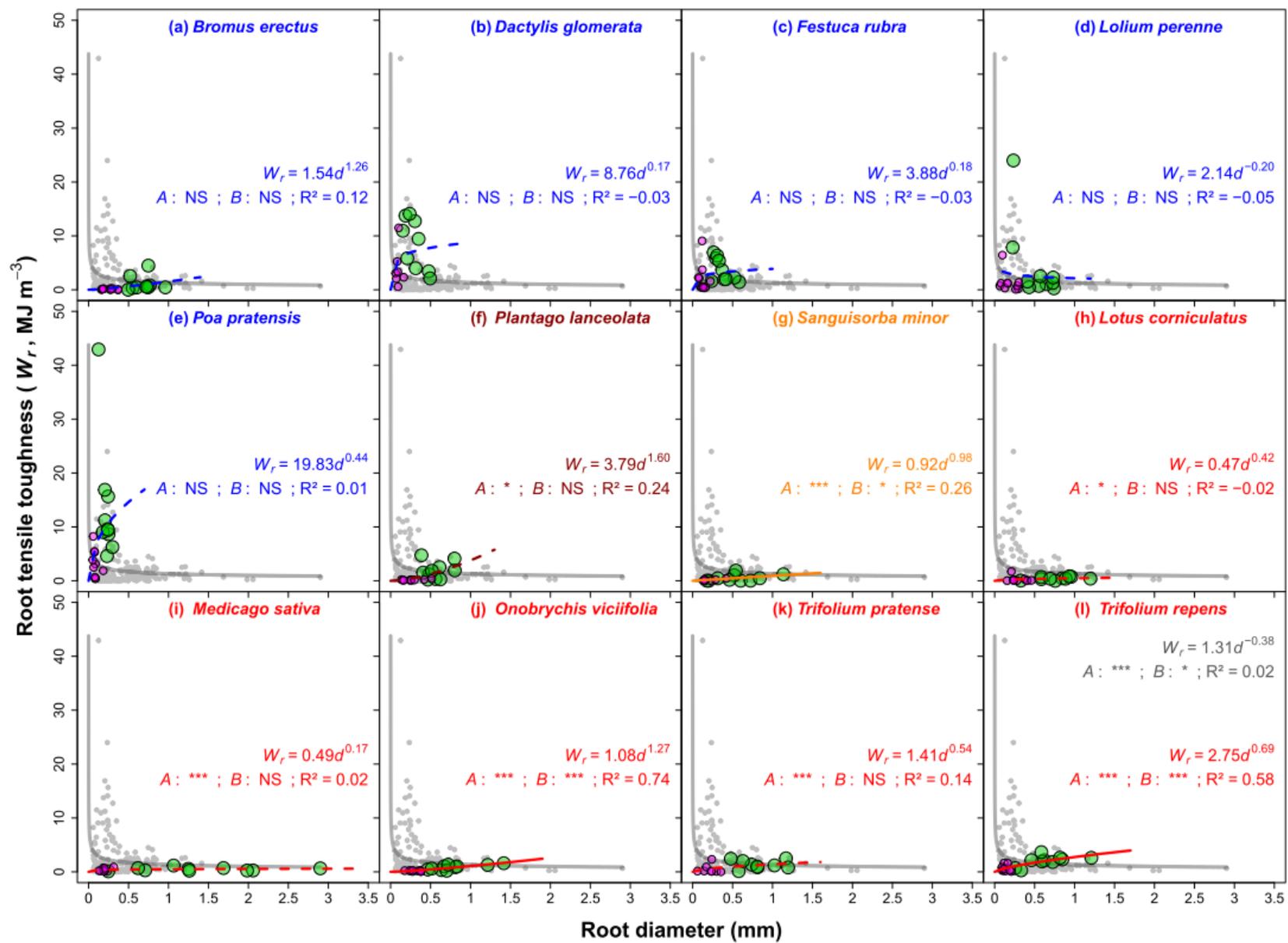


Figure 5

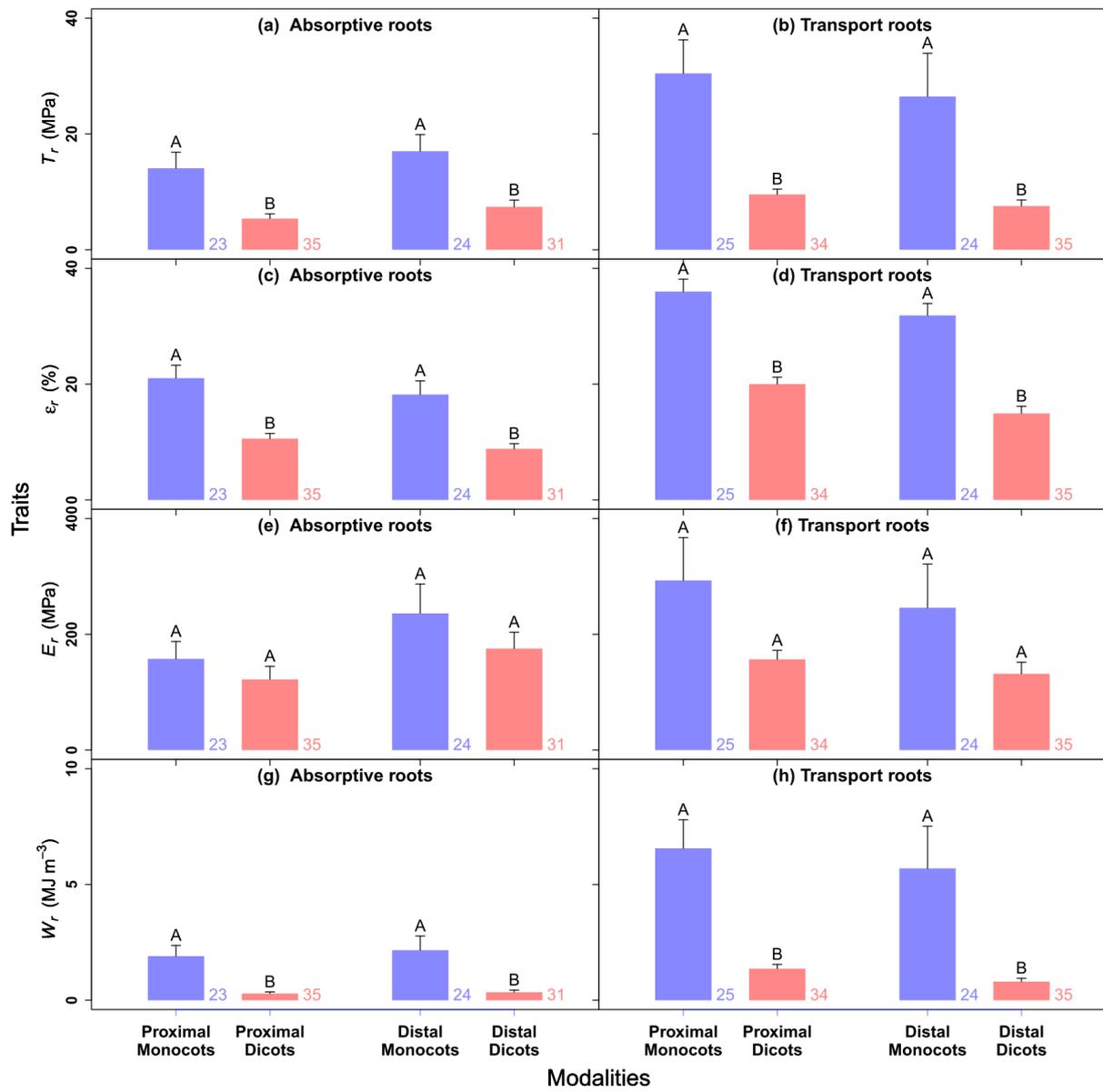


Figure 6

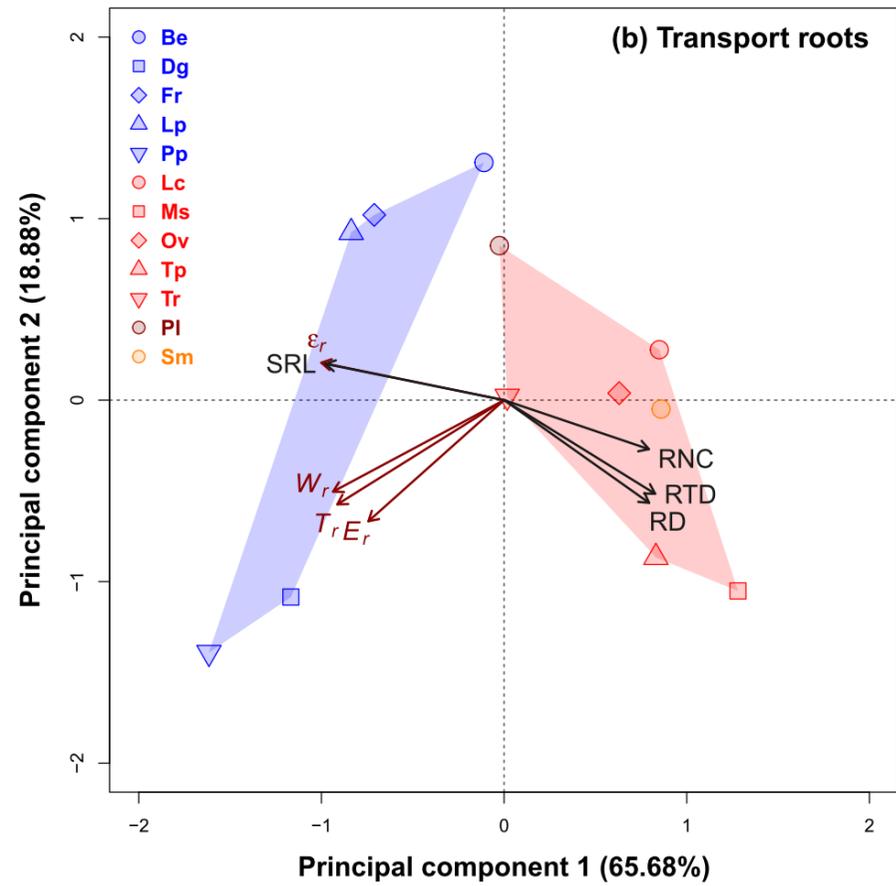
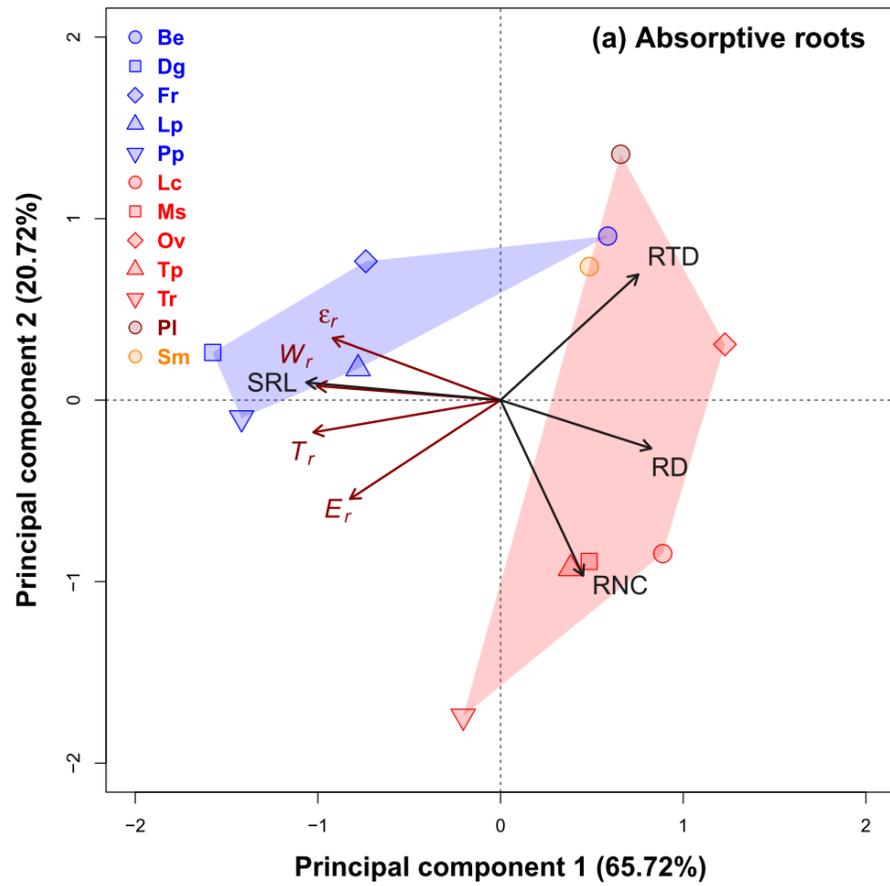


Figure 7