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1 **Root architecture and hydraulics converge for acclimation to changing water**
2 **availability**

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11

12 **Abstract.** Because of intense transpiration and growth, the needs of plants for water can be
13 immense. Yet, water in the soil is most often heterogeneous if not scarce due to more and more
14 frequent and intense drought episodes. The converse context, flooding, is often associated with
15 marked oxygen deficiency and can also challenge the plant water status. Under our feet roots
16 achieve an incredible challenge to meet the water demand of the plant's aerial parts under such
17 dramatically different environmental conditions. For this, they continuously explore the soil, building
18 a highly complex, branched architecture. On shorter time scales, roots keep adjusting their water
19 transport capacity (their so-called hydraulics), locally or globally. While the mechanisms that directly
20 underlie root growth and development and tissue hydraulics are being uncovered, the signalling
21 mechanisms that govern their local and systemic adjustments as a function of water availability
22 remain largely unknown. A comprehensive understanding of root architecture and hydraulics as a
23 whole (in other terms, root hydraulic architecture) is needed to apprehend the strategies used by
24 plants to optimize water uptake and possibly improve crops for this crucial trait.

25 **Word count: 3871**

26

27 **Introduction**

28 Water is certainly the most limiting environmental factor for agricultural production, whether in arid
29 or temperate areas. Climate change exacerbates this threat by inducing increasingly frequent and
30 intense drought episodes. While droughts can dramatically alter plant productivity and survival,
31 water excess is not a lesser evil ¹. With notable exceptions such as rice and Rumex, complete

32 submergence of the plant results in a full growth arrest ¹ and under waterlogging conditions several
33 plant species exhibit a paradoxical wilting phenotype due to transpiration while root water uptake
34 capacity has been reduced ². Thus, both water deficit and excess negatively impact agriculture and
35 result in significant economical losses. For instance, a global analysis including drylands and non-
36 drylands worldwide showed that crops as important as wheat and maize show a yield reduction by
37 21% and 39%, respectively, at approximately 40% water reduction ³. According to recent estimates,
38 Europe loses up to 5 billion euros of agricultural harvests every year, due to river overflows. These
39 losses may double by 2080 due to climate change ⁴. Thus, understanding the overall modes of
40 response of plant to water availability is of utmost agronomic importance ¹.

41 Several directions are currently followed, regarding water use. Foremost is irrigation, which
42 has traditionally been used to counteract insufficient precipitation, although it is associated with
43 significant economic and environmental costs. Soil drainage is also central to combat the detrimental
44 effects of waterlogging ⁵. Although novel water management and predictive practices ⁵⁻⁷ have been
45 explored to increase the efficiency of water usage ⁸, developing drought- or flood-tolerant crop
46 cultivars promises to be another main path to progress ^{1,8,9}. In particular, drought-tolerant crops are
47 plants that are adapted to water-challenged climates that, most importantly, maintain a stable yield
48 despite annual variations in precipitation. To reach this goal, breeders have focused on exploiting
49 plant phenology as a means to protect the reproductive stage (the most drought-sensitive
50 developmental stage in some crops). Breeding work has also been aimed at transpiration or leaf
51 growth in order to prevent water loss, thereby achieving significant genetic progress in plant
52 resistance to drought ¹⁰. In contrast, most breeders have avoided the selection of root traits,
53 although they fulfil key functions for the plant such as soil water uptake, which is absolutely essential
54 during droughts and is challenged under waterlogging conditions. One reason is that roots vary with
55 soil type and rainfall and require considerable investment for functional assays or growth monitoring
56 in the field. Efforts to phenotype root systems in real soils, using X-ray computed tomography or
57 shovelomics, or in adapted devices such as rhizotrons or transparent soils have led to significant
58 technical progresses on how to capture the complexity and dynamics of root architecture and
59 anatomy (see ¹¹ for a recent review). Yet, the functionality of root systems cannot be fully addressed
60 using these phenotyping devices. In the present Perspective, we point to recent fundamental
61 advances in root biology that open exciting avenues in several directions related to water uptake and
62 ultimately crop improvement.

63 **Elucidating root hydraulic architecture**

64 Roots fulfil their anchoring and foraging functions through continuous growth and branching,
65 thereby producing a highly complex and specialized network, the so called root system architecture

66 (RSA) (Fig. 1a). Experimentally, RSA can be defined by length (depth) of the main root(s), the density
67 and elongation of lower order roots, their gravitropic setpoint angle, and the possible presence of
68 crown roots or adventitious roots. A large body of research has addressed the elementary
69 mechanisms that determine each of these individual traits and emphasized the role of hormones,
70 including auxin, abscisic acid (ABA), cytokinins and ethylene¹²⁻¹⁴. Other studies have addressed the
71 adaptive significance of varying RSA. In a search for root ideotypes that could provide cereal crops
72 with an adaptive advantage under drought, deep rooting has been proposed as a key trait, as it
73 permits access to unexploited water resources when the soil surface desiccates¹⁵. Yet, this ideotype
74 may not be optimal for quick recovery after drought in seasonal precipitation regimes¹⁶, or for
75 acquisition of nutrients such as phosphate¹⁷. One initial approach to investigate the role of roots
76 during drought consisted of searching for correspondences between Quantitative Trait Loci (QTLs)
77 for specific root morphological traits and whole-plant performance under water deficit^{18,19}. In
78 grasses, for instance, suppression of crown roots was found to promote drought tolerance^{20,21}. In
79 addition, plant geneticists have recently succeeded in cloning such critical genes as rice *DRO1*, which
80 determines root growth angle and thereby enhances rice performance under drought by favoring
81 deep rooting²². A natural variation approach, but in *Arabidopsis*, led to identification of
82 *EXOCYST70A3*, an exocyst factor which also interferes with root growth orientation and root system
83 depth by acting on expression of auxin efflux carriers in the root tip¹⁶. Although the two studies
84 point to the central role of auxin in regulating RSA, they identify opposite and species-specific
85 strategies for soil exploration under water deficit. More generally, much of the physiological and
86 genetic components that shape the adaptive value of RSA under natural conditions are as yet
87 unknown. To address these, elaborate time-lapse 3D imaging and mathematical modelling
88 approaches are under development to capture the great complexity of RSA, and its intra- and
89 interspecific variations²³⁻²⁵.

90 Water uptake is not simply a matter of root growth. It is also critically determined by the
91 intrinsic water transport capacity of the roots, *i.e.* their hydraulics (Fig. 1b). Water is first transported
92 radially from the soil to the stele, through concentric layers of root cells, loaded into xylem vessels,
93 and then transported axially up to the shoots. Our biophysical and physiological understanding of
94 these processes has made significant progress in the last two decades^{26,27}. Molecular physiological
95 studies have shown that water channel proteins named aquaporins facilitate water diffusion across
96 cell membranes and therefore contribute to cell-to-cell transport^{26,28}. Yet, many other components
97 of root hydraulics are to be discovered. For instance, the crucial role of lignified and suberized
98 barriers differentiated in the walls of exo- and endodermal cells has long remained elusive but can
99 now be explored using genetic materials recently arising from sharp molecular dissection of these
100 barriers²⁹. Such studies have revealed however the intricate regulatory pathways connecting the cell

101 wall (apoplastic) and cell-to-cell (aquaporin-dependent) water transport paths³⁰. While root growth
102 or leaf water relation traits have been the subject of extensive direct genetic analyses, it is only
103 recently that these approaches have been extended to root hydraulics. For instance, QTL analysis of a
104 biparental recombinant population of *Arabidopsis* led to the molecular cloning of *Hydraulic*
105 *Conductivity of Root 1 (HCR1)*³¹. HCR1 encodes a raf-like MAP3K protein kinase which
106 characterization has revealed unexpected hydraulic regulation under the combined effects of
107 potassium and oxygen (O₂) availabilities (see below) (Fig. 2a,b). With respect to the strategy used for
108 *HCR1* mapping and cloning, Genome Wide Association Studies (GWAS) have recently provided a
109 more direct approach for isolating genes controlling root hydraulic conductivity³². These studies
110 uncovered XYLEM NAC DOMAIN 1 (*XND1*), a transcription factor that acts as a negative regulator of
111 xylem differentiation and as a consequence of root hydraulics, thereby providing novel insights into
112 the long-lasting debate on the possibly limiting role of xylem vessels in axial water transport (Fig. 1b).
113 In relation with its effects on root water transport, *XND1* negatively acts on drought stress tolerance
114³² (Fig. 2c). Overall, natural variation at *HCR1* and *XND1* points to the critical role of root hydraulics in
115 plant adaptation to water excess or deficit in natural habitats. More broadly, these studies indicate
116 how root hydraulics contributes to integrative response of plants to combined abiotic and biotic
117 stresses (Fig. 2). Future development of such genetic approaches in crops will be crucial for dissecting
118 and possibly improving root hydraulic performance under agricultural conditions.

119 Full comprehension of the ability of roots to capture soil water requires consideration of the
120 root architecture and hydraulics as a whole. Mathematical modelling approaches have therefore
121 attempted to integrate root local water transport properties within the RSA, thereby representing
122 the so-called root hydraulic architecture³³⁻³⁵. Several recent works have aimed at a better match
123 between root anatomy and architecture and water transport properties³⁶⁻³⁸. Nevertheless, there is
124 still too little experimental data to support or challenge these models^{27,38-40}. Consequently, although
125 this is a crucial integrative trait for plant performance, root hydraulic architecture has largely been
126 neglected by plant breeding efforts. In addition to RSA phenotyping, crude evaluation of root water
127 uptake capacity in breeding materials, by direct measurements in pot or hydroponically grown plants
128⁴¹, or indirectly through transpiration in grafted species⁴², would certainly help estimate the
129 potentialities of these materials. Another key issue is the interconnection between hydraulics and
130 growth. While it is well supported in shoots, it is just emerging in roots. For instance, auxin-
131 controlled aquaporins allow directing water flows in lateral primordia thereby reducing the
132 mechanical resistance of overlaying cells and favoring the emergence of the newly formed lateral
133 roots⁴³. This study establishes a unique physiological link between root hydraulics and branching.

134 **Root plasticity under varying water availability**

135 Root growth and hydraulics are both highly plastic, and are continuously adjusted in response to a
136 large variety of soil signals with potentially antagonistic or synergistic effects. For instance, water and
137 phosphorus deprivation can induce the formation of deep or shallow roots, respectively, while they
138 both down-regulate aquaporins (root hydraulic conductivity)^{25,26}. In addition, water and mineral
139 resources are far from uniform and can dramatically vary between soil patches or strata. A key
140 enigma in root research is therefore to resolve how plant roots, which lack a centralized information
141 processing system, can integrate signals from a heterogeneous environment to design the optimal
142 short- and long-term strategies for soil resource acquisition.

143 There is no need to say that, due to their great agronomical importance, these questions have
144 been raising a strong interest. A large body of literature shows that water availability exerts multiple
145 short- or long-term effects on root growth and hydraulics, with a sharp dose-dependency. For
146 instance, moderate water deprivation enhances primary root growth and lateral root formation,
147 whereas a strong water deficit exerts opposite inhibitory effects^{12,44,45}. In addition, sensitivity of
148 these responses can vary between the primary root and lateral roots of different orders, or between
149 segments of a same axial root⁴⁶. Root hydraulics is also dynamically regulated by water deficit, with
150 species- or cultivar-specific profiles and, in most cases, an early inhibition of aquaporin function^{47,48}.
151 In maize, root aquaporins can also integrate diurnal changes in shoot water demand (transpiration),
152 through a circadian regulation mechanism that shows a higher response amplitude under soil water
153 deficit⁴⁹. On a longer term, drought acts on root hydraulics by enhancing suberization of the
154 endodermis, or interfering with xylem differentiation (Fig. 1a). For instance, water deficit triggers in
155 the *Arabidopsis* root a non-cell-autonomous pathway involving endodermal ABA signaling. The
156 hormone enhances the accumulation of microRNA165, which migrates into the stele to act on
157 transcription factors determining xylem identity⁵⁰.

158 Recently, there have been attempts to understand how these responses integrate with each
159 other to determine whole root functionality. Analysis of both root architecture and hydraulics under
160 exogenous-ABA treatments and in ABA-biosynthesis and signalling mutants has revealed striking
161 parallels indicating that ABA, that accumulates under water deficit, acts as an integrator of root
162 responses to the associated stress⁴⁶. Yet, the picture is definitely more complex as ABA acts within a
163 hormonal interaction network involving auxin, ethylene and cytokinins^{51,52}. Future studies will also
164 have to address the issue of local heterogeneity in water availability, which, besides overall water
165 deficit, can occur in the absence of any water stress for the plant. Indeed, local variations can orient
166 root growth (hydrotropism)⁵³ or lateral root formation (hydropatterning)^{54,55} (Fig. 1a). Orman-Lipeza
167 et al.⁵⁶ recently described a related response, called xerobranching, which reflects the repression of
168 lateral root formation when a root grows through a large air-filled soil macropore, thereby feeling a
169 transient water deficit. In all cases, root tip growth and root branching are positioned towards

170 regions of higher water availability (Fig. 1a). While much mechanistic details are being uncovered
171 from laboratory experiments ⁴⁵, it will be fascinating to understand how these tropic responses
172 mutually interact and operate during growth of roots in real, drying soils and how they allow
173 optimizing soil foraging and water uptake.

174 Water excess reduces root hydraulic conductivity in most plant species, with early effects
175 being mediated through proton-dependent gating of aquaporins due to metabolically-induced cell
176 acidosis ^{2,57}. On a longer term, water excess exerts profound effects on root anatomy and ultimately
177 RSA. In some wetland species, hypoxia promotes suberin and lignin deposition in the outer layers of
178 the roots (rhizodermis) to create a barrier for lateral diffusion of O₂ from the root to the water
179 logged soil ⁵⁸. More generally, and to facilitate root aeration, roots differentiate internal air spaces
180 called aerenchyma, which can be either constitutive in species such as rice or inducible by hypoxia.
181 While the role of ethylene and ROS in aerenchyma induction under hypoxic stress is now well
182 assessed, a central role of auxin in constitutive aerenchyma formation was recently uncovered ⁵⁹.
183 Interestingly, the auxin pathway involved shares commonalities with the AUX/IAA- and ARF-
184 dependent pathway responsible for lateral root formation. Yet, the two responses are somewhat
185 distinct since auxin operates in two adjacent cell territories, e.g. cortex and pericycle. Concerning
186 root growth, hypoxia can induce root slanting, to possibly escape from deeper layers in water logged
187 soils ⁶⁰, due in part to a recently uncovered cytokinin-dependent mechanism that delays the
188 gravitropic response of lateral roots ⁶¹. More severe O₂ deprivation can result in tip growth arrest if
189 not death, and inhibition of lateral root formation ^{1,58}. To possibly alleviate defects of the primary
190 root system, flooding also promotes the formation of adventitious roots at the shoot basis of flood-
191 tolerant species, a process that is primarily induced by tissue accumulation of ethylene ¹. While
192 effects of energy depletion on transport activities in hypoxic roots have been largely identified ⁶², the
193 significance with respect to water uptake of hypoxia-induced root developmental reprogramming is
194 as yet unclear. Thus, the notion of root hydraulic architecture in flooded plants will require as much
195 attention as in droughted plants.

196 **Sensing water availability**

197 The molecular and cellular mechanisms underlying the early perception of water availability by roots
198 and downstream signalling processes have become a crucial area in plant research. Interestingly,
199 candidate genes involved in sensing water deficit are now emerging ^{63,64} and associated signalling
200 events involving ROS and calcium are being elucidated ^{65,66}. These studies, which deal with local
201 effects of water deficit, typically relate to root responses to pronounced drought. Yet, the capacity of
202 roots to acclimate to heterogeneous water resources or changing water demands of shoots, indicate

203 that roots must continuously emit or sense systemic signals transferred within the root system or
204 between roots and shoots^{67,68}. A dehydration-induced peptide that relays root ABA signalling
205 towards shoots was recently uncovered⁶⁹ but other physical (*e.g.* hydraulic) or chemical (*e.g.*
206 hormones, ions, ROS) signals are surely serving in root responses to heterogeneous or varying water
207 availabilities .

208 Robbins and Dinneny⁷⁰ have recently explored the initial steps of hydropatterning and used a
209 thoughtful modelling approach to show that perception of water availability is necessarily linked to
210 growth. In brief, they showed that growth allows to locally sustain a water potential gradient across
211 the root radial plane whereas such gradient rapidly dissipates in a non-growing zone. These findings
212 echo an independent experimental work showing that signal perception triggering the hydrotropic
213 response of Arabidopsis roots occurs in the elongating cortex⁷¹. Thus, the general principles
214 governing root responses to water availability are emerging and we now know where to look for
215 'water sensing' and early signalling mechanisms! A first significant step was recently taken by Orosa-
216 Puente et al.⁷². These authors showed how the hydropatterning response relies on a chain of
217 negative regulations which locally repress lateral root formation. In brief, local water deficit acts on
218 SUMO protease function to enhance sumoylation of auxin response factor ARF7, which in turn
219 accumulates and represses the downstream expression of root-inducing transcription factor LBD16.
220 It is still disputed whether xerobranching is an extreme case of hydropatterning or would involve a
221 fully distinct mechanism^{45,56}. The authors showed that xerobranching can be mimicked by a transient
222 ABA accumulation and response due to local water deficit, which would somewhat antagonize
223 constitutive auxin-dependent root branching. However, this model awaits validation using ABA
224 signaling mutants⁴⁵. Nevertheless, this hormonal regulation is different from previously described
225 root responses to long-term exposure to ABA or water deficit. In all cases, a deep interconnection
226 between ABA and auxin is emerging⁴⁵.

227 The perception of water excess relies on a completely different mechanism involving a class
228 (class VII) of transcription factors which are homologous to Ethylene Responsive Factors (ERF) and
229 are specifically oxidized and degraded by the O₂ and nitric oxide (NO) sensing branch of the
230 PROTEOLYSIS 6 (PRT6) N-degron pathway^{1,73}. Under flooding (O₂ deprivation) conditions, these so-
231 called ERF-VII factors are stabilized to trigger a core anaerobic transcriptional response. Recent work
232 indicate that this core mechanism is itself regulated by multiple hormonal and environmental cues.
233 For instance, ethylene, which accumulates in the early phases of submergence and pre-acclimates
234 plant to hypoxia stress, was shown to stabilize ERF-VII factors by increasing the expression of
235 PHYTOGLOBIN1, which in turn scavenges NO⁷⁴. The HCR1 protein kinase was also shown to stabilize
236 one such factor (RAP2.12), specifically in the presence of K⁺, thereby potentiating this response, and
237 promoting by as yet unknown mechanisms the inhibition of root hydraulic conductivity³¹. What

238 might be the significance of this joint response pathway to O₂ and K⁺ availability? Whereas O₂
239 deprivation directly reports on the intensity of flooding stress, K⁺ availability could reflect the growth
240 capacity of the plant depending on soil washing⁵. As a major intracellular cation, K⁺ indeed
241 contributes to turgor maintenance and thereby growth. In this context, HCR1 activation in the
242 presence of K⁺ would promote the plant's metabolic acclimation to flooding stress, thereby providing
243 an enhanced growth capacity during the recovery phase (Fig. 2b). Depending on its intensity, flooding
244 can result in soil water logging or full plant submergence that impact with different extent the water
245 status and growth of plants¹. It was proposed that natural alleles of *HCR1* with distinct functionalities
246 may have distinct adaptive values in these different scenarios.

247 ERF-VII transcription factors also play a role in the growth responses of Arabidopsis roots to
248 hypoxia by repressing the slanting response of the primary root to hypoxia⁶⁰ and promoting
249 elongation of adventitious roots⁷⁵. We also note that the capacity of plant roots to sense and
250 acclimate to O₂ availability goes beyond their responses to flooding stress. Hypoxic niches that
251 naturally occur under aerobic conditions were recently shown to play significant roles in root
252 development. Starting from the observation that hypoxic-responsive genes are induced during the
253 late phases of lateral root formation, Shukla et al.⁷⁶ showed how ERF-VII transcription factors bind to
254 auxin-responsive transcriptional complexes to repress the expression of master regulators of lateral
255 root formation, thereby contributing to the termination of this process.

256 **Conclusions**

257 Roots can be seen as a biological network integrating three main functions: growth, water transport,
258 and water perception and signalling. The first two functions yield the root hydraulic architecture, an
259 underexplored yet key trait. One main question is to understand how this architecture evolves in
260 time and space by integrating local and systemic signals reporting on the availability of water. The
261 present review indicates that the modes and mechanisms of response of roots to water deficit or
262 excess are fundamentally distinct. While ABA emerges as a coordinator of root hydraulic architecture
263 under drought⁴⁶, we miss corresponding information on integrative hydraulic responses of roots to
264 flooding stress. Also, a large focus has been made on aquaporin regulation under drought, whereas
265 the significance of suberization and xylem differentiation with respect to root hydraulics remains
266 disputed. More generally, future research will have to uncover the main principles and variety of
267 strategies used by plant roots to optimize soil water uptake and maintain the plant water status
268 under varying water availabilities. In these respects, mathematical modeling will be crucial to
269 integrate functional and architectural components of whole root systems. In particular, a specific
270 challenge will be to determine and possibly design root genotypes which are the best adapted to
271 specific drought or flooding scenarios or culture practices such as deficit irrigation or partial root

272 zone drying. More generally, a better integration of root functions and their relations to soil in crop
273 models would certainly aid crop improvement.

274 Recent progress in plant molecular genetics now makes it possible to directly address these
275 issues in the most relevant crops. Besides genome editing using CRISPR-Cas9 which now offers a
276 powerful approach to knock down genes of interest ⁷⁷, GWAS provide a potentially direct and rapid
277 approach to the identification of genes controlling a trait of interest. For instance, this approach has
278 been successfully used to isolate genes contributing to drought tolerance in crop plants with complex
279 genomes such as maize ^{78,79} and it can now be used to target specific root traits. Cereals which
280 display an elaborate embryonic and postembryonic root developmental program also hold promises
281 for exciting discoveries in root functionalization.

282

283 **Figure legends**

284 **Fig. 1| The water uptake capacity of a root system is determined by both its architecture and**
285 **hydraulics.**

286 **a)** The root system architecture is determined in part by soil water availability which can be highly
287 heterogeneous depending on soil layers. As shown in the inset, these local heterogeneities can
288 orientate root tip growth (hydrotropism) and lateral root formation (hydropatterning). **b)** Water
289 uptake can be decomposed in radial water transport from the soil to the root stele and axial
290 transport along the xylem vessels. Aquaporins, which contribute to transcellular water flows during
291 radial transport, determine to a large extent the root hydraulic conductivity. Suberized and lignified
292 endodermis or exodermis (not shown) can also impact radial transport.

293

294 **Fig. 2| Quantitative genetics allowed the identification of novel genes involved in the regulation of**
295 **root hydraulics under composite stress conditions.**

296 **a)** Optimal growth and transpiration of a plant in a fully aerated (O_2), irrigated (H_2O) and fertilized
297 (K^+) soil. The load of soil pathogenic bacteria (bacteria) is maintained at a minimum. The water
298 uptake capacity of the root system is accounted for by its hydraulic conductivity (Lp_r). **b)** Flooding
299 results in oxygen deficiency (hypoxia) of the root system. In the presence of nutriment (K^+),
300 induction of the Hydraulic Conductivity of Root 1 (HCR1) pathway enhances the core anaerobic
301 transcriptional response (anaerobic metabolism) and inhibits water uptake (Lp_r). These responses
302 promote plant acclimation to submergence and a better growth during the recovery phase. **c)** The
303 Xylem NAC Domain 1 (XND1) transcription factor negatively regulates xylem differentiation and as a
304 consequence Lp_r . Pathogenic bacteria can penetrate the root and move axially through its
305 vasculature. They also enhance the expression of XND1. Reduced xylem differentiation is detrimental
306 under water deficit (brown) and results in plant wilting. Yet, it restricts the proliferation of vascular
307 pathogens and therefore diminishes the susceptibility of the plant to bacterial wilt. Thus, XND1
308 determines a trade-off between responses to abiotic and biotic stresses.

309

310

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492

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497 C.M. wrote this article which was discussed with and corrected by P.N.

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500 **Competing interests**

501 The authors declare no competing interests

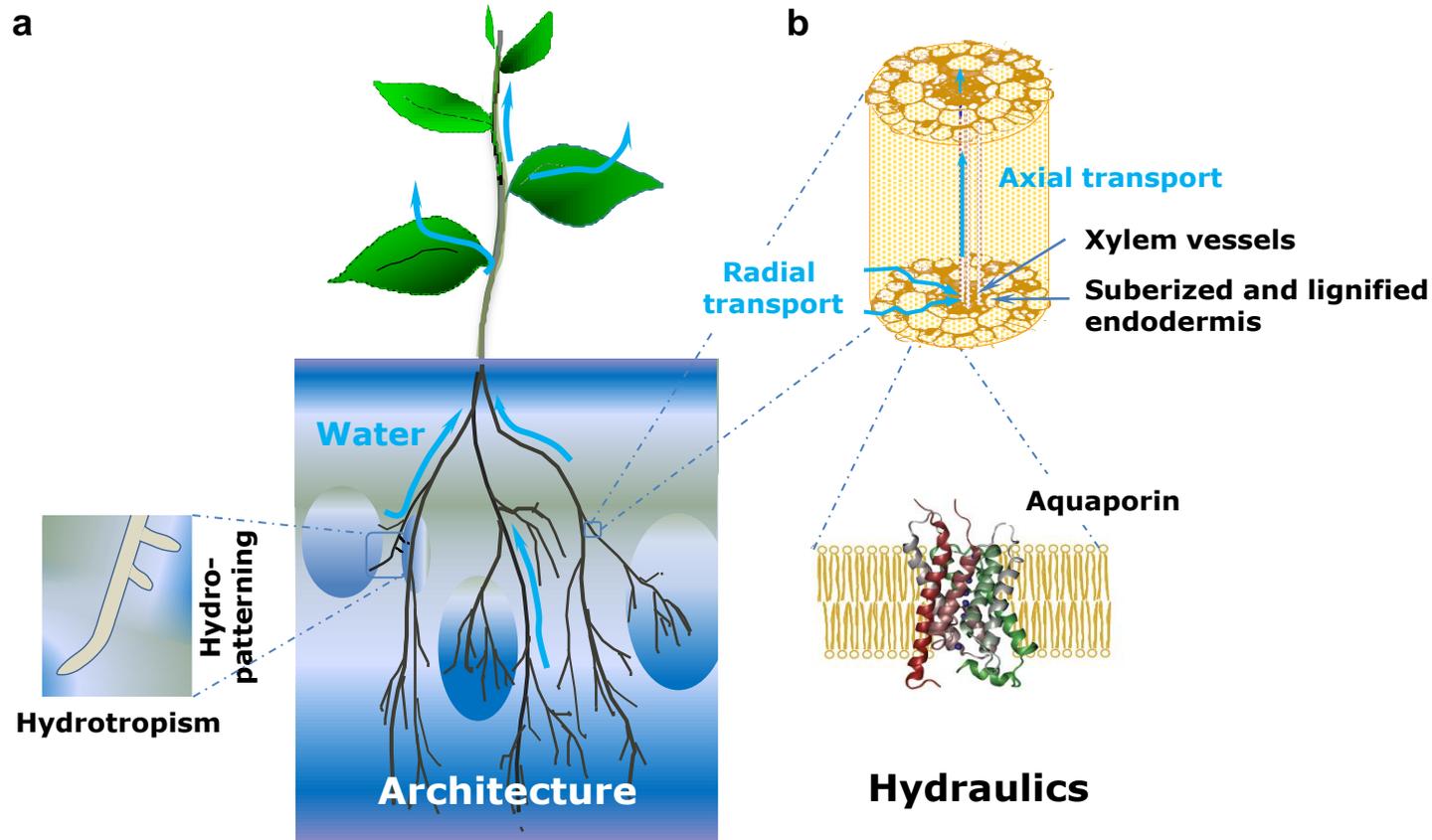


Figure 1

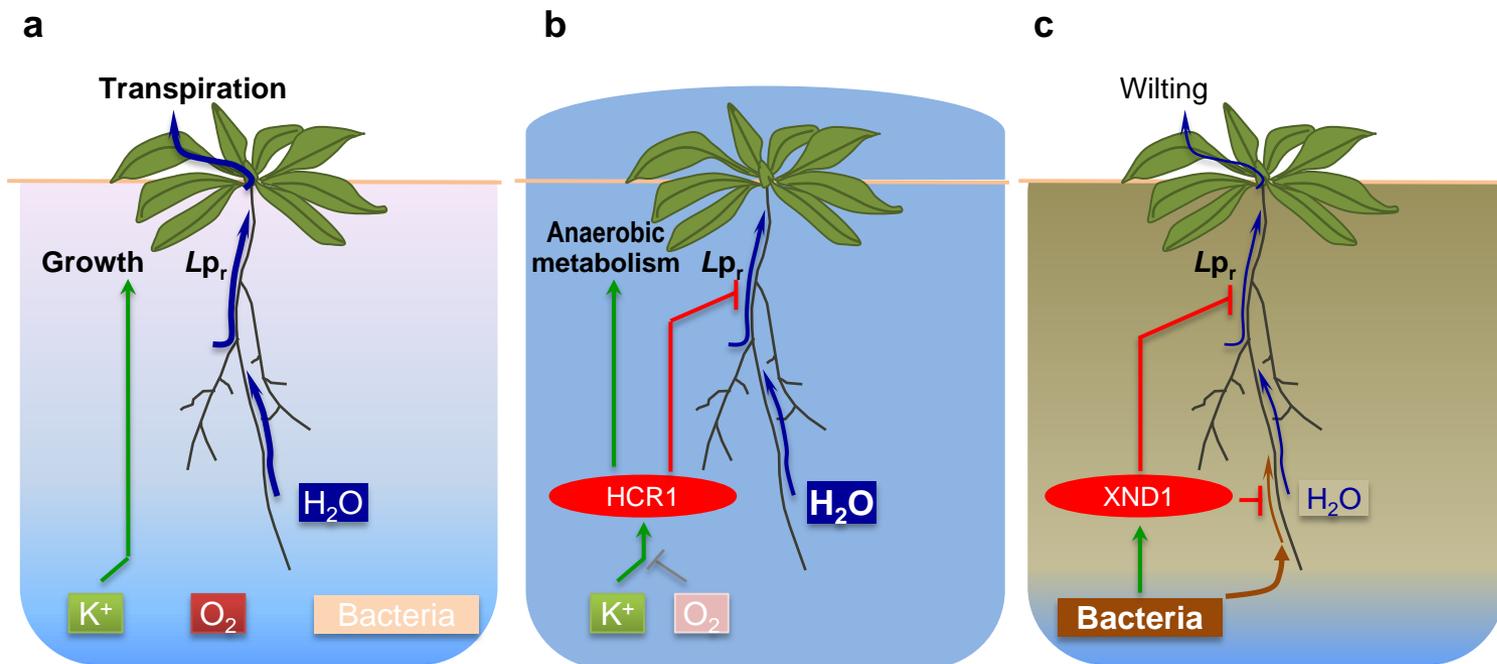


Figure 2