

# Root hydraulic properties: an exploration of their variability across scales

## Authors

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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 (Steudle,  
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 (Steudle,  
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 ( $\psi$ , 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 (Steudle, 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 ( $k_{\text{root}}$ ) 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 ( $K_{\text{rs}}$ ) 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 (Wullschleger *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 (Vadéz,  
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-](https://roothydraulic-properties.shinyapps.io/database/)  
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<sub>3</sub> grass (wheat), a C<sub>4</sub> 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

were extracted from the database and from modelling (Doussan *et al.*, 1998) and used to parametrize MARSHAL.  $k_r$  and  $k_x$  are age-dependent and vary among root types (Figure S1). To account for the uncertainty in their parameterization, a sensitivity analysis was performed by varying  $k_r$ ,  $k_x$  or the  $k_r/k_x$  within the range of variation and the spatial heterogeneity observed in the literature (Figure S1). Modeled  $K_{rs}$  corresponds to the mean  $\pm$  standard error of all simulations, for each individual crop. Modeling results were contrasted with data gathered from the review, specifically for crop species (dicot crops and C<sub>3</sub> and C<sub>4</sub> grasses) measured using a hydrostatic driving force.

## 3 Results and discussion

### 3.1 Range of variability of root hydraulic properties

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

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

$K_{rs}$  is often reported in the literature on the basis of a measure of root size, to facilitate the comparison among plants of different age, with root surface area ( $K_{rs\_area}$ ) being the normalization most widely used (see Table 1 for other common normalizations). Our results indicated that the range of variation of  $K_{rs\_area}$  was indeed factors of magnitude smaller than 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 large range of variation was also observed within each PFT ( $\approx 1\text{--}3$  orders of magnitude), indicating large intrinsic differences among species and/or experimental design of the studies. 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 ( $3.3 \times 10^{-8}$  –  
255  $1.0 \times 10^{-7}$  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 =  $4.7 \times 10^{-9}$  –  
259  $1.2 \times 10^{-5}$  m MPa $^{-1}$  s $^{-1}$ , Figure 2), but also within individual PFTs (ranges  $\approx$  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 ( $3.4 \times 10^{-8}$  –  $1.8 \times 10^{-7}$  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 =  $3.1 \times 10^{-13}$  –  $3.5 \times 10^{-9}$  m $^4$  MPa $^{-1}$  s $^{-1}$ ) and on a cross sectional area basis ( $k_{x\_cs}$ , range  
266 =  $1.1 \times 10^{-7}$  –  $2.7 \times 10^{-1}$  m $^2$  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  $3.1 \times 10^{-13}$  –  $3.0 \times 10^{-10}$  m $^4$  MPa $^{-1}$  s $^{-1}$ , with C<sub>4</sub> grasses showing the  
271 lowest ( $5.5 \times 10^{-12}$  m $^4$  MPa $^{-1}$  s $^{-1}$ ) and dicot crops the highest ( $2.4 \times 10^{-11}$  m $^4$  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  $2.2 \times 10^{-4}$  –  $2.7 \times 10^{-1}$   
274 m $^2$  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 =  $1.1 \times 10^{-7}$  –  $1.1 \times 10^{-4}$  m $^2$  MPa $^{-1}$  s $^{-1}$ ) and confirm the results from previous  
277 metaanalyses (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 ( $1.2 \times 10^{-5}$  in *V. faba* and  $7.4 \times 10^{-6}$  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  $\approx 1\text{--}3$  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 systematically 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 C<sub>3</sub> grasses and the remaining  
432 PFTs, and also very large discrepancies within the C<sub>3</sub> 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<sub>3</sub> 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<sub>4</sub> grasses) ( $p = 0.16$ ). Also, across all studies and species ( $n=30$ ), the  $K_{rs}$  response  
460 to drought varied greatly, between ≈98% decrease (i.e., a decline of almost two orders of  
461 magnitude) and ≈35% increase. On the contrary,  $K_{rs}$  responded negatively to AQP inhibition,  
462 without exception ( $n=25$ ), with the decrease ranging between ≈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; Baugé *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<sub>3</sub> and C<sub>4</sub>) 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<sub>4</sub> grass, ≈44%) under drought was considerably  
474 weaker than that of tomato (dicot crop, ≈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<sub>3</sub> grasses seven out of 9  
478 studies were conducted with rice, and a similar behavior was observed for C<sub>4</sub> 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<sub>3</sub> 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-](https://roothydraulic-properties.shinyapps.io/database/)  
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

VC: Formal Analysis, Writing - review and editing

DB: Writing - review and editing

TG: Funding Acquisition, Writing - review and editing

THN: Writing - review and editing

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

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## **Conflict of interest statement**

No conflict of interest declared

## References

**Abdalla M, Ahmed MA. 2021.** Arbuscular mycorrhiza symbiosis enhances water status and soil-plant hydraulic conductance under drought. *Frontiers in Plant Science* **12**: 722954.

**Abdalla M, Ahmed MA, Cai G, Wankmüller F, Schwartz N, Litig O, Javaux M, Carminati A. 2022.** Stomatal closure during water deficit is controlled by below-ground hydraulics. *Annals of Botany* **129**: 161–170.

**Ahmed MA, Zarebanadkouki M, Meunier F, Javaux M, Kaestner A, Carminati A. 2018.** Root type matters: measurement of water uptake by seminal, crown, and lateral roots in maize. *Journal of Experimental Botany* **69**: 1199–1206.

**Ainsworth EA, Long SP. 2005.** What have we learned from 15 years of free-air CO<sub>2</sub> enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO<sub>2</sub>. *New Phytologist* **165**: 351–372.

**Altmann A, Tološi L, Sander O, Lengauer T. 2010.** Permutation importance: a corrected feature importance measure. *Bioinformatics* **26**: 1340–1347.

**Aroca R, Porcel R, Ruiz-Lozano JM. 2011.** Regulation of root water uptake under abiotic stress conditions. *Journal of Experimental Botany* **63**: 43–57.

**Baca Cabrera JC. 2023.** *Root-hydraulic-properties*: v1.0.0. doi: 10.5281/zenodo.10195243.

**Barrios-Masias FH, Knipfer T, McElrone AJ. 2015.** Differential responses of grapevine rootstocks to water stress are associated with adjustments in fine root hydraulic physiology and suberization. *Journal of Experimental Botany* **66**: 6069–6078.

**Bárzana G, Aroca R, Paz JA, Chaumont F, Martínez-Ballesta MC, Carvajal M, Ruiz-Lozano JM. 2012.** Arbuscular mycorrhizal symbiosis increases relative apoplastic water flow in roots of the host plant under both well-watered and drought stress conditions. *Annals of Botany* **109**: 1009–1017.

**Bates D, Mächler M, Bolker B, Walker S. 2015.** Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**: 1–48.

**Bauget F, Protto V, Pradal C, Boursiac Y, Maurel C. 2023.** A root functional structural model allows assessment of the effects of water deficit on water and solute transport parameters. *Journal of Experimental Botany* **74**: 1594–1608.

**Bouda M, Brodersen C, Saiers J. 2018.** Whole root system water conductance responds to both axial and radial traits and network topology over natural range of trait variation. *Journal of Theoretical Biology* **456**: 49–61.

**Boursiac Y, Pradal C, Bauget F, Lucas M, Delivoras S, Godin C, Maurel C. 2022a.** Phenotyping and modeling of root hydraulic architecture reveal critical determinants of axial water transport. *Plant Physiology* **190**: 1289–1306.

**Boursiac Y, Protto V, Rishmawi L, Maurel C. 2022b.** Experimental and conceptual approaches to root water transport. *Plant and Soil* **478**: 349–370.

**Bramley H, Turner NC, Turner DW, Tyerman SD. 2007.** Comparison between gradient-dependent hydraulic conductivities of roots using the root pressure probe: the role of pressure propagations and implications for the relative roles of parallel radial pathways. *Plant, Cell & Environment* **30**: 861–874.

**Bramley H, Turner NC, Turner DW, Tyerman SD. 2009.** Roles of morphology, anatomy, and aquaporins in determining contrasting hydraulic behavior of roots. *Plant Physiology* **150**: 348–364.

**Cai G, König M, Carminati A, Abdalla M, Javaux M, Wankmüller F, Ahmed MA. 2022.** Transpiration response to soil drying and vapor pressure deficit is soil texture specific. *Plant and Soil* **45**: 650–663.

**Chaumont F, Tyerman SD. 2014.** Aquaporins: highly regulated channels controlling plant water relations. *Plant Physiology* **164**: 1600–1618.

**Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, et al. 2012.** Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752–755.

**Couvreur V, Faget M, Lobet G, Javaux M, Chaumont F, Draye X. 2018.** Going with the flow: multiscale insights into the composite nature of water transport in roots. *Plant Physiology* **178**: 1689–1703.

**Couvreur V, Vanderborght J, Beff L, Javaux M. 2014.** Horizontal soil water potential heterogeneity: simplifying approaches for crop water dynamics models. *Hydrology and Earth System Sciences* **18**: 1723–1743.

**Couvreur V, Vanderborght J, Javaux M. 2012.** A simple three-dimensional macroscopic root water uptake model based on the hydraulic architecture approach. *Hydrology and Earth System Sciences* **16**: 2957–2971.

**Cowan IR. 1965.** Transport of water in the soil-plant-atmosphere system. *Journal of Applied Ecology* **2**: 221–239.

**Ding L, Gao C, Li Y, Li Y, Zhu Y, Xu G, Shen Q, Kaldenhoff R, Kai L, Guo S. 2015.** The enhanced drought tolerance of rice plants under ammonium is related to aquaporin (AQP). *Plant Science* **234**: 14–21.

**Domec J-C, Schäfer K, Oren R, Kim HS, McCarthy HR. 2010.** Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO<sub>2</sub> concentration. *Tree Physiology* **30**: 1001–1015.

**Doussan C, Pierret A, Garrigues E, Pagès L. 2006.** Water uptake by plant roots: II – Modelling of water transfer in the soil root-system with explicit account of flow within the root system – comparison with experiments. *Plant and Soil* **283**: 99–117.

**Doussan C, Vercambre G, Pagès L. 1998.** Modelling of the hydraulic architecture of root systems: an integrated approach to water absorption distribution of axial and radial conductances in maize. *Annals of Botany* **81**: 225–232.

**Frensch J, Steudle E. 1989.** Axial and radial hydraulic resistance to roots of maize (*Zea mays L.*). *Plant Physiology* **91**: 719–726.

**Gallardo M, Eastham J, Gregory PJ, Turner NC. 1996.** A comparison of plant hydraulic conductances in wheat and lupins. *Journal of Experimental Botany* **47**: 233–239.

**Gambetta GA, Knipfer T, Fricke W, McElrone AJ. 2017.** Aquaporins and root water uptake. In: Chaumont F, Tyerman SD, eds. *Plant aquaporins, signaling and communication in plants*. Springer International Publishing, 133–153.

**Garthwaite AJ, Steudle E, Colmer TD. 2006.** Water uptake by roots of *Hordeum marinum*: formation of a barrier to radial O<sub>2</sub> loss does not affect root hydraulic conductivity. *Journal of Experimental Botany* **57**: 655–664.

**Hacke UG, Jansen S. 2009.** Embolism resistance of three boreal conifer species varies with pit structure. *New Phytologist* **182**: 675–686.

**Hedges LV, Gurevitch J, Curtis PS. 1999.** The meta-analysis of response ratios in experimental ecology. *Ecology* **80**: 1150–1156.

**Hess L, Meir P, Bingham IJ. 2015.** Comparative assessment of the sensitivity of oilseed rape and wheat to limited water supply. *Annals of Applied Biology* **167**: 102–115.

**Huang B, Nobel PS. 1992.** Hydraulic conductivity and anatomy for lateral roots of *Agave deserti* during root growth and drought-induced abscission. *Journal of Experimental Botany* **43**: 1441–1449.

**Huang B, Nobel PS. 1994.** Root hydraulic conductivity and its components, with emphasis on desert succulents. *Agronomy Journal* **86**: 767–774.

**Kim YX, Ranathunge K, Lee S, Lee Y, Lee D, Sung J. 2018.** Composite transport model and water and solute transport across plant roots: an update. *Frontiers in Plant Science* **9**.

**Knipfer T, Fricke W. 2011.** Water uptake by seminal and adventitious roots in relation to whole-plant water flow in barley (*Hordeum vulgare L.*). *Journal of Experimental Botany* **62**: 717–733.

**Kreszies T, Eggels S, Kreszies V, Osthoff A, Shellakkutti N, Baldauf JA, Zeisler-Diehl VV, Hochholdinger F, Ranathunge K, Schreiber L. 2020.** Seminal roots of wild and cultivated barley differentially respond to osmotic stress in gene expression, suberization, and hydraulic conductivity. *Plant, Cell & Environment* **43**: 344–357.

**Lambers H, Oliveira RS. 2019.** Plant water relations. In: Lambers H, Oliveira RS, eds. *Plant physiological ecology*. Springer International Publishing, 187–263.

**Landsberg JJ, Fowkes ND. 1978.** Water movement through plant roots. *Annals of Botany* **42**: 493–508.

**Leitner D, Klepsch S, Knieß A, Schnepf A. 2010.** The algorithmic beauty of plant roots – an L-System model for dynamic root growth simulation. *Mathematical and Computer Modelling of Dynamical Systems* **16**: 575–587.

**Leitner D, Meunier F, Bodner G, Javaux M, Schnepf A. 2014.** Impact of contrasted maize root traits at flowering on water stress tolerance A simulation study. *Field Crops Research* **165**: 125–137.

**Lian H-L, Yu X, Ye Q, Ding X-S, Kitagawa Y, Kwak S-S, Su W-A, Tang Z-C. 2004.** The role of aquaporin RWC3 in drought avoidance in rice. *Plant and Cell Physiology* **45**: 481–489.

**Liaw A, Wiener M. 2002.** Classification and regression by randomForest. *R News* **2**: 18–22.

**Lobet G, Pagès L, Draye X. 2014.** A modeling approach to determine the importance of dynamic regulation of plant hydraulic conductivities on the water uptake dynamics in the soil-plant-atmosphere system. *Ecological Modelling* **290**: 65–75.

**Luke SG. 2017.** Evaluating significance in linear mixed-effects models in R. *Behavior Research Methods* **49**: 1494–1502.

**Lynch JP, Chimungu JG, Brown KM. 2014.** Root anatomical phenes associated with water acquisition from drying soil: Targets for crop improvement. *Journal of Experimental Botany* **65**: 6155–6166.

**Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB. 2006.** Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant, Cell & Environment* **29**: 571–583.

**Maurel C, Simonneau T, Sutka M. 2010.** The significance of roots as hydraulic rheostats. *Journal of Experimental Botany* **61**: 3191–3198.

**Melchior W, Steudle E. 1993.** Water transport in onion (*Allium cepa* L.) roots (changes of axial and radial hydraulic conductivities during root development). *Plant Physiology* **101**: 1305–1315.

**Meunier F, Couvreur V, Draye X, Vanderborght J, Javaux M. 2017a.** Towards quantitative root hydraulic phenotyping: novel mathematical functions to calculate plant-scale hydraulic parameters from root system functional and structural traits. *Journal of Mathematical Biology* **75**: 1133–1170.

**Meunier F, Draye X, Vanderborght J, Javaux M, Couvreur V. 2017b.** A hybrid analytical-numerical method for solving water flow equations in root hydraulic architectures. *Applied Mathematical Modelling* **52**: 648–663.

**Meunier F, Heymans A, Draye X, Couvreur V, Javaux M, Lobet G. 2019.** MARSHAL, a novel tool for virtual phenotyping of maize root system hydraulic architectures. *in silico Plants* **2**: diz012.

**Meunier F, Zarebanadkouki M, Ahmed MA, Carminati A, Couvreur V, Javaux M. 2018.** Hydraulic conductivity of soil-grown lupine and maize unbranched roots and maize root-shoot junctions. *Journal of Plant Physiology* **227**: 31–44.

**Moraes MT de, Debiasi H, Franchini JC, Mastroberti AA, Levien R, Leitner D, Schnepf A. 2020.** Soil compaction impacts soybean root growth in an Oxisol from subtropical Brazil. *Soil and Tillage Research* **200**: 104611.

**Morandage S, Vanderborght J, Zörner M, Cai G, Leitner D, Vereecken H, Schnepf A.** 2021. Root architecture development in stony soils. *Vadose Zone Journal* **20**: e20133.

**Nguyen TH, Langensiepen M, Vanderborght J, Hüging H, Mboh CM, Ewert F.** 2020. Comparison of root water uptake models in simulating CO<sub>2</sub> and H<sub>2</sub>O fluxes and growth of wheat. *Hydrology and Earth System Sciences* **24**: 4943–4969.

**Nobel PS, Cui M.** 1992. Hydraulic conductances of the soil, the root-soil air gap, and the root: Changes for desert succulents in drying soil. *Journal of Experimental Botany* **43**: 319–326.

**North GB, Peterson CA.** 2005. Water flow in roots: structural and regulatory features. In: Holbrook NM, Zwieniecki MA, eds. *Vascular transport in plants*. Burlington: Academic Press, 131–156.

**Poulter B, MacBean N, Hartley A, Khlystova I, Arino O, Betts R, Bontemps S, Boettcher M, Brockmann C, Defourny P, et al.** 2015. Plant functional type classification for earth system models: results from the European Space Agency's Land Cover Climate Change Initiative. *Geoscientific Model Development* **8**: 2315–2328.

**Pratt RB, Jacobsen AL, Golgotiu KA, Sperry JS, Ewers FW, Davis SD.** 2007. Life history type and water stress tolerance in nine California chaparral species (*Rhamnaceae*). *Ecological Monographs* **77**: 239–253.

**Pratt RB, North GB, Jacobsen AL, Ewers FW, Davis SD.** 2010. Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings. *Functional Ecology* **24**: 70–81.

**R Core Team.** 2023. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

**Rieger M, Litvin P.** 1999. Root system hydraulic conductivity in species with contrasting root anatomy. *Journal of Experimental Botany* **50**: 201–209.

**Rishmawi L, Bauget F, Protto V, Bauland C, Naqry P, Maurel C.** 2023. Natural variation of maize root hydraulic architecture underlies highly diverse water uptake capacities. *Plant Physiology* **192**: 2404–2418.

**Rohatgi A.** 2023. *WebPlotDigitizer*. URL <https://github.com/ankitrohatgi/WebPlotDigitizer>.

**Sanderson J, Whitbread FC, Clarkson DT.** 1988. Persistent xylem cross-walls reduce the axial hydraulic conductivity in the apical 20 cm of barley seminal root axes: implications for the driving force for water movement. *Plant, Cell & Environment* **11**: 247–256.

**Schnepf A, Leitner D, Landl M, Lobet G, Mai TH, Morandage S, Sheng C, Zörner M, Vanderborght J, Vereecken H.** 2018. CRootBox: a structural functional modelling framework for root systems. *Annals of Botany* **121**: 1033–1053.

**Steudle E.** 1990. *Methods for studying water relations of plant cells and tissues*. San Diego, USA: Academic Press.

**Steudle E.** 2000a. Water uptake by plant roots: an integration of views. *Plant and Soil* **226**: 45–56.

**Steudle E.** 2000b. Water uptake by roots: effects of water deficit. *Journal of Experimental Botany* **51**: 1531–1542.

**Steudle E. 2001.** The cohesion-tension mechanism and the acquisition of water by plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**: 847–875.

**Steudle E, Meshcheryakov AB. 1996.** Hydraulic and osmotic properties of oak roots. *Journal of Experimental Botany* **47**: 387–401.

**Strock CF, Burridge JD, Niemiec MD, Brown KM, Lynch JP. 2021.** Root metaxylem and architecture phenotypes integrate to regulate water use under drought stress. *Plant, Cell & Environment* **44**: 49–67.

**Sulis M, Couvreur V, Keune J, Cai G, Trebs I, Junk J, Shrestha P, Simmer C, Kollet SJ, Vereecken H, et al. 2019.** Incorporating a root water uptake model based on the hydraulic architecture approach in terrestrial systems simulations. *Agricultural and Forest Meteorology* **269-270**: 28–45.

**Tyerman SD, Wignes JA, Kaiser BN. 2017.** Root hydraulic and aquaporin responses to N availability. In: Chaumont F, Tyerman SD, eds. *Plant aquaporins. Signaling and communication in plants*. Cham: Springer International Publishing, 207–236.

**Tyree MT. 2003.** Hydraulic properties of roots. In: Kroon H de, Visser EJW, eds. *Ecological Studies*. Berlin, Heidelberg: Springer, 125–150.

**Tyree MT, Patiño S, Bennink J, Alexander J. 1995.** Dynamic measurements of roots hydraulic conductance using a high-pressure flowmeter in the laboratory and field. *Journal of Experimental Botany* **46**: 83–94.

**Vadez V. 2014.** Root hydraulics: the forgotten side of roots in drought adaptation. *Field Crops Research* **165**: 15–24.

**Vanderborght J, Couvreur V, Meunier F, Schnepf A, Vereecken H, Bouda M, Javaux M. 2021.** From hydraulic root architecture models to macroscopic representations of root hydraulics in soil water flow and land surface models. *Hydrology and Earth System Sciences* **25**: 4835–4860.

**Vansteenkiste J, Van Loon J, Garré S, Pagès L, Schrevens E, Diels J. 2014.** Estimating the parameters of a 3-D root distribution function from root observations with the trench profile method: case study with simulated and field-observed root data. *Plant and Soil* **375**: 75–88.

**Vercambre G, Doussan C, Pages L, Habib R, Pierret A. 2002.** Influence of xylem development on axial hydraulic conductance within prunus root systems. *Trees* **16**: 479–487.

**Wullschleger SD, Epstein HE, Box EO, Euskirchen ES, Goswami S, Iversen CM, Kattge J, Norby RJ, Bodegom PM van, Xu X. 2014.** Plant functional types in earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany* **114**: 1–16.

**Zhang J, Zhang X, Liang J. 1995.** Exudation rate and hydraulic conductivity of maize roots are enhanced by soil drying and abscisic acid treatment. *New Phytologist* **131**: 329–336.

## 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 $k_{\text{root}}$ 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)
$k_{\text{root}}$	(Total) root hydraulic conductivity	Individual roots or root segments	$\text{m MPa}^{-1} \text{s}^{-1}$	$L_{\text{pr}}$ (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 $k_x$ )
$K_{\text{rs}}$	Whole root system conductance	Entire root system	$\text{m}^3 \text{MPa}^{-1} \text{s}^{-1}$	$K_{\text{root}}$ (Cai <i>et al.</i> , 2022); $L_p$ (Lambers & Oliveira, 2019); $L_{\text{pr}}$ (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.
$K_{\text{rs\_norm}}$	$K_{\text{rs}}$ 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: $K_{\text{rs\_area}}$ ( $\text{m MPa}^{-1} \text{s}^{-1}$ ) Root fresh or dry weight: $K_{\text{rs\_weight}}$ ( $\text{m}^3 \text{MPa}^{-1} \text{s}^{-1} \text{g}^{-1}$ ) Root length: $K_{\text{rs\_length}}$ ( $\text{m}^3 \text{MPa}^{-1} \text{s}^{-1} \text{m}^{-1}$ ) Root volume: $K_{\text{rs\_vol}}$ ( $\text{m}^3 \text{MPa}^{-1} \text{s}^{-1} \text{m}^{-3}$ )

**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.

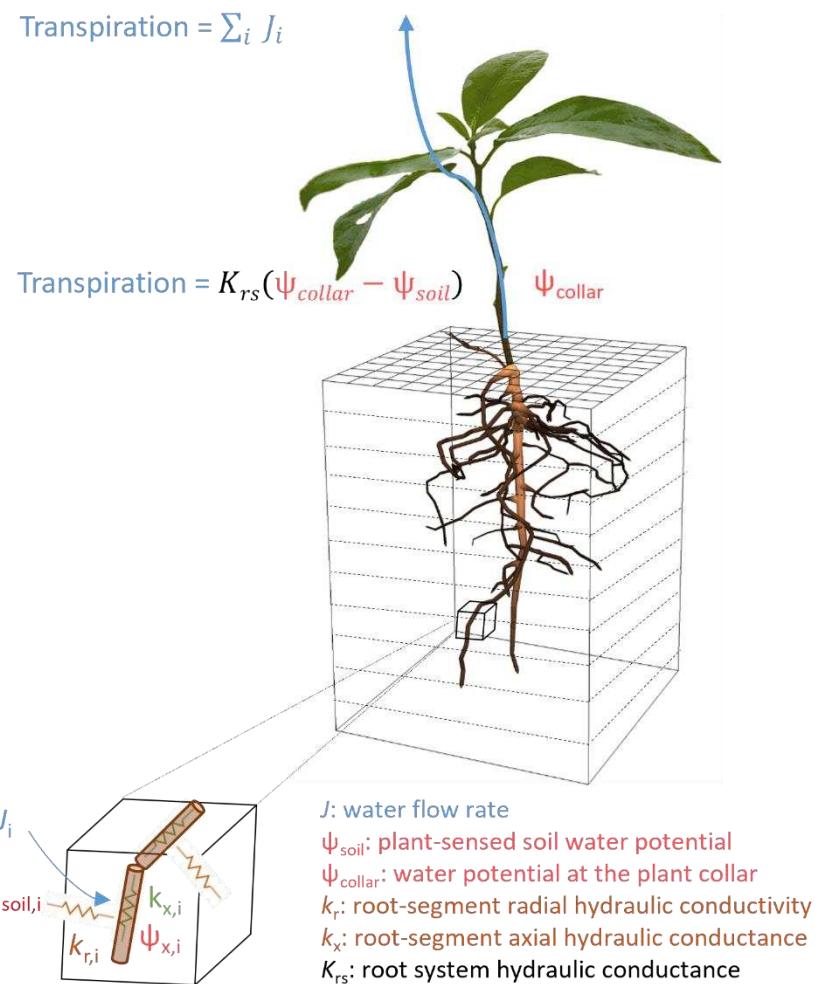
PFT	Description	Species examples	Nr. species	Nr. genera	Nr. studies
Crop herbaceous	Herbaceous crop species (legumes and non-legumes), excluding all C <sub>3</sub> and C <sub>4</sub> grasses	Tomato, soybean, lupin	23	17	50
Crop woody	Woody crop species	Cotton, grapevine	2	2	11
C <sub>3</sub> grass	Grass species with a C <sub>3</sub> photosynthetic pathway. Most species investigated corresponded to grasses used as crops	Barley, rice, wheat	9	7	50
C <sub>4</sub> grass	Grass species with a C <sub>4</sub> 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.

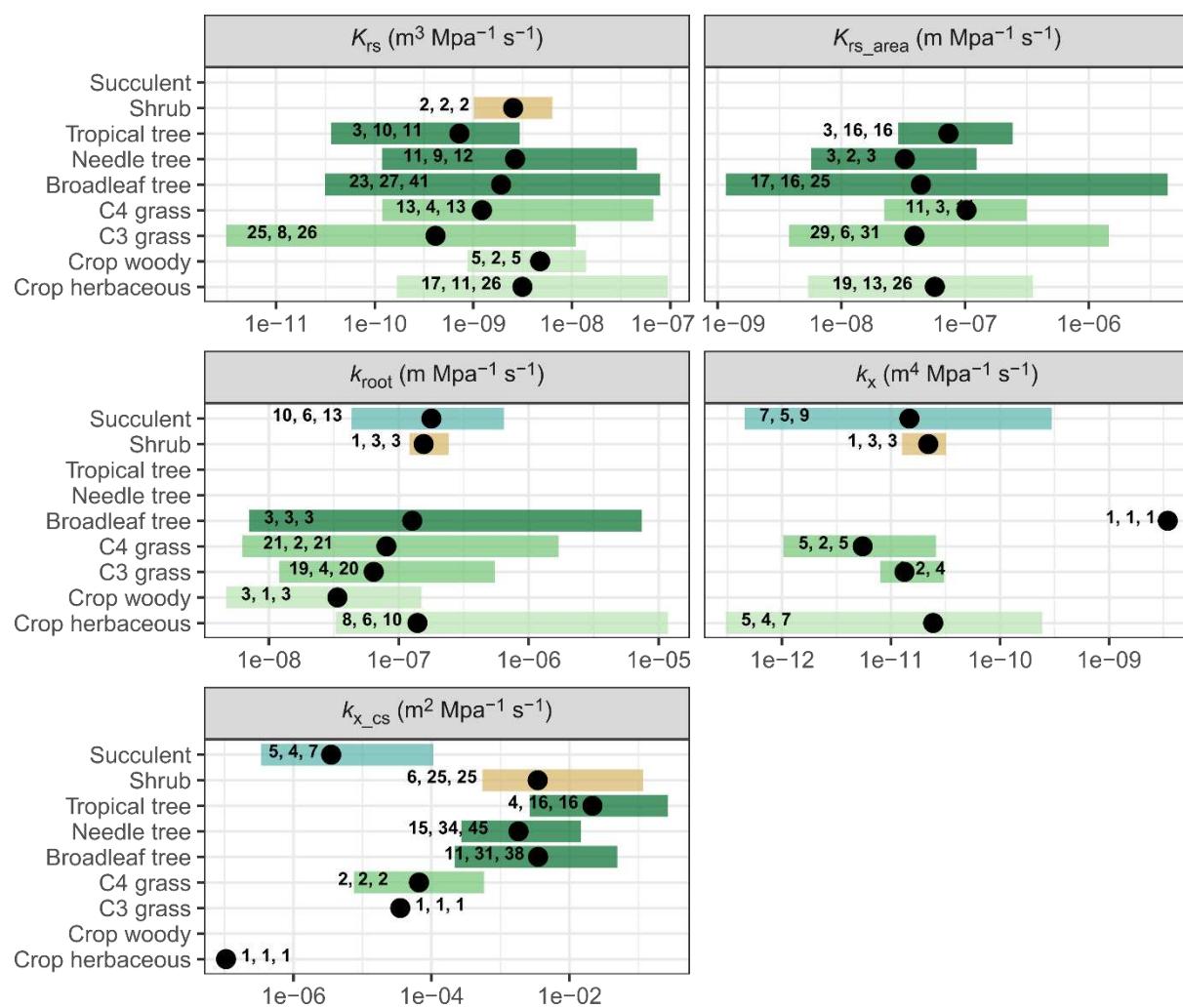
Factor	Description	Factor levels or range
PFT	Plant functional types, according to the classification in Table 2	Nine different PFTs
Age	Root system age. Data principally corresponds to dicot crops and grasses. Root system age of trees and shrubs scarcely reported, mainly restricted to studies with seedlings	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).

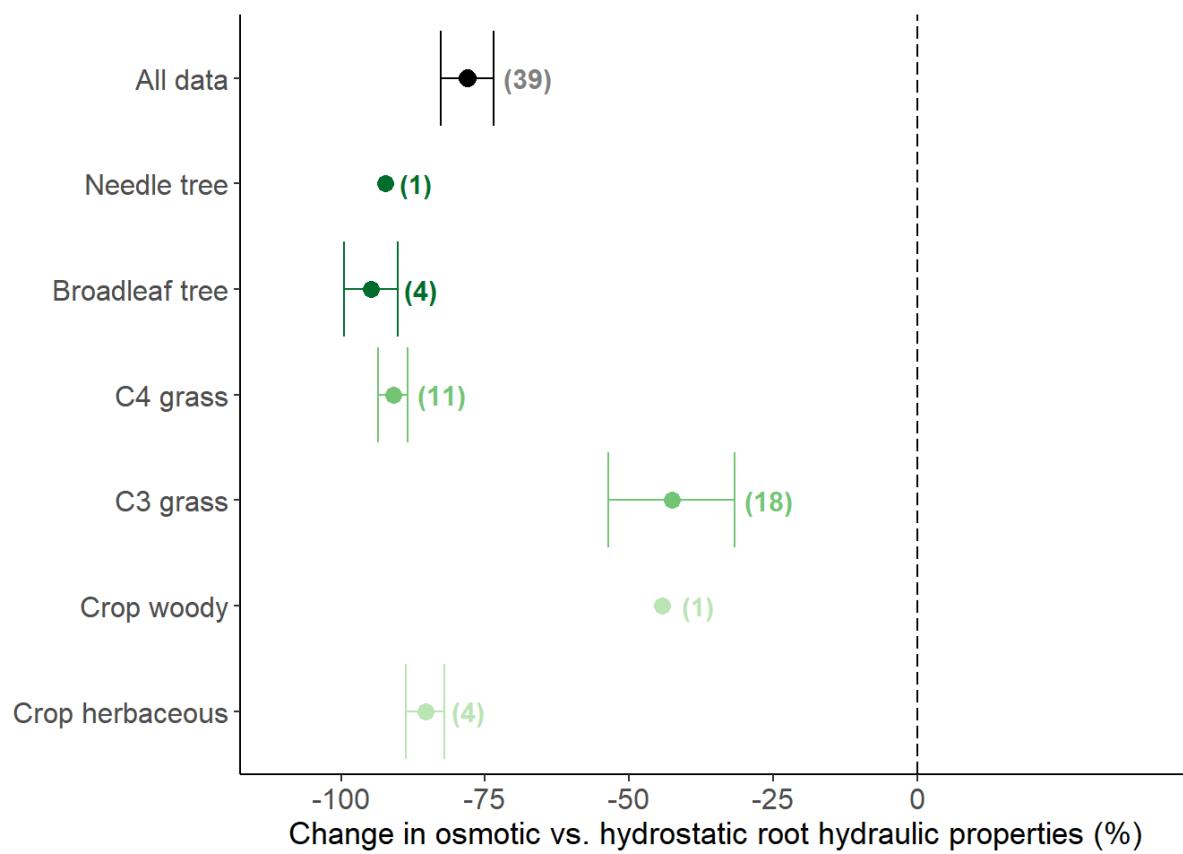
Factor	Drop in mean square error				<i>p</i> -value (Satterthwaite)			
	<i>K<sub>rs</sub></i>	<i>K<sub>rs_area</sub></i>	<i>k<sub>root</sub></i>	<i>k<sub>x_cs</sub></i>	<i>K<sub>rs</sub></i>	<i>K<sub>rs_area</sub></i>	<i>k<sub>root</sub></i>	<i>k<sub>x_cs</sub></i>
PFT	<b>2.07</b>	0.98	<b>0.91</b>	<b>7.39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



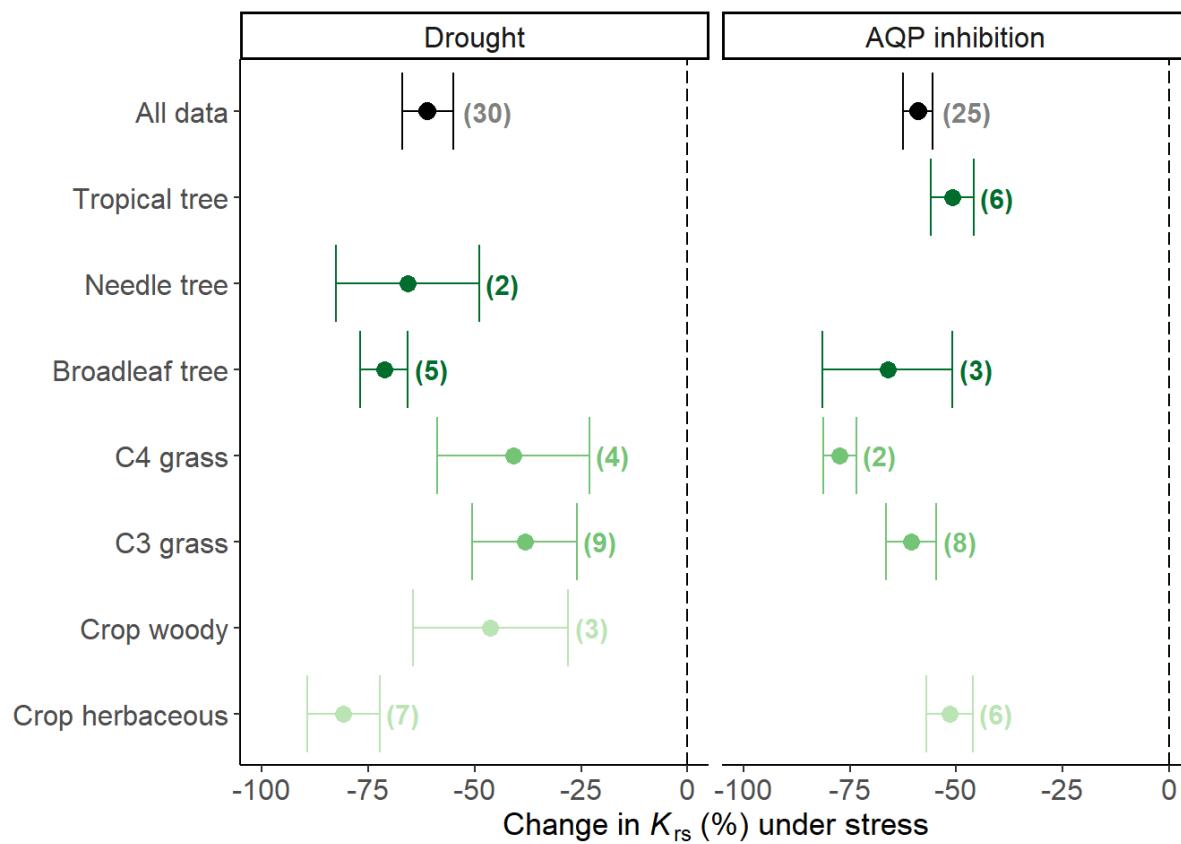
**Figure 1: Root hydraulic properties and water flow in the soil-plant-atmosphere continuum.** Figure adapted from Vanderborght *et al.* (2021)



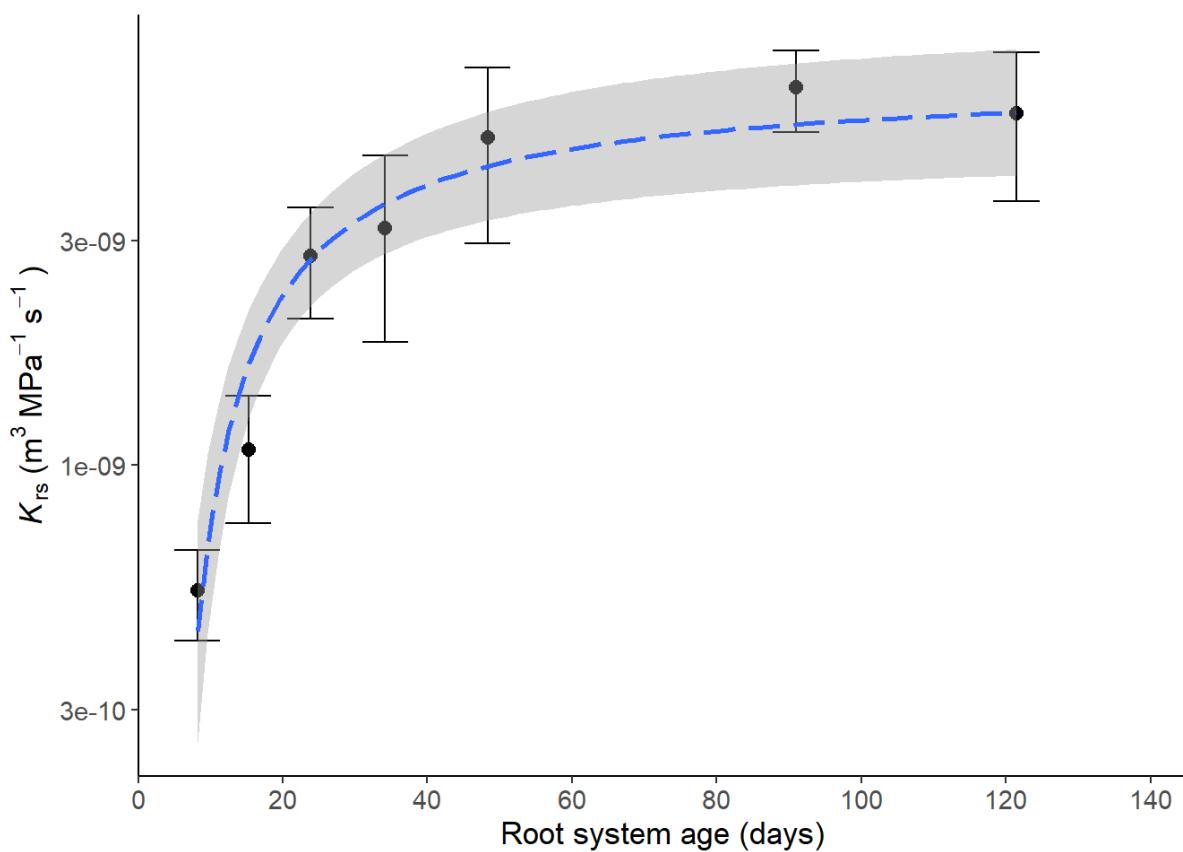
**Figure 2: Range of variation in root hydraulic properties.** Geometric means (filled circles) and range of variation (bars) of root hydraulic properties (see Table 1 for detailed definitions) for different plant functional types. The total number of studies, species, and individual data points for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



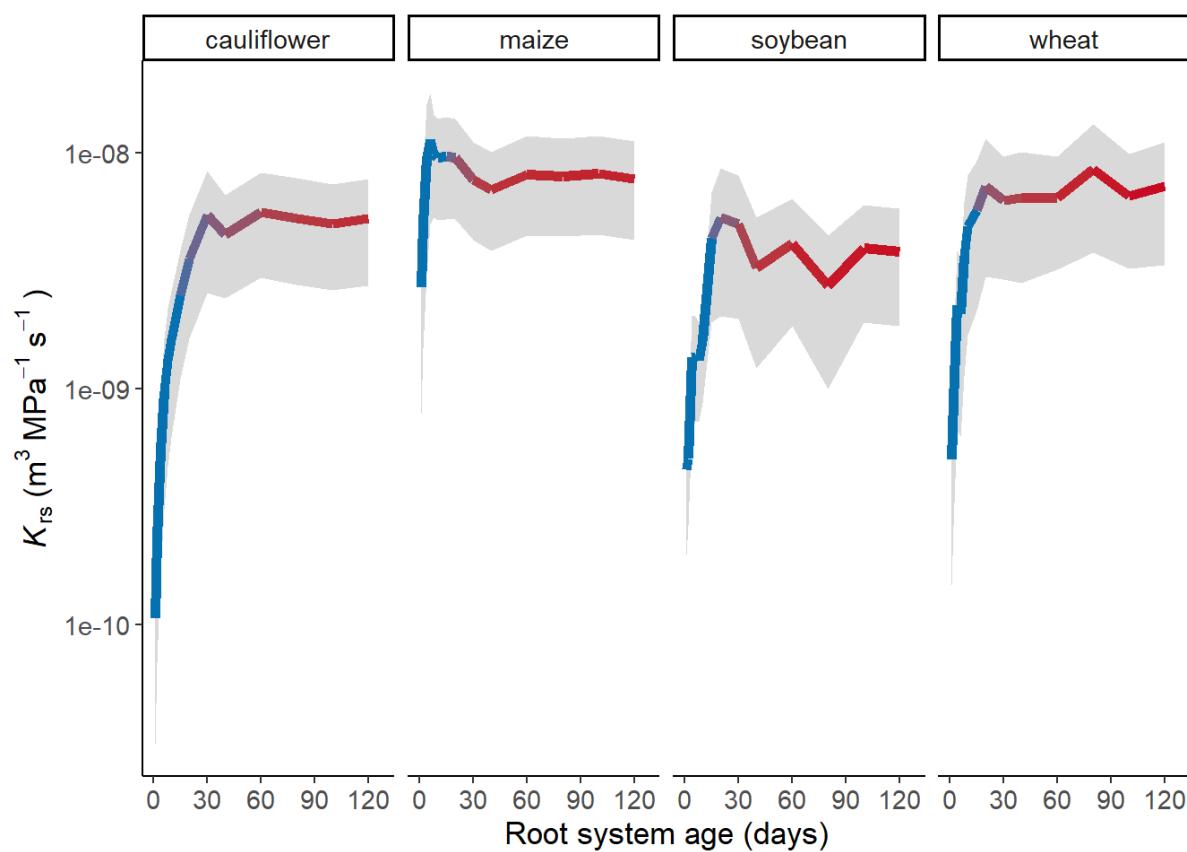
**Figure 3: Difference between osmotic vs. hydrostatic root hydraulic properties.** Data points and error bars represent the mean  $\pm$  the standard error for each PFT (sample size  $n$  reported on the side). The mean value for all samples is represented with a black circle. Individual values were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



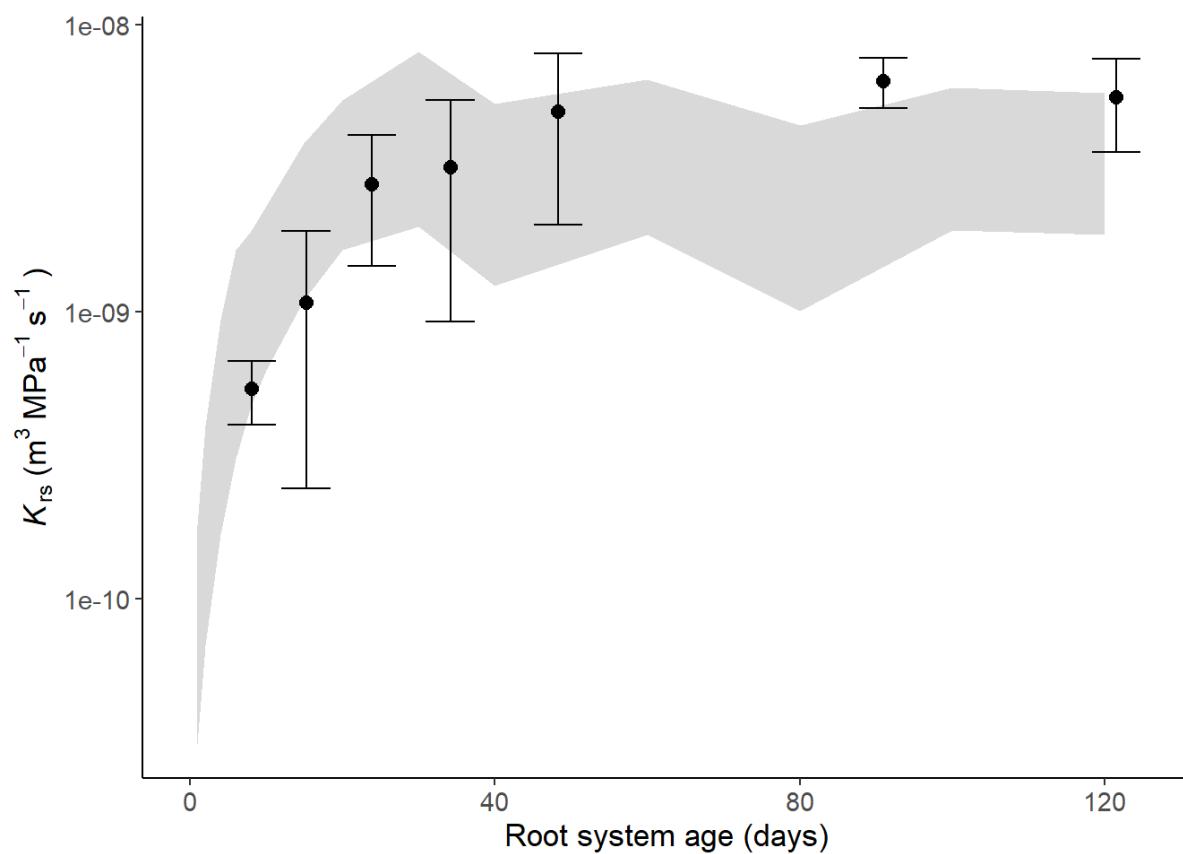
**Figure 4: Response of  $K_{rs}$  to stress treatments.** Changes in  $K_{rs}$  under drought stress (left panel) and aquaporin inhibition (right panel). Data points and error bars represent the mean  $\pm$  the standard error for each PFT (sample size  $n$  reported on the side). The mean value for 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).