

Root hydraulic properties: an exploration of their variability across scales

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1 **Abstract**

2 Root hydraulic properties are key physiological traits that determine the capacity of root
3 systems to take up water, at a specific evaporative demand. They can strongly vary among
4 species, cultivars or even within the same genotype, but a systematic analysis of their variation
5 across plant functional types (PFTs) is still missing. Here, we reviewed published empirical
6 studies on root hydraulic properties at the segment-, individual root-, or root system scale and
7 determined its variability and the main factors contributing to it.

8 We observed an extremely large range of variation (of orders of magnitude) in root hydraulic
9 properties, but this was not caused by systematic differences among PFTs. Rather, the
10 (combined) effect of factors such as root system age, driving force used for measurement, or
11 stress treatments shaped the results. We found a significant decrease in root hydraulic
12 properties under stress conditions (drought and aquaporin inhibition) and a significant effect of
13 the driving force used for measurement (hydrostatic or osmotic gradients). Furthermore, whole
14 root system conductance increased significantly with root system age across several crop
15 species, causing very large variation in the data (> 2 orders of magnitude). Interestingly, this
16 relationship showed an asymptotic shape, with a steep increase during the first days of growth
17 and a flattening out at later stages of development. This behaviour was also observed in
18 simulations with computational plant models, suggesting common patterns across studies and
19 species.

20 These findings provide better understanding of the main causes of root hydraulic properties
21 variations observed across empirical studies. They also open the door to better representation
22 of hydraulic processes across multiple plant functional types and at large scales. All data
23 collected in our analysis has been aggregated into an open access database
24 (<https://roothydraulic-properties.shinyapps.io/database/>), fostering scientific exchange.

25

26 **Key words:** root hydraulic properties variability, open access database, plant functional types,
27 whole root system conductance, review, plant modelling.

28 1 Introduction

29 Root water uptake is a fundamental mechanism essential for the survival of plants. The ability
30 of plants to absorb water through their roots and transport it to the plant's above-ground tissues
31 is crucial for enabling key physiological processes such as photosynthesis, nutrient absorption,
32 and cell expansion (Lambers & Oliveira, 2019). The effectiveness of root systems in absorbing
33 water allows plants to regulate their water balance, postpone or avoid water stress, regulate
34 canopy temperature, and sustain physiological functions at their optimum (Stedde,
35 2000a; Lynch *et al.*, 2014; Abdalla *et al.*, 2022).

36 Water uptake is a passive process driven by the water potential gradients in the soil-plant-
37 atmosphere continuum (catenary process, Cowan, 1965), where water is pulled up from the
38 soil into the root xylem and up to the leaf following the cohesion-tension principle (Stedde,
39 2001). Water flow through the root system can be described analogously to electric current
40 through a network of resistances (Landsberg & Fowkes, 1978). The water flow rate (J , $\text{m}^3 \text{s}^{-1}$)
41 between any two points is dependent on the water potential difference (ψ , MPa) and the
42 hydraulic conductance (K , $\text{m}^3 \text{MPa}^{-1} \text{s}^{-1}$, the inverse of a resistance) between these points. In
43 that, root water uptake from the root-soil interface to the above ground organs is affected by
44 root hydraulic properties (the individual resistances) and the root system architecture (the way
45 resistances are connected to form a network) (Doussan *et al.*, 1998; Leitner *et al.*,
46 2014; Lobet *et al.*, 2014) (Figure 1).

47 Root hydraulic properties can be expressed at different tissue scales, from root segments up to
48 the whole root system (Figure 1, Table 1). The radial conductivity (k_r) represents the capacity
49 of roots to transport water from the root-soil interface to the root-xylem across their radial
50 pathways, and depends on several anatomical features (Stedde, 2000a; North & Peterson,
51 2005) and aquaporin expression (Gambetta *et al.*, 2017). The axial conductance k_x refers to the
52 ability of roots to transport water longitudinally, which is a function of the number and diameter
53 of xylem vessels (Hacke & Jansen, 2009). The resulting total conductivity of individual roots
54 or root segments (k_{root}) can be limited by its radial (Bramley *et al.*, 2009) or axial
55 components (Sanderson *et al.*, 1988; Bouda *et al.*, 2018; Boursiac *et al.*, 2022a). The whole
56 root system conductance (K_{rs}) integrates the contribution of all individual conductances along
57 the root system, i.e., it depends on k_r and k_x (Bouda *et al.*, 2018; Meunier *et al.*, 2019) but also
58 on the root system architecture (Doussan *et al.*, 2006), and reflects the overall hydraulic
59 efficiency of the root system in transporting water from the soil to the above-ground tissues

60 (see Table 1 for details). Understanding the variability in these key hydraulic properties among
61 and within plant species and in response to changing environmental conditions and
62 environmental stresses is essential for the study of plant water relations (Gallardo *et al.*,
63 1996; Lambers & Oliveira, 2019).

64 A large range of empirical methods has been developed for the determination of root hydraulic
65 properties, from the cell and tissue level (Steudle, 1990) up to the whole root system (Tyree *et*
66 *al.*, 1995), with the pressure chamber, the High Pressure Flow Meter (HPFM) and root
67 exudation being the most common ones (Boursiac *et al.*, 2022b). While these methods rely on
68 the direct measurement of water flow across root tissues, also more indirect methods based on
69 observations of soil water content and transpiration changes in combination with modelling
70 have been applied (Abdalla & Ahmed, 2021; Abdalla *et al.*, 2022). However, different
71 measurement methods may produce different results, especially when comparing methods that
72 rely on a hydrostatic driving force for water flow against those using an osmotic one (Kim *et*
73 *al.*, 2018). Additionally, empirical studies have shown that root hydraulic properties can
74 strongly vary (up to orders of magnitude) among species (Steudle, 2000a; Bramley *et al.*,
75 2009; Pratt *et al.*, 2010), but also among genotypes of one species (Rishmawi *et al.*, 2023) or
76 even among individuals of the same genotype (Steudle, 2000a). This large variability can be
77 explained, at least partially, by the function of roots as hydraulic rheostats, i.e., the dynamic
78 changes that root hydraulic properties undergo during development and in response to
79 environmental stimuli (Maurel *et al.*, 2010). Interestingly, though, a systematic study of the
80 range of variability of root hydraulic properties across multiple plant functional types (PFTs),
81 experimental treatments and measurement techniques is still missing. PFTs provide a
82 simplified description of plant diversity, facilitating the representation of ecosystem processes
83 and vegetation dynamics (Wullschlegel *et al.*, 2014). Understanding the variability of root
84 hydraulic properties among and within PFTs is therefore key for a better modelling
85 representation of root water uptake processes across scales (Sulis *et al.*, 2019; Nguyen *et al.*,
86 2020; Nguyen *et al.*, 2022).

87 In this context, the present study focused on improving the understanding of the variability of
88 root hydraulic properties observed across species and PFTs. For this, we systematically
89 reviewed published empirical studies and addressed the following questions: (i) what is the
90 total range of variation in root hydraulic properties observed in the literature?; (ii) are there
91 systematic differences in root hydraulic properties among PFTs and which other factors affect
92 root hydraulic properties variability?; (iii) are the responses of root hydraulic properties to

93 environmental stresses consistent across PFTs?; and (iv) how are root hydraulic properties
94 affected by root development (root age)?

95 Given the large amount of data obtained in the review and its complexity (see 2.2 for a detailed
96 data description), the results presented in this study have a stronger focus on K_{rs} , a key trait that
97 might determine the water use of plants under changing environmental conditions (Vadez,
98 2014) and integrates the variability of k_r , k_x and root architecture. But, all original data that was
99 collected in the review has been aggregated to an open access database, which can be easily
100 accessed through a web application (Baca Cabrera, 2023), facilitating data access and further
101 use. Furthermore, we complemented our review by using functional-structural modelling, to
102 improve our understanding of the mechanisms behind the emerging patterns in the empirical
103 data.

104 **2 Methods**

105 **2.1 Literature review selection criteria**

106 The main goal of this study was to obtain an overview about the range of variation in root
107 hydraulic properties observed experimentally, and the main factors contributing to it. For this,
108 we reviewed scientific articles in which whole root system hydraulic conductance, root
109 hydraulic conductivity, radial conductivity and/or axial conductance were determined
110 experimentally. The Web of Science search engine was used for the review, and following
111 search terms and keywords were included: “*root hydraulic conduct**” AND *measur** or “*root*
112 *axial hydraulic conduct**” AND *measur** or “*root radial hydraulic conduct**” AND *measur**.
113 The boolean operator AND was used to limit the search to studies in which root hydraulic
114 properties were directly measured and not indirectly modelled from soil water content and/or
115 plant transpiration or theoretically derived. All papers resulting from the search were revised
116 in detail and only those which met the selection criteria were retained in the database.

117 In a second step, we checked the citations included in the selected papers to look for additional
118 publications that may meet the selection criteria. Additionally, we looked at previous meta-
119 analyses (Meunier *et al.*, 2018; Bouda *et al.*, 2018), reviews (Nobel & Cui, 1992; Huang &
120 Nobel, 1994; Steudle, 2000a; North & Peterson, 2005; Maurel *et al.*, 2010; Aroca *et al.*,
121 2011; Gambetta *et al.*, 2017; Kim *et al.*, 2018) and the Xylem Functional Traits
122 Database (Choat *et al.*, 2012) to check for missing publications that should be included in our
123 review. In total, we reviewed 241 papers, which comprises the vast majority of experimental

124 studies on root hydraulic properties published between 1973-2023. A complete list of
125 references included in the database is presented in Table S1.

126 **2.2 Root hydraulic properties database**

127 As part of the review process, we created an open access root hydraulic properties database,
128 which aggregates all extracted data. Root hydraulic properties data were extracted manually
129 and the software WebPlotDigitizer (Rohatgi, 2023) was used for digitalizing figures. The
130 database contains detailed references to the original studies and provides easy, systematized
131 access to the following data: root hydraulic properties (K_{rs} , k_{root} , k_r and/or k_x), plant functional
132 type (PFT, Table 2), growth form (a coarser classification than PFT, i.e. tree, shrub, succulent,
133 graminoid and forb), tissue measured (whole root system, individual roots or root segments),
134 root section (whole root or distal, mid-root or basal segments) measurement method, driving
135 force for measurement, and experimental treatment(s) applied. When reported, plant age and
136 morphological data were also included. The values stored in the database correspond to average
137 values per study, species, factor (with factor being one or many among experimental treatment,
138 tissue, root section, measurement method and driving force) and age. This means, for example,
139 that a study reporting on K_{rs} of maize, based on two different measurement methods, with two
140 treatments at three developmental stages generated a total of $1 \times 2 \times 2 \times 3 = 12$ data points.
141 Therefore, the number of data points aggregated to the database from each study varied greatly.
142 All digitized data is available for download in the database repository.

143 Based on the digitalized data, we developed a web application ([https://roothydraulic-
144 properties.shinyapps.io/database/](https://roothydraulic-properties.shinyapps.io/database/)) that facilitates data selection, manipulation, visualization,
145 and download. The main results presented in this study can be reproduced using the dynamic
146 tools included there, and interested users are also encouraged to use these tools for their own
147 research. The root hydraulic properties database, together with the web application, is
148 conceived as a dynamic tool that will be updated continuously with newly reviewed studies.
149 Readers are encouraged to share in the repository their new work or previously published work
150 that may have been overlooked in our review process, by using the data sharing template
151 available in the web application. The data included in the database is provided with free and
152 unrestricted access for scientific (non-commercial) use (ODC-BY 1.0 license). Data users are
153 requested to acknowledge the original data source and reference this review in resulting
154 publications.

155 **2.3 Data analysis and statistics**

156 The data stored in the database was used for a comprehensive analysis on root hydraulic
157 properties variability, excluding data that could not be classified into any PFT (defined as
158 “Other”, see Table 2). The data was highly imbalanced, and there were large differences in the
159 number of studies and species investigated for the different PFTs and root hydraulic properties.
160 Accordingly, appropriate data analysis methods had to be selected. Although applying a strict
161 meta-analysis (Hedges *et al.*, 1999) could have been reasonable for this purpose, we discarded
162 this approach because of two reasons: too few articles reported all the information needed for
163 performing a meta-analysis (i.e., sample size and standard deviations for each experimental
164 factor); and the experimental factors varied extremely among studies (Table S1), which
165 hampered an evaluation of their individual effects and interactions. Instead, we followed an *ad-*
166 *hoc* step-wise approach, and performed a series of independent analyses that quantified the
167 variability in root hydraulic properties observed across studies and evaluated some of the (most
168 important) factors causing it (see Table 3 for factor description). This analysis was performed
169 for all individual root hydraulic properties except for k_r , for which a very limited number of
170 species and studies ($n=12$, in both cases) was available. Due to the large skewness in the
171 original data, values were log transformed before data analysis, and then back transformed.
172 Thus, the presented results correspond to geometric averages. Approximate standard deviations
173 and standard errors were calculated using the Delta Method (Cramér, 1999).

174 In a first step, we calculated the range of variation (i.e., minimum, mean and maximum values)
175 for each of the PFTs described in Table 2. For this, we first calculated the geometric means for
176 the different studies and of each species investigated. These values were considered
177 independent and suited for the analysis and were used for the calculation of the range of
178 variation. The results corresponded to geometric means and range of variation for each PFT
179 and root hydraulic property investigated (3.1).

180 Secondly, Random Forest (RF) models were run and the drop in accuracy of the model –a
181 permutation feature importance metric (Altmann *et al.*, 2010)– was calculated to rank the
182 importance of several factors on the variability of root hydraulic properties. Next, linear mixed
183 models were fitted to test for significant differences in root hydraulic properties among PFTs.
184 PFT and two other highest ranked factors according to the RF model (excluding taxonomical
185 features) were defined as the fixed effects, and study and experimental treatment were defined
186 as the random effects. Given the extremely large dissimilarity in experimental designs among
187 publications (see Table S1 for treatment list), we simplified the factor experimental treatment
188 to four levels: control (defined as such in the publications), stress (any treatment that causes

189 stress, e.g., drought, salt stress, nutrient limitation), other (any treatment that cannot be strictly
190 defined as control or stress. e.g., different soil types, genotypes, season) and no treatment
191 (studies where no treatments were applied). Type III ANOVA with the Satterthwaite's method
192 (Luke, 2017) was used for evaluating factor significance. The R-packages randomForest (Liaw
193 & Wiener, 2002) and lme4 (Bates *et al.*, 2015) were used for fitting the models.

194 Finally, we evaluated in more detail three factors that have been repeatedly reported to affect
195 root hydraulic properties: driving force used for measurement, drought stress, and aquaporin
196 (AQP) inhibition (see e.g., Aroca *et al.*, 2011; Gambetta *et al.*, 2017; Kim *et al.*, 2018). For
197 this, the natural log response ratio ($\ln(r) = \ln(\text{treatment}) - \ln(\text{control})$) (Hedges *et al.*, 1999) was
198 calculated for each individual study and species in which root hydraulic properties were
199 measured under both treatment and control conditions. The results were reported as the mean
200 percentage change $((r - 1) * 100)$ (Ainsworth & Long, 2005) and response significance was
201 tested with one-sample t-tests (on the log transformed data). Differences in the responses
202 among PFTs were evaluated with one-way ANOVA tests. All data and statistical analyses were
203 conducted in R v.4.3.1 (R Core Team, 2023).

204 **2.4 Modelling the relationship between K_{rs} and root system age**

205 The results of the RF and linear mixed models (see Section 3.2) indicated a significant and
206 (probably) non-linear relationship between root system age and K_{rs} (and K_{rs_area}). To investigate
207 this relationship in more detail, we modeled the response of K_{rs} to the increase in root system
208 age (and size) over time, using the functional-structural plant models CPlantBox (Schnepf *et*
209 *al.*, 2018) and MARSHAL (Meunier *et al.*, 2019). Because data on root age was extremely
210 scarce for trees and shrubs (see Table 3), this analysis was restricted to crop species
211 (herbaceous crops and grasses).

212 CPlantBox was used to simulate the root system development of four different crops over a
213 120-day period: a C_3 grass (wheat), a C_4 grass (maize), a forb (cauliflower) and a legume
214 (soybean). The species were selected based on plant-functional diversity and data availability.
215 The XML-input parameters were obtained from the literature (Leitner *et al.*, 2010;
216 Vansteenkiste *et al.*, 2014; Moraes *et al.*, 2020; Morandage *et al.*, 2021). CPlantBox outputs
217 (i.e., the root architecture at each time step) were coupled to MARSHAL to simulate water
218 flow from the soil-root interfaces to xylem vessels at the plant collar, using the analytical
219 solution of water flow within infinitesimal subsegments (Meunier *et al.*, 2017b), and to
220 calculate the macroscopic parameter K_{rs} (Couvreur *et al.*, 2012). Segment-scale k_r and k_x values

221 were extracted from the database and from modelling (Doussan *et al.*, 1998) and used to
222 parametrize MARSHAL. k_r and k_x are age-dependent and vary among root types (Figure S1).
223 To account for the uncertainty in their parameterization, a sensitivity analysis was performed
224 by varying k_r , k_x or the k_r/k_x within the range of variation and the spatial heterogeneity observed
225 in the literature (Figure S1). Modeled K_{rs} corresponds to the mean \pm standard error of all
226 simulations, for each individual crop. Modeling results were contrasted with data gathered from
227 the review, specifically for crop species (dicot crops and C₃ and C₄ grasses) measured using a
228 hydrostatic driving force.

229 **3 Results and discussion**

230 **3.1 Range of variability of root hydraulic properties**

231 In this work, we reviewed a total of 241 root hydraulic properties publications, comprising 215
232 species from 124 genera (complete list of references and species in Table S1). From this total,
233 165 studies focused on K_{rs} , 60 on k_{root} (including k_r) and 46 on k_x (some studies measured
234 multiple hydraulic properties, simultaneously). We observed an extremely large range of
235 variation (of orders of magnitude) in all root hydraulic properties, whereby this was especially
236 pronounced for K_{rs} (Figure 2).

237 Reported K_{rs} values varied extremely across studies, species, and plant functional types,
238 ranging between 3.1×10^{-12} (measured in barley) to $9.4 \times 10^{-8} \text{ m}^3 \text{ MPa}^{-1} \text{ s}^{-1}$ (measured in
239 common bean). A very large range of variation was also observed within PFTs, with K_{rs}
240 showing a range of variation of ≈ 2 – 3 orders of magnitude in all PFTs, except for shrubs (for
241 which only two studies were available). This was considerably larger than the differences in
242 the geometric means among PFTs, which varied between 4.1×10^{-10} (C₃ grasses) and 4.8×10^{-9}
243 $\text{m}^3 \text{ MPa}^{-1} \text{ s}^{-1}$ (woody crops). Due to the very large intra-PFT variability, possible systematic
244 differences among PFTs could have been obscured (but see 3.2.1).

245 K_{rs} is often reported in the literature on the basis of a measure of root size, to facilitate the
246 comparison among plants of different age, with root surface area (K_{rs_area}) being the
247 normalization most widely used (see Table 1 for other common normalizations). Our results
248 indicated that the range of variation of K_{rs_area} was indeed factors of magnitude smaller than
249 that of K_{rs} , but it was still extremely large ($1.2 \times 10^{-9} - 4.3 \times 10^{-6} \text{ m MPa}^{-1} \text{ s}^{-1}$) (Figure 2). A very
250 large range of variation was also observed within each PFT (≈ 1 – 3 orders of magnitude),
251 indicating large intrinsic differences among species and/or experimental design of the studies.
252 Surprisingly, even, both the lowest and the highest K_{rs_area} values found in the literature

253 corresponded to broadleaf tree species (*Q. petraea* and *P. tremula* × *tremuloides*). On the
254 contrary, the geometric mean of K_{rs_area} varied comparatively slightly among PFTs (3.3×10^{-8} –
255 1.0×10^{-7} m MPa⁻¹ s⁻¹).

256 Published root hydraulic properties data of individual roots and/or root segments (total, radial,
257 and axial) also showed very large variability. The total conductance k_{root} (which is often
258 reported as a proxy of k_r in the literature) varied extremely across studies (range = 4.7×10^{-9} –
259 1.2×10^{-5} m MPa⁻¹ s⁻¹, Figure 2), but also within individual PFTs (ranges ≈ 1–3 orders of
260 magnitude). This large variation was observed despite the few species that have been
261 investigated (2–6 species for the different PFTs). Additionally, the geometric means
262 of k_{root} showed small variation among PFTs (3.4×10^{-8} – 1.8×10^{-7} m MPa⁻¹ s⁻¹), and this range
263 was almost identical to that of K_{rs_area} .

264 Axial conductance also showed a very large variability, both for published data reported
265 as k_x (range = 3.1×10^{-13} – 3.5×10^{-9} m⁴ MPa⁻¹ s⁻¹) and on a cross sectional area basis (k_{x_cs} , range
266 = 1.1×10^{-7} – 2.7×10^{-1} m² MPa⁻¹ s⁻¹). However, we found very few studies on k_x (20
267 publications), and they were unevenly distributed across PFTs. While succulent species were
268 the most frequently reported (7 studies, 5 species), only one tree species was available and
269 showed by far the largest k_x (1-3 order of magnitudes larger than any other value). Excluding
270 that species, k_x ranged between 3.1×10^{-13} – 3.0×10^{-10} m⁴ MPa⁻¹ s⁻¹, with C₄ grasses showing the
271 lowest (5.5×10^{-12} m⁴ MPa⁻¹ s⁻¹) and dicot crops the highest (2.4×10^{-11} m⁴ MPa⁻¹ s⁻¹) geometric
272 means among PFTs. At the same time, k_{x_cs} has been widely reported for woody vegetation (26
273 publications, 105 species) and showed a range of variation between 2.2×10^{-4} – 2.7×10^{-1}
274 m² MPa⁻¹ s⁻¹, with tropical trees showing the highest values. These values were systematically
275 higher than k_{x_cs} of the very few non-woody species for which data was available (8 species,
276 range = 1.1×10^{-7} – 1.1×10^{-4} m² MPa⁻¹ s⁻¹) and confirm the results from previous
277 meta-analyses (Bouda *et al.*, 2018). However, our review also highlights the difficulty of
278 comparing axial conductance of woody and non-woody vegetation, with the former almost
279 entirely being reported as k_{x_cs} and the latter as k_x .

280 **3.2 Understanding root hydraulic properties variability**

281 The results in Section 3.1 showed an extremely large range of variation in root hydraulic
282 properties across published studies. Here, we further investigated to which degree the observed
283 variability could be explained by the response of root hydraulic properties to the following

284 factors: systematic differences among PFTs, driving force used for measurement (hydrostatic
285 or osmotic), effect of environmental stresses, and root system age.

286 3.2.1 Main factors affecting root hydraulic properties and differences among PFTs

287 One central question we addressed in this study was whether the observed variability in root
288 hydraulic properties could be attributed to systematic differences among PFTs. For this, we
289 first used Random Forest (RF) regressions to compare the importance of PFT with other
290 variables that have been reported to affect root hydraulic properties. This included factors such
291 as root system age, the driving force used for measurement (hydrostatic or osmotic), root
292 section and root type, experimental treatment, or variation within species. According to the
293 “drop in accuracy” metric (Table 4, more details in 2.3), root system age had the highest
294 importance to explain the variability in K_{rs} , which agrees with the general positive relationship
295 between K_{rs} and root system size observed in the literature (Tyree, 2003). This is the case, as
296 with increasing age the root system grows, adding conductances (new root segments) in parallel
297 in a hydraulic network, which increases the total conductance of that network. Interestingly,
298 root system age also showed the highest importance for K_{rs_area} , suggesting complex
299 interactions between root system growth and K_{rs} development (see 3.2.4 for further discussion).
300 The importance of PFT for K_{rs} was 27.4% smaller (and 26.9% smaller for K_{rs_area}) than that of
301 root system age and was similar to the importance of driving force or species and only clearly
302 larger than that of experimental treatment (Table 4). These results indicate that the large
303 variability of K_{rs} observed in the literature cannot be explained by systematic differences
304 among PFTs, alone, but rather by the added effect of multiple factors.

305 We also analyzed the importance of PFT for k_{root} (Table 4) and observed that it was lower than
306 the importance of driving force (-4.2 %) and slightly higher to that of species, root type
307 (seminal, adventitious, lateral) or root section (distal, mid-root, basal or entire root). This
308 suggests that the observed variability of k_{root} is caused by the added effect of multiple factors
309 and their interactions, rather than by systematic differences among PFTs. However, care must
310 be taken in the interpretation of these results, due to the rather small number of species
311 investigated (26) and the extremely low number of studies (5) in which species belonging to
312 different PFTs were investigated simultaneously. On the contrary, the importance of PFT
313 for k_{x_cs} variability was much larger (at least more than twice) than that of any other factor,
314 except for growth form, confirming the clear, systematic difference between woody and non-
315 woody species depicted in Figure 2 and the observations of Bouda *et al.* (2018). These results
316 are probably associated with large increases in axial conductance (2-3 orders of magnitude)

317 following secondary growth in woody roots (Vercambre *et al.*, 2002) and with large differences
318 in xylem cross sections between woody and non-woody vegetation.

319 To confirm the results of the RF models and further investigate systematic differences in root
320 hydraulic properties among PFTs, individual linear mixed models for K_{rs} , K_{rs_area} , k_{root} and k_{x_cs}
321 were run, with PFT and additional non-taxonomical features (i.e. root system age, driving
322 force, root section or root type, detailed factor and model description in Section 2.2–2.3) as
323 fixed effects, and study and treatment as random effects.

324 We found no significant effect of PFT on K_{rs} ($p = 0.20$), K_{rs_area} ($p = 0.84$) and k_{root} ($p = 0.92$),
325 but k_{x_cs} varied highly significantly ($p < 0.001$) among PFTs (Table 4), which agrees with the
326 results of the RF analysis and its conclusions. On the contrary, a highly significant effect of
327 driving force ($p < 0.001$) on K_{rs} , K_{rs_area} and k_{root} was found, indicating systematic difference in
328 root hydraulic properties measured using a hydrostatic driving force, against those using an
329 osmotic driving force (see 3.2.2 for a detailed analysis). Additionally, root system age showed
330 a highly significant positive effect on K_{rs} ($p < 0.01$), probably associated with an increase
331 of K_{rs} with increasing root system size. Conversely, root system age had no effect on K_{rs_area}
332 ($p = 0.38$), contradicting the high importance that root age had for K_{rs_area} prediction, according
333 to the RF model. Interestingly, though, the linear mixed model showed a negative (albeit non-
334 significant) relationship between K_{rs_area} and root age and this negative relationship became
335 significant ($p < 0.05$) when a negative exponential function was fitted to the data, instead of a
336 linear relationship. This implies a decrease in K_{rs} per unit root surface over time, a phenomenon
337 that could be associated with the decrease in segment-scale radial conductivity with age, but
338 also with axial transport limitation with increasing root length (Meunier *et al.*, 2017b; Bouda *et*
339 *al.*, 2018, see also discussion in Section 3.2.4). Clearly, the relationship between root age
340 and K_{rs} (and K_{rs_area}) observed in our review is complex and was therefore explored in more
341 detail in section 3.2.4.

342 The linear mixed models also showed a highly significant ($p < 0.001$) effect of root section—a
343 factor describing whether root hydraulic properties were measured on basal, mid-root or distal
344 root segments or on entire roots—on k_{root} and k_{x_cs} , suggesting the presence of spatial gradients
345 in roots across species and PFTs. Spatial variation alongside roots in k_r and k_x (and
346 consequently in k_{root}) has been reported for the grass species maize (Frensch & Steudle,
347 1989; Doussan *et al.*, 1998; Meunier *et al.*, 2018) and barley (Knipfer & Fricke, 2011) and
348 for *A. deserti* (Huang & Nobel, 1992), with radial conductivity decreasing from root tip to root
349 base, while the opposite was the case for axial conductance (see also Figure S1). Variation can

350 be caused by changes in root anatomy and function (e.g., formation of apoplastic barriers,
351 increase in xylem diameter and density, differences in aquaporin expression) with increasing
352 age. However, similar gradients were not evident (particularly in the case of k_r and k_{root}) in
353 onion (Melchior & Steudle, 1993) or lupin (Doussan *et al.*, 2006; Meunier *et al.*, 2018),
354 questioning the idea that they are ubiquitous across species and PFTs. Our review cannot
355 answer this, because most of the studies reported data for one root section only, hampering
356 systematic comparison among sections. For instance, the two largest k_{root} values in our review
357 (1.2×10^{-5} in *V. faba* and 7.4×10^{-6} in *P. trichocarpa x deltoides*) corresponded to measurements
358 in distal segments, but unfortunately no other root section was investigated in those studies.
359 Nevertheless, the statistical results underscore the significance of spatial gradients as a factor
360 of variability in root hydraulic properties and stress the need for further investigations on this
361 topic, focusing on the differences (or lack thereof) among species from different PFTs.

362 In general, the statistical analyses did not reveal systematic differences in root hydraulic
363 properties among PFTs, apart from the highly significant effect of PFT on axial conductance,
364 a feature that has been reported previously. Rather, the results imply that the variation in
365 multiple factors such as age, driving force, or root section analyzed (and probably their
366 interactions) determined the extremely large variability observed here. This would also explain
367 why root hydraulic properties varied so much within PFTs (Figure 2) or even within species.
368 Accordingly, a detailed analysis on the influence of several factors on root hydraulic properties
369 variability (with the main focus on K_{rs}) was also performed in this review, and the results are
370 presented in the following sections (3.2.2 – 3.2.4).

371 To our knowledge, this is the first systematic review on the topic of root hydraulic properties
372 and their variability across PFTs, leaving little room for the comparison of our results with
373 previous investigations. However, we cannot discard the possibility that systematic differences
374 among PFTs –which we did not find– were obscured by the dissimilarity in experimental
375 design among the publications. Actually, less than 10% of the reviewed studies included
376 species corresponding to more than one PFT, and the hydraulic properties investigated there
377 were unevenly distributed: while K_{rs} and k_{root} studies mostly focused on dicot and monocot
378 crop species (Gallardo *et al.*, 1996; Bramley *et al.*, 2007; e.g. Hess *et al.*, 2015), broadleaf and
379 needle trees were predominant in k_x (or rather k_{x_cs}) studies (e.g. Maherali *et al.*, 2006; Domec
380 *et al.*, 2010). In fact, we only found one study in which root hydraulic properties of trees and
381 herbaceous vegetation were measured simultaneously (Rieger & Litvin, 1999). Thus, more

382 studies comparing root hydraulic properties across species and PFTs are needed to confirm (or
383 reject) the results in this review.

384 3.2.2 *The driving force matters*

385 According to the results from the previous section, the driving force used for measurement was
386 a key factor for explaining the very large variability observed in this review. Here, we
387 quantified in more detail the differences in root hydraulic properties
388 (specifically K_{rs} and k_{root} ; k_x data is not relevant for this analysis) estimated under osmotic
389 gradients (hereafter osmotic root hydraulic properties), compared to those estimated under
390 hydrostatic gradients (hereafter hydrostatic root hydraulic properties), based on the log
391 response ratio of pairwise comparisons (methodological details in 2.3).

392 A total of 39 data pairs, corresponding to 29 studies and 16 species were investigated, whereby
393 only four species (maize, barley, rice, and wheat) accounted for >60% of all values (see Table
394 S2 for all studies and species included). On average, osmotic root hydraulic properties were
395 78.1% smaller than hydrostatic ones, and this effect was highly significant ($p < 0.001$). More
396 interestingly, the observed response varied significantly among PFTs ($p < 0.001$), showing
397 average decreases ranging from 42.6% (C_3 grasses) to 94.9% (broadleaf trees). In that,
398 C_3 grasses showed a much lower decrease compared to the remaining PFTs, which varied very
399 slightly among each other (range = 94.9 – 85.4%; woody crops were not included in this
400 comparison, because only one value was available). For all PFTs, the reported decrease in
401 osmotic root hydraulic properties (Figure 3) was significantly different from zero ($p < 0.05$).

402 Clearly, the driving force affects the measurements of root hydraulic properties. Across all
403 studies, the largest difference was observed in K_{rs} of oak trees and reached almost two orders
404 of magnitude (Steudle & Meshcheryakov, 1996). On average, a decrease of $\approx 78\%$ of osmotic
405 compared with hydrostatic root hydraulic properties was observed, and in four PFTs (broadleaf
406 and needle trees, C_4 grasses and dicot crops) a decrease of $\approx 90\%$ (i.e., 1 order of magnitude)
407 was reached. Considering that the total range of variation within PFTs was $\approx 1-3$ orders of
408 magnitude (Figure 2), the driving force can be described as one of the most important factors
409 for explaining the variability in root hydraulic properties reported in this review.

410 That osmotic root hydraulic properties are systemically lower than hydrostatic ones has been
411 reported before (Steudle, 2000a; Kim *et al.*, 2018). In line with the principles of the composite
412 transport model (Steudle, 2000a), the comparison between osmotic and hydrostatic root
413 hydraulic properties has been widely used to differentiate the cell-to-cell path (obtained from

414 osmotic measurements) from the overall path for water flow (i.e. cell-to-cell + apoplastic paths,
415 obtained from hydrostatic measurements) and how the contribution of the former might change
416 under conditions of environmental stress (see e.g. Garthwaite *et al.*, 2006; Barrios-Masias *et*
417 *al.*, 2015; Kreszies *et al.*, 2020). According to this approach, our results would imply that the
418 cell-to-cell path had a (much) smaller contribution than the apoplastic path to the total water
419 flow across PFTs, with the cell-to-cell contribution to total water flow being the lowest in
420 broadleaf trees (4.9%) and the highest in C₃ grasses (36.5%). However, the accuracy of this
421 approach has been questioned (Chaumont & Tyerman, 2014), as multiscale studies do not
422 support this common assumption and rather indicate that the differences between osmotic and
423 hydrostatic root hydraulic properties may stem from an erroneous estimation of the osmotic
424 driving pressure and therefore of hydraulic properties (Bramley *et al.*, 2007; Couvreur *et al.*,
425 2018). Cell-scale simulations of the advection-diffusion of osmolytes suggest that their
426 accumulation at apoplastic barriers (e.g. Casprian strip) may alone generate a 5-fold
427 overestimation of the effective water potential gradient across the endodermis (Knipfer &
428 Fricke, 2011, Steudle, 2008; Couvreur *et al.*, 2018), while apoplastic, symplastic and
429 transmembrane modes of water transport would vary radially regardless of whether the water
430 potential difference between root surface and xylem is due to pressure or osmolytes.
431 Nevertheless, the data clearly showed a differentiation between C₃ grasses and the remaining
432 PFTs, and also very large discrepancies within the C₃ grasses: while osmotic and hydrostatic
433 root hydraulic properties were almost equal in barley ($\approx 6\%$ higher osmotic root hydraulic
434 properties, in average), osmotic root hydraulic properties were much smaller than hydrostatic
435 ones in wheat and rice ($\approx 55\%$ and $\approx 63\%$ in average, respectively). To which degree these
436 differences indicate functional heterogeneity in water transport patterns among species lies
437 beyond the scope of this review, but the data presented here could be used to identify species
438 or PFTs of interest for future studies.

439 *3.2.3 Responses to drought and AQP inhibition*

440 Environmental stress has been widely reported as a factor affecting root hydraulic
441 properties (Steudle, 2000b; Maurel *et al.*, 2010; Aroca *et al.*, 2011; Gambetta *et al.*, 2017).
442 Interestingly, though, our analysis showed that experimental treatment had the lowest
443 importance of all variables in explaining the range of variation in K_{rs} , K_{rs_area} , k_{root} and k_{x_cs}
444 observed in the literature (Table 4). Two aspects could explain these results: (1) the variation
445 across studies and PFTs was so large, that it obscured the effects of experimental treatments
446 observed in individual studies; and (2) experimental treatments differed extremely among

447 studies (Table S1), hindering a systematic analysis of the effect of environmental stress on root
448 hydraulic properties variability. Thus, for the purpose of this review, the response of root
449 hydraulic properties to stress was narrowed to two factors: drought stress and aquaporin (AQP)
450 inhibition. For this, 28 studies on the effect of drought stress and 19 studies on the effect of
451 AQP inhibition on K_{rs} (or its normalized values) were analyzed.

452 There was a significant decrease in K_{rs} under both drought stress and AQP inhibition ($p < 0.001$
453 in both cases). On average, K_{rs} decreased 61% under drought conditions and the decrease under
454 AQP inhibition was very similar (59%). However, the K_{rs} response to drought showed more
455 variation across PFTs, studies or species than that to AQP inhibition. The average K_{rs} decrease
456 under drought varied among PFTs in a range between 80.8% (in dicot crops) and 38.3% (in
457 C_3 grasses), and this variation was marginally significant ($p = 0.07$) (Figure 4). Meanwhile,
458 K_{rs} decreased under AQP inhibition in a smaller range between 50.9% (in tropical trees) to
459 77.4% in (C_4 grasses) ($p = 0.16$). Also, across all studies and species ($n=30$), the K_{rs} response
460 to drought varied greatly, between $\approx 98\%$ decrease (i.e., a decline of almost two orders of
461 magnitude) and $\approx 35\%$ increase. On the contrary, K_{rs} responded negatively to AQP inhibition,
462 without exception ($n=25$), with the decrease ranging between $\approx 22\%$ – 86% .

463 The average decline in K_{rs} under drought agrees with the conclusions of previous
464 reviews (Aroca *et al.*, 2011). This response corresponds to a water saving strategy under
465 condition of limited water availability, which can be induced by short-term responses
466 (e.g., changes in the aquaporin gating), but also on long-term drought-driven anatomical
467 changes (e.g., formation of apoplastic barriers, aerenchyma, changes in xylem vessel size) or
468 changes in root size (Aroca *et al.*, 2011; Vadez, 2014; Bauget *et al.*, 2023). Furthermore, our
469 review revealed differences among PFTs (albeit non-significant, probably due to a small
470 sample size), with grasses (both C_3 and C_4) showing a weaker response to drought than trees
471 or dicot crops. In fact, the only three studies in which an increase in K_{rs} under drought was
472 reported, were conducted with rice (Lian *et al.*, 2004; Ding *et al.*, 2015) and maize (Zhang *et*
473 *al.*, 1995). Also, the K_{rs} decrease of maize (C_4 grass, $\approx 44\%$) under drought was considerably
474 weaker than that of tomato (dicot crop, $\approx 63\%$), in the only study where grass and non-grass
475 species were directly compared (Bárzana *et al.*, 2012), supporting the overall trends reported
476 here. However, the shown differences among PFT might be conditioned by the low number of
477 species investigated within each PFT. For example, in the case of C_3 grasses seven out of 9
478 studies were conducted with rice, and a similar behavior was observed for C_4 grasses (all 4
479 studies with maize) or dicot crops (4 out of 7 studies with tomato). But, regardless of these

480 limitations, our results contribute to a better understanding of the expected root hydraulic
481 properties variability under drought conditions across species and PFTs.

482 On the other hand, a negative response of K_{rs} to AQP inhibition was observed across all PFTs
483 and species investigated. This effect is driven by a decrease in the cell-to-cell radial water
484 flow (Aroca *et al.*, 2011; Chaumont & Tyerman, 2014), such that the large range
485 in K_{rs} responses to AQP inhibition ($\approx 22\%$ – 86% decrease across studies) could be associated
486 with differences in aquaporin activity of root cells among the investigated species and PFTs.
487 However, we did not observe systematic differences among PFTs in our analysis. In a previous
488 review on aquaporins and root water uptake, Gambetta *et al.* (2017) also identified a very large
489 range in the response of root hydraulic properties to AQP inhibition, and mainly attributed this
490 to variability in the experimental approach across studies. As such, further examinations of the
491 responses exhibited by distinct tissues, species, and/or plant functional types (PFTs) are
492 essential to enhance our understanding of water flow dynamics under stress conditions, and
493 how this might impact the overall variability of root hydraulic properties.

494 3.2.4 Non-linear K_{rs} increase with increasing root system age in crops and grasses

495 Root system age is a key factor for explaining the large variability in K_{rs} observed in this review
496 (see 3.2.1). Here, we investigated this relationship in more detail, for hydrostatic K_{rs} of dicot
497 crops and grass species (selection criteria described in 2.4). Across studies and species, there
498 was a significant increase in K_{rs} with increasing age of the root system ($p < 0.01$), with the
499 relationship exhibiting a non-linear pattern (Figure 5). K_{rs} increased abruptly during the first
500 20–30 days of root development, and then slowly flattened out, with a total range of variation
501 between $\approx 6 \times 10^{-11} - 2 \times 10^{-8} \text{ m}^3 \text{ MPa}^{-1} \text{ s}^{-1}$. The steep increase in K_{rs} during the first days of
502 development is probably caused by the growth of the root system adding new conductances
503 (new roots) to the root hydraulic network, thus increasing the total conductance of the network.
504 However, the asymptotic behaviour after days 30-40 suggests a partial decoupling between
505 root size and K_{rs} at later stages of development. Unfortunately, root size data (e.g., root surface
506 area or total root length) was not reported ubiquitously across studies, impeding the analysis of
507 the interactions between K_{rs} , root age and root size. Interestingly, though, an analogous
508 asymptotic relationship between root length and K_{rs} has been previously reported in a
509 modelling study (Meunier *et al.*, 2017a).

510 To explore the K_{rs} development with age in more detail, we modeled this relationship for four
511 selected crop species, using CPlantBox coupled with MARSHAL (see 2.4 for details on data

512 selection and model parametrization). Despite large differences in root size and root
513 architecture (Figure S2), all species exhibited a very similar non-linear pattern, i.e., a
514 pronounced increase in K_{rs} with age during the first 20 days, followed by rather constant values
515 from day 20 onwards (Figure 6). This behaviour was not related to cessation in root growth, as
516 total root length showed a continuous increase during the 120 days of simulation (Figure S2).
517 But, with increasing root age the proportion of “old” root segments (> 10-day old segments)
518 also increased (Figure 6). This could have impacted the development of K_{rs} , as the radial (k_r)
519 and axial (k_x) hydraulic properties of root segments –which, together with the root architecture,
520 determine K_{rs} – are age dependent (Doussan *et al.*, 1998). Specifically, k_r strongly decreases
521 with age (Figure S1), and the radial pathway is commonly considered to be the more limiting
522 one for water transport (Frensch & Steudle, 1989; Lynch *et al.*, 2014). Thus, the counteracting
523 effect of an increase in less conductive tissues (i.e., older root segments) proportionally to total
524 root growth would explain the constancy in K_{rs} at later stages of development. Additionally, it
525 has been shown that even under constant k_r and k_x , K_{rs} can display an asymptotic behavior for
526 roots due to axial flow limitations with increasing root length (Meunier *et al.*, 2017a).
527 Furthermore, the modeled K_{rs} response to age strongly resembled the one observed in the
528 empirical data. In fact, average K_{rs} values at different ages obtained from the review lay within
529 (or very near) the range of variation of the models (Figure 7), indicating that the modelling
530 results were representative of common patterns across studies and species. Whether the
531 mechanisms observed in the models also explain the patterns evidenced in the review remains
532 to be investigated.

533 The non-linear relationship between K_{rs} and root system age presented here has been reported
534 previously. For instance, a similar pattern was observed in a modelling study with 10,000
535 virtual maize root systems (Meunier *et al.*, 2019). However, our work is the first –at least to
536 our knowledge– to demonstrate a common pattern across studies and species in both
537 experimental data and modelling and to quantify the associated range of variation in K_{rs} over
538 time. Also, the combination of literature data and modelling gave insights about the (possible)
539 causes for the emerging patterns. These results are therefore of relevance and can be a valuable
540 input for the description of root water uptake processes at plant, field or regional
541 scales (Couvreur *et al.*, 2014; Sulis *et al.*, 2019; Nguyen *et al.*, 2020; Vanderborght *et al.*,
542 2021; Nguyen *et al.*, 2022; Jorda *et al.*, 2022).

543

544 **4 Conclusions and outlook**

545 Here, we presented an extensive review on root hydraulic properties, their variability and some
546 of the factors affecting them. A very large range of variation (orders of magnitude)
547 in K_{rs} , k_{root} , k_r and k_x reported in the literature was identified, but this was not caused by
548 systematic differences among plant functional types (with the only exception of significant
549 differences between axial conductance of woody vs. non-woody species), but rather by the
550 (combined) effect of factors such as root system age, driving force used for measurement, root
551 tissue measured, environmental stress or intra-specific variation. As a result, a closer
552 examination was undertaken to explore the influence of some of these factors on root hydraulic
553 properties. This yielded new insights on root hydraulic properties variability, some of which
554 could not be analyzed here in detail, due to the inherent limitations of a broad review, but
555 should be targeted specifically in future studies. The following topics are of special interest:
556 (1) the difference between osmotic and hydrostatic root hydraulic properties was much lower
557 in C_3 grasses (particularly in barley) than in other PFTs; how is this reflected in the water
558 transport patterns of these species?; (2) a large range of variation was observed in the response
559 of root hydraulic properties to drought, with some indications of differences among PFTs, but
560 clear conclusions were hindered by the extremely low number of studies comparing multiple
561 species and PFTs. Hence, do species corresponding to different PFTs (e.g. dicot crops
562 vs. grasses) respond differently to drought under the same environmental conditions?; and (3)
563 a common non-linear relationship between root system age and K_{rs} was identified for several
564 crop species, according to both literature data and modelling. Is such a pattern also present in
565 species from other PFTs (e.g., shrubs or young trees) and how is it reflected in the seasonality
566 of perennial species?

567 In summary, the present study represents an overview of root hydraulic properties variability
568 across plant functional types, species and experimental conditions and their associated
569 responses. The new insights obtained here, together with the accompanying data (stored in a
570 database and easily accessible through the web application, [https://roothydraulic-
571 properties.shinyapps.io/database/](https://roothydraulic-properties.shinyapps.io/database/)) and additional tools like modelling –as we applied in this
572 study– should be a valuable input for future studies on the role of root hydraulics and root water
573 uptake processes under changing environmental conditions.

Author contributions

JCBC: Conceptualization, Software, Formal Analysis, Investigation, Data Curation, Visualization, Writing - original draft, Writing - review and editing

JV: Formal Analysis, Funding Acquisition, Writing - review and editing

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TG: Funding Acquisition, Writing - review and editing

THN: Writing - review and editing

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Conflict of interest statement

No conflict of interest declared

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Tables and Figures

Table 1: Root hydraulic properties definitions

Symbol	Definition	Tissue level	Units	Alternative symbols used in the literature	Specification
k_r	Radial hydraulic conductivity	Individual roots or root segments	$\text{m MPa}^{-1} \text{ s}^{-1}$	L_r (Huang & Nobel, 1994; North & Peterson, 2005; Doussan <i>et al.</i> , 2006)	Usually not directly measured, but calculated using k_{root} and k_x measurements, based on the model of Landsberg & Fowkes (1978).
k_x	Specific axial hydraulic conductance	Individual roots or root segments	$\text{m}^4 \text{ MPa}^{-1} \text{ s}^{-1}$	K_h (Huang & Nobel, 1994; North & Peterson, 2005; Doussan <i>et al.</i> , 2006); K_x (Ahmed <i>et al.</i> , 2018); L_x (Frensch & Steudle, 1989; Melchior & Steudle, 1993)	The ability of roots to transport water longitudinally
k_{x_cs}	k_x normalized by cross sectional area	Individual roots or root segments	$\text{m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$	K_s (Pratt <i>et al.</i> , 2007; Choat <i>et al.</i> , 2012)	k_x data for woody species is very commonly reported on a cross sectional area basis (sapwood, stele, total root cross section)
k_{root}	(Total) root hydraulic conductivity	Individual roots or root segments	$\text{m MPa}^{-1} \text{ s}^{-1}$	L_{pr} (Steudle, 2000a; Kim <i>et al.</i> , 2018; Boursiac <i>et al.</i> , 2022b); L_p (Huang & Nobel, 1994; North & Peterson, 2005; Gambetta <i>et al.</i> , 2017; Lambers & Oliveira, 2019)	The total water transport capacity of an individual root or a root segment. It can be separated into its radial and axial components. Often assumed to be an approximation of k_r in the literature (i.e. water transport only limited by k_r , not by k_x)
K_{rs}	Whole root system conductance	Entire root system	$\text{m}^3 \text{ MPa}^{-1} \text{ s}^{-1}$	K_{root} (Cai <i>et al.</i> , 2022); L_p (Lambers & Oliveira, 2019); L_{pr} (Steudle, 2000a; Kim <i>et al.</i> , 2018), L_0 (Maurel <i>et al.</i> , 2010; Tyerman <i>et al.</i> , 2017; Boursiac <i>et al.</i> , 2022b)	The water transport capacity of the entire root system.
K_{rs_norm}	K_{rs} normalized by a measure of the root system size	Entire root system	Depends on normalization		Most common normalizations found in the literature include: Root surface area: K_{rs_area} ($\text{m MPa}^{-1} \text{ s}^{-1}$) Root fresh or dry weight: K_{rs_weight} ($\text{m}^3 \text{ MPa}^{-1} \text{ s}^{-1} \text{ g}^{-1}$) Root length: K_{rs_length} ($\text{m}^3 \text{ MPa}^{-1} \text{ s}^{-1} \text{ m}^{-1}$) Root volume: K_{rs_vol} ($\text{m}^3 \text{ MPa}^{-1} \text{ s}^{-1} \text{ m}^{-3}$)

Table 2: Plant functional type (PFT) classification. Selected PFTs and corresponding number of species, genera and studies for which root hydraulic properties were investigated. PFTs were defined based on commonly used classifications in land surface models (Poulter *et al.*, 2015), and additional features such as growth form, differentiation between woody and herbaceous vegetation and agronomical importance.

PFT	Description	Species examples	Nr. species	Nr. genera	Nr. studies
Crop herbaceous	Herbaceous crop species (legumes and non-legumes), excluding all C ₃ and C ₄ grasses	Tomato, soybean, lupin	23	17	50
Crop woody	Woody crop species	Cotton, grapevine	2	2	11
C ₃ grass	Grass species with a C ₃ photosynthetic pathway. Most species investigated corresponded to grasses used as crops	Barley, rice, wheat	9	7	50
C ₄ grass	Grass species with a C ₄ photosynthetic pathway. All species investigated corresponded to grasses used as crops	Maize, sorghum, pearl millet	4	4	40
Broadleaf tree	Deciduous and evergreen broadleaf tree species, including fruit trees	Quercus spp., Populus spp., Apple	64	30	54
Needle tree	Deciduous and evergreen needle tree species	Pinus spp., Picea spp., Abies spp.	39	12	28
Tropical tree	Broadleaf tree species from tropical ecosystems	Piper spp., Shorea spp.	37	31	9
Shrub	Deciduous and evergreen shrub species	Juniperus spp., Rhamnus spp.	29	17	10
Succulent	Succulent species from arid ecosystems	Agave spp., Opuntia spp.	6	3	10
Other	All species that could not be assigned to any of the defined PFTs	Arabidopsis thaliana., Dendrobium, Iris germanica	3	3	6

Table 3: Factors affecting root hydraulic properties variability. Factors analyzed and their ranges (or factor levels) observed in the database.

Factor	Description	Factor levels or range
PFT	Plant functional types, according to the classification in Table 2	Nine different PFTs
Age	Root system age. Data principally corresponds to dicot crops and grasses. Root system age of trees and shrubs scarcely reported, mainly restricted to studies with seedlings	3–150 days (herbaceous crops and grasses) 12-485 days (woody crops)
Driving force	Driving force used for measurement of root hydraulic properties	Hydrostatic or osmotic driving force
Genus	Taxonomic genus	124 distinct genera
Growth form	A coarser classification than PFT	Tree, shrub, succulent, graminoid or dicot crops
Root section	Section of the root (segment) for which root hydraulic properties were determined. Several investigations measured whole roots instead of specific segments	Whole root or distal, mid-root or basal segments
Root type	Type of root investigated	Primary, tap, seminal, lateral, adventitious, whole root system
Species	Species investigated	214 distinct species
Treatment	Simplified classification of the experimental treatments applied in the studies	Control, stress, other or no treatment

Table 4: Statistics of Random Forest and linear mixed models. Importance of several factors (as described in Table 3) for root hydraulic properties variability, according to the drop in accuracy metric (Random Forest); *p*-value of the same factors, using Type III ANOVA tests (linear-mixed models); and total variance explained by the fitted Random Forest models. Data in bold indicate the 3 highest ranked factors (Random Forest models) and effect significance ($p < 0.05$, ANOVA tests).

Factor	Drop in mean square error				<i>p</i> -value (Satterthwaite)			
	<i>K_{rs}</i>	<i>K_{rs_area}</i>	<i>k_{root}</i>	<i>k_{x_cs}</i>	<i>K_{rs}</i>	<i>K_{rs_area}</i>	<i>k_{root}</i>	<i>k_{x_cs}</i>
PFT	2.07	0.98	0.91	7.39	0.20	0.84	0.92	<0.001
Age	2.85	1.34	-	-	<0.001	0.38		
Driving force	1.63	1.1	0.95	-	<0.001	<0.001	<0.001	
Genus	1.84	1.05	0.89	1.81	-	-	-	-
Growth form	1.14	0.41	0.68	6.72	-	-	-	-
Root section	-	-	0.64	2.47			<0.01	<0.001
Root type	-	-	0.75	1.79	-	-	-	-
Species	1.99	1.12	0.76	1.8	-	-	-	-
Treatment	0.67	0.33	0.31	0.41	-	-	-	-
	-	-	-	-	-	-	-	-
Total variance explained (%)	76.9	65.9	64.3	83.6	-	-	-	-

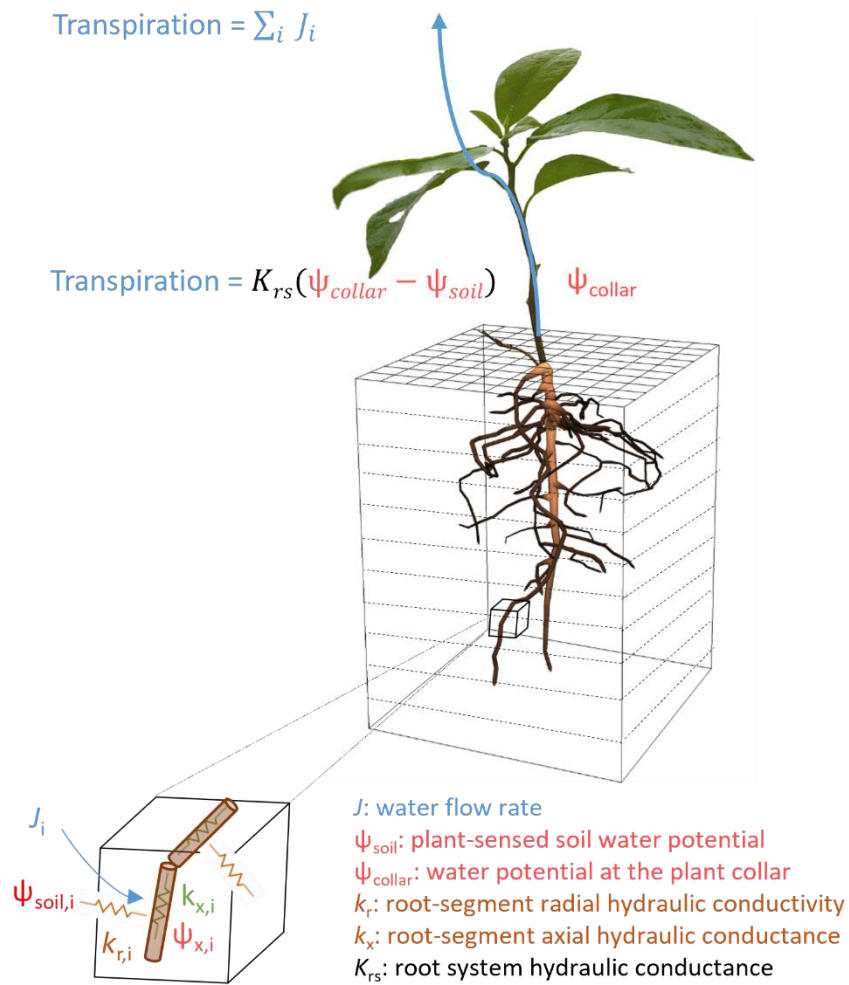


Figure 1: Root hydraulic properties and water flow in the soil-plant-atmosphere continuum. Figure adapted from Vanderborgh *et al.* (2021)

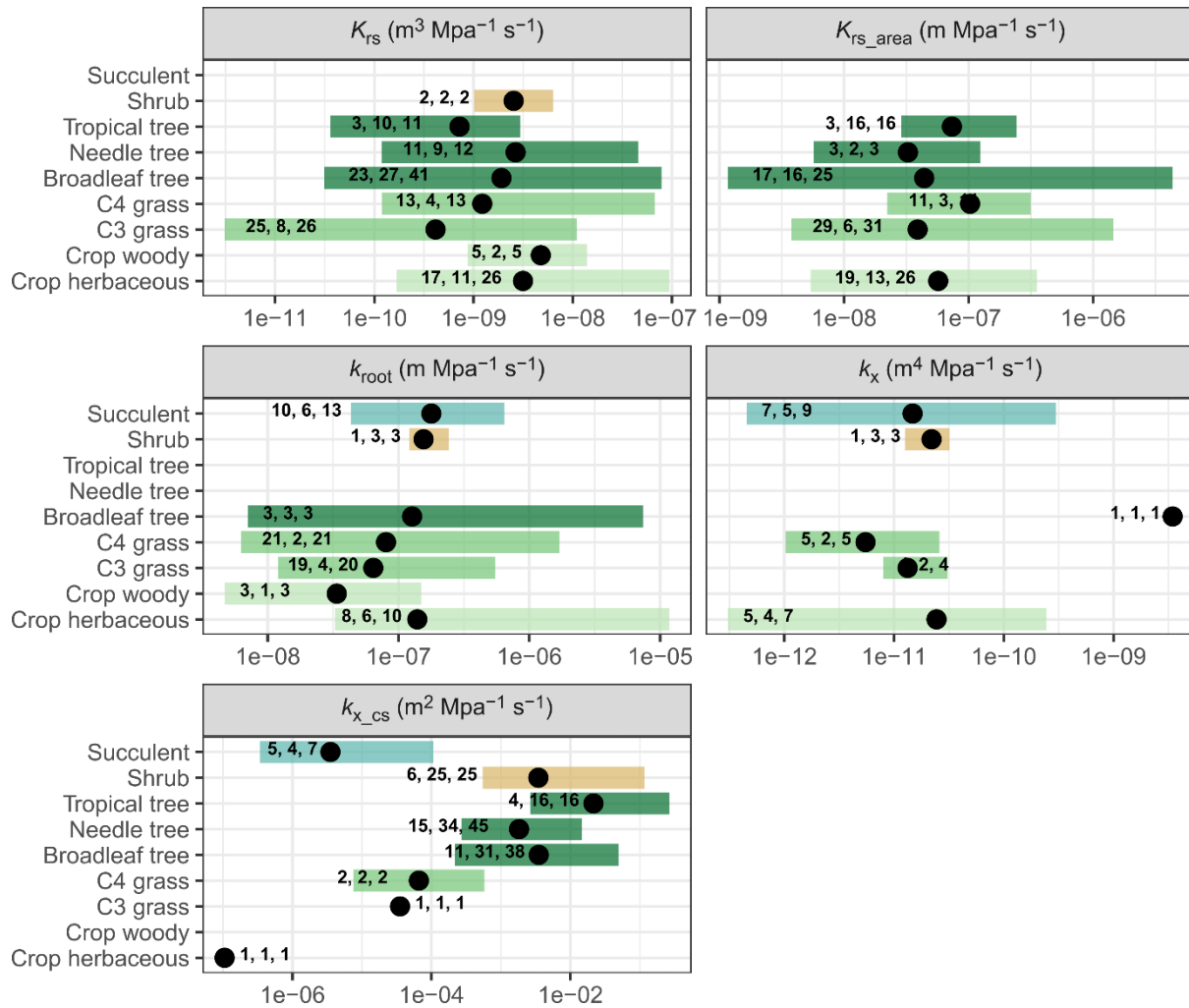


Figure 2: Range of variation in root hydraulic properties. Geometric means (filled circles) and range of variation (bars) of root hydraulic properties (see Table 1 for detailed definitions) for different plant functional types. The total number of studies, species, and individual data points for each PFT are indicated in bold (see 2.3 for details on the calculation).

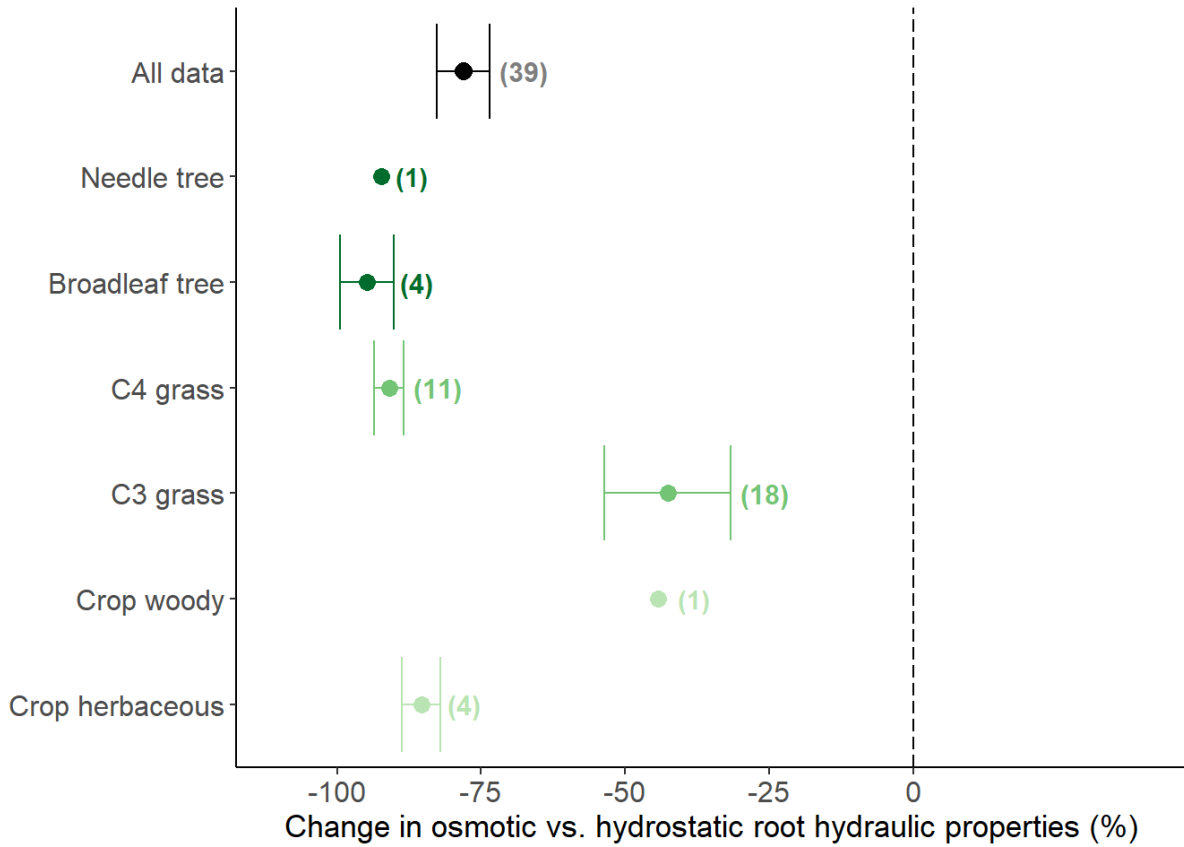


Figure 3: Difference between osmotic vs. hydrostatic root hydraulic properties. Data points and error bars represent the mean \pm the standard error for each PFT (sample size n reported on the side). The mean value for all samples is represented with a black circle. Individual values were calculated based on the log response ratio.

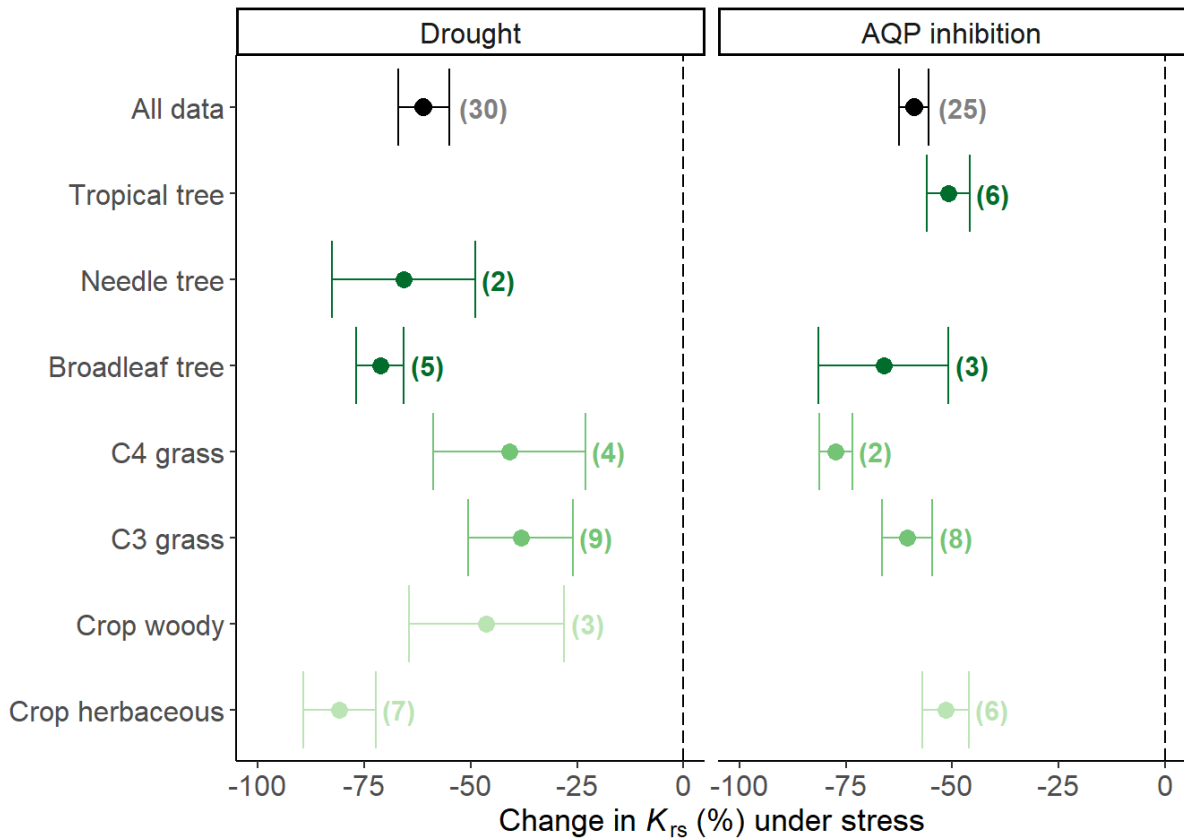


Figure 4: Response of K_{rs} to stress treatments. Changes in K_{rs} under drought stress (left panel) and aquaporin inhibition (right panel). Data points and error bars represent the mean \pm the standard error for each PFT (sample size n reported on the side). The mean value for all samples is represented with a black circle. Individual values were calculated based on the log response ratio.

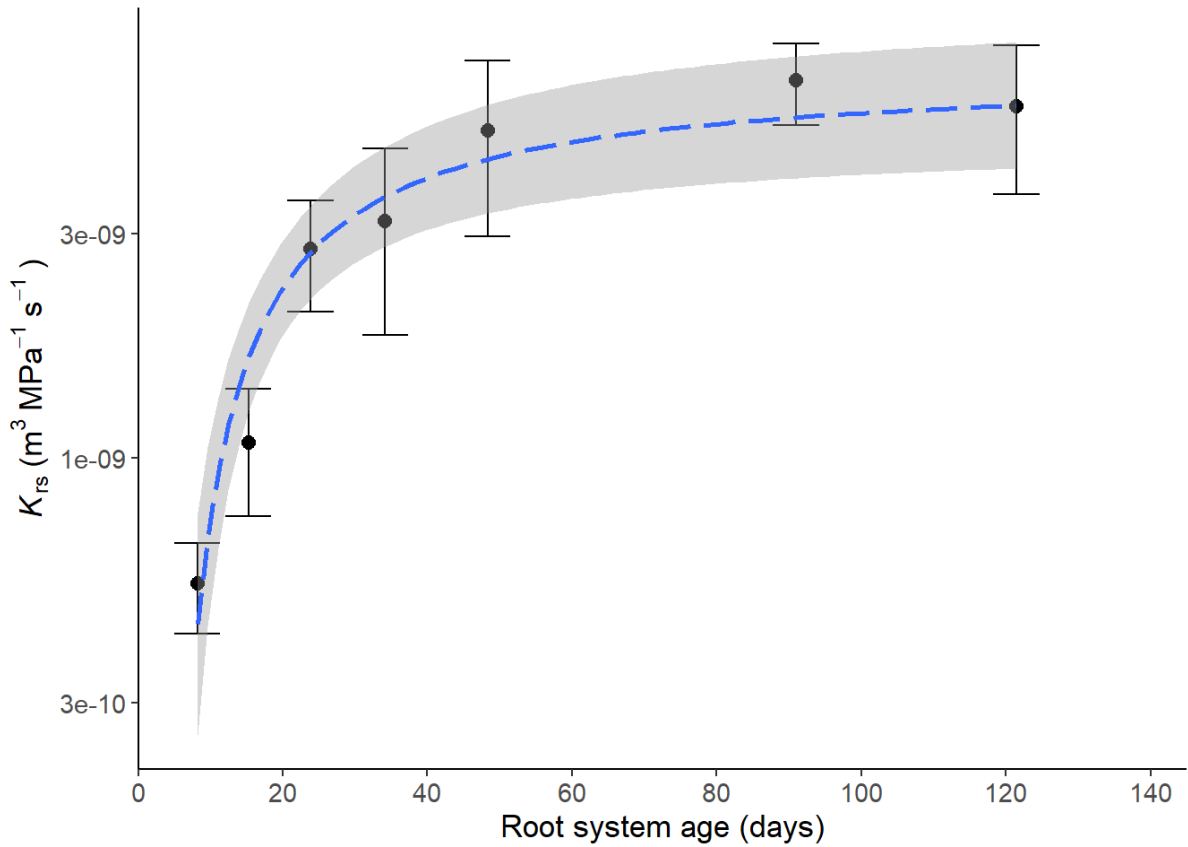


Figure 5: Relationship between root system age and K_{rs} . Data points and error bars represent K_{rs} (mean \pm standard error) of crop species grouped according to age (0–10, 10–20, 20–30, 30–40, 40–60, 60–100, >100 days). The dashed blue line and the shaded area represent a fitted exponential model (\pm standard error).

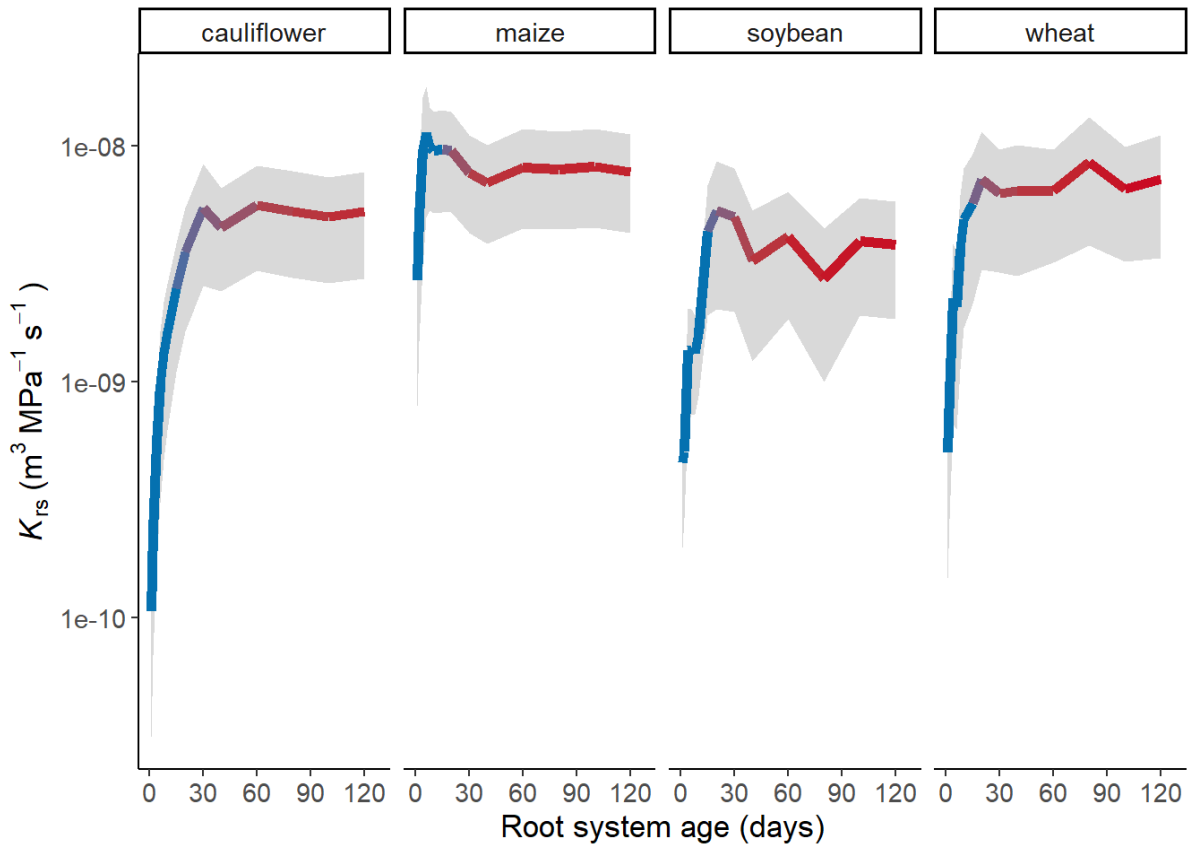


Figure 6: Modelled K_{rs} development with age. Colored lines and shaded areas represent K_{rs} (mean \pm standard error) of simulations using CPlantBox coupled with MARSHAL, for four different crops. The color scale indicates the proportion of old (>10 days) root segments in the total root system.

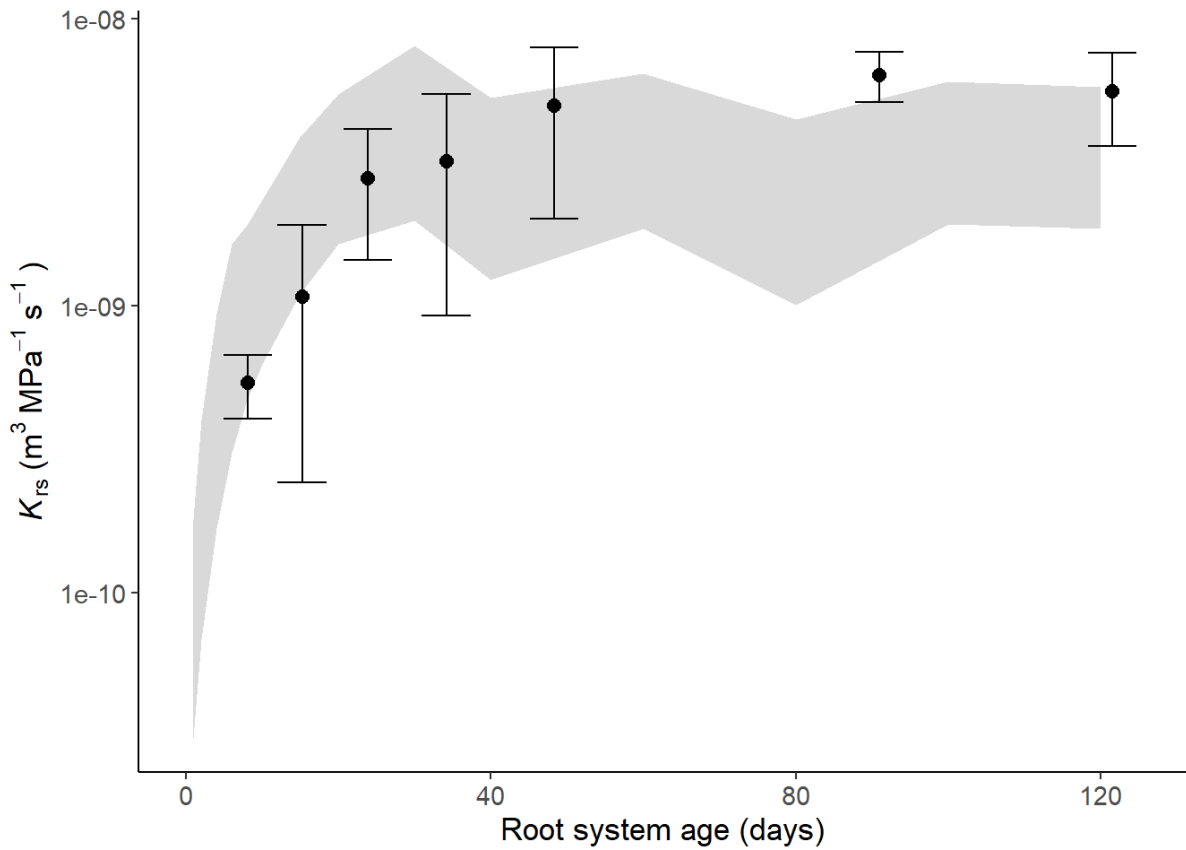


Figure 7: Modelled and observed K_{rs} development with age. Data points and error bars represent K_{rs} (mean \pm standard error) of crop species from the review and the shadowed area represents the total range of variation in K_{rs} according to simulations (CPlantBox coupled with MARSHAL).