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1 **Keep in touch: the soil-root hydraulic continuum and its role in drought resistance in**
2 **crops**

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9 **Highlight**

10 Rapid soil drying in the vicinity of the root is a major challenge for plant during drought. Plants
11 can adapt to this stress by shaping the root-soil interface.

12

13 **Abstract**

14 Drought is a major threat to food security worldwide. Recently, the root-soil interface has
15 emerged as a major site of hydraulic resistance during water stress. Here, we review the impact
16 of soil drying on whole plant hydraulics and discuss mechanisms by which plants can adapt by
17 modifying the properties of the rhizosphere either directly or through interactions with the soil
18 microbiome.

19

20 **Keywords**

21 Root architecture, rhizodeposition, root hairs, mucilage, rhizosheath, EPS, AMF

22 **Introduction**

23 Water stress is the main factor affecting crop yield worldwide (Hammer et al., 2021) and the
24 impact of water stress on agriculture is expected to augment with increased frequency and
25 intensity of drought spells predicted in most future climate scenarios (Fahad et al., 2017;
26 Potopová et al., 2016). Understanding the factors that control water acquisition and use in plants
27 is critical to adapt agriculture to future dry climate (Tardieu 2022).

28 The hydraulic network at the whole plant scale can be described using a demand and supply
29 scheme (Figure 1). Water loss occurs mostly in leaves by transpiration through stomata, small
30 pores where gas exchange with the atmosphere occurs and whose opening is tightly regulated
31 by the plant water status (Wang et al., 2022). Transpiration is driven by the difference of vapour
32 pressure between the stomatal cavity and the atmosphere, which ultimately creates a gradient
33 of increasing bulk water potentials from the leaves to the roots. This gradient of water potential
34 drives water from the soil within the plant only when the water potential of the root is more
35 negative than that of the surrounding soil. In wet soils and under high transpiration demand the
36 largest drop in water potential is within the plant, and in these conditions, the main hydraulic
37 resistance corresponds to the active regulation of transpiration by stomata. As the soil dries, an
38 important resistance occurs in the soil surrounding the roots. In these conditions, plant traits
39 that impact the water flow to the root surface are relevant for controlling leaf water potential
40 and plant water status.

41 Here, we describe the impacts of the drop in soil matric potential on plant hydraulics in
42 drying soil and discuss mechanisms by which plants cope with the reduction in soil hydraulic
43 conductivity by modifying the properties of the rhizosphere. We further illustrate how a
44 complex interplay between roots and the soil microbiome contributes to sustain the water flow
45 across the soil-root interface under drought.

46 **The soil-root hydraulic continuum and its impact on drought tolerance**

47 Although the soil dries over weeks during a cropping season, millimetre-scale gradients of
48 soil moisture develop around roots over minutes when the transpiration demand cannot be
49 matched by the flow of water from the soil. These gradients are the result of the nonlinearity of
50 the soil hydraulic conductivity, which decreases by several orders of magnitude as the soil
51 matric potential drops, and of the radial geometry of the flow towards roots. Gradients of water
52 potential around the roots were predicted since the early work by Gardner (1960). The concept
53 of matric flux potential allowed more accurate calculation of these gradients (e.g. van Lier et
54 al. 2008; 2013). Despite the improvements in modelling, these gradients remain challenging to
55 measure. An experimental set-up developed by Passioura, (1980) was used to estimate gradients
56 in soil water potential toward the root from the deviation of the leaf water potential from its
57 linear trajectory. Nonlinearity in the relationship between transpiration and leaf water potential
58 were interpreted as the consequence of a loss in the hydraulic conductivity (defined as the
59 intrinsic ability of a material to conduct water, expressed in $\text{m}\cdot\text{s}^{-1}$) of the soil, of the root, or of
60 the root-soil interface. We refer to the hydraulic conductance (defined as the relationship
61 between conductivity and driving force, expressed in $\text{m}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ – conductance is the inverse
62 of resistance) of the root-soil continuum as the combination of the hydraulic conductance of the
63 soil, the root and their interface; precisely, as it is a flow in series, it is the harmonic mean of
64 the conductance of the three elements.

65 Plants continuously adapt to variable atmospheric and soil conditions by altering the
66 hydraulic conductivity of key elements below and above ground. Although the occurrence of
67 these alterations is well accepted, our quantitative understanding of this hydraulic
68 acclimatisation and its impact is incomplete. In wheat (*Triticum aestivum*), neither xylem
69 collapse and cavitation nor a decrease in leaf conductance drive stomatal closure (Corso et al.,
70 2020). Instead, decrease in soil-root hydraulic conductance was the main driver of stomatal
71 closure during soil drying in tomato (Abdalla et al., 2021) and in olive trees (Dominguez and

72 Brodribb, 2020). Under drought, stomatal closure was controlled by a drop in soil water
73 potential at the root-soil interface (Abdalla et al., 2022). These results demonstrate that losses
74 in root hydraulic conductance, which could be due to (i) a disconnection of the root from the
75 soil during moderate water stress and/or (ii) collapse of root xylem conduits, are profound and
76 sufficient to induce stomatal closure. In a recent review, Cai et al. (2022) investigated, across
77 11 crops and 10 contrasting soil textures, the interplay between soil and root hydraulic
78 properties on water uptake during soil drying. The authors found that root water uptake was
79 constrained within a wide range of soil water potential (-6 to -1000 kPa), depending on both
80 soil and root hydraulic properties (Cai et al., 2022). Furthermore, transpiration response to both
81 soil drying and vapour pressure deficit was also found to be soil texture specific (Cai et al.,
82 2022; Koehler et al., 2022). The accumulation of salts at the root surface, which is likely to
83 occur in soil drying conditions and at high transpiration rates, is an additional process hindering
84 water flow across the root-soil interface. Salinity not only induced a more negative predawn
85 leaf water and reduced transpiration rate during soil drying, but also caused a reduction in root
86 hydraulic conductance (Abdalla et al., 2022).

87 Altogether, this shows that the root-soil interface is a major site of hydraulic resistance
88 during drought. Accordingly, plants have developed ways of coping with the creation of
89 gradients of soil water potential near the root during soil drying.

90 **Root traits contribute to maintenance of soil-root hydraulic continuum**

91 Root architecture can impact water acquisition efficiency while root anatomy and
92 physiology control the water transport capacity of the root (Lynch, 1995; Lynch, 2022).
93 Accordingly, root system architectures that would optimise water acquisition in different
94 environments have been proposed based in large part on *in silico* simulations (e.g. Leitner et al
95 2014; Koch et al 2019; Lynch, 2022). Maintenance of the root-soil hydraulic continuum is
96 important in root zones that actively acquire water. In maize, water uptake occurs mainly

97 through seminal roots and their laterals at early developmental stages (Ahmed et al., 2016b).
98 As the root system develops, crown roots appear and become the main contributors of water
99 uptake (Ahmed et al. 2018b). Similarly, crown roots have a higher contribution to water
100 acquisition than primary roots in barley and wheat (Krassovsky et al. 1926, Sallans et al. 1942).
101 Moreover, water uptake and water radial/axial hydraulic conductivity are not homogeneous
102 along the root (Javaux 2008). In maize, water acquisition occurs mainly in the apical parts in
103 the seminal root (close to the tip; Zwieniecki, 2003). Besides, branching density as well as
104 lateral root length impact the ability of the root to acquire water. For instance, larger root surface
105 area attenuates water potential gradients in the rhizosphere due to a lower water flux at the root-
106 soil interface (Abdalla et al., 2022; Cai et al., 2022). Similarly, higher axial hydraulic
107 conductivity in the apical segments combined with shorter and fewer laterals leads to a more
108 uniform repartition of water potential along crown roots in maize (Ahmed et al., 2018b).
109 Therefore, root water uptake is not homogeneous between and along root types and the
110 maintenance of the root-soil hydraulic continuum in drying soils appears crucial in crown root
111 apical zones and highly branched regions.

112 Root traits have been associated with improved root-soil hydraulic continuity in conditions
113 of water stress. Root hairs are tubular extensions of epidermal cells that increase the root surface
114 area in contact with the soil (Ohlert., 1837; Haling et al., 2013). The role of root hairs for
115 nutrient acquisition is well documented, but their role in water uptake remains controversial
116 (Cai and Ahmed et al. 2022). Barley plants with relatively long root hairs showed increased
117 water uptake in drying soils (Carminati et al., 2017; Marin et al., 2021). On the other hand, no
118 differences in water uptake were observed between the *rth3* root hair less maize mutant and its
119 corresponding wild type (Cai et al., 2021; Jorda et al. 2022). It was suggested that short root
120 hairs (as in maize) have little contribution to root water uptake as opposed to relatively longer
121 root hairs (as in barley; Cai and Ahmed, 2022). Barley roots also show denser root hairs as

122 compared to maize which increase the soil-root contact and reduce the radial hydraulic
123 resistance at the root-soil interface (Aslam et al., 2022). Dense root hairs also influence soil
124 density and porosity close to the root by aggregating soil particles (Hallett et al. 2022).
125 Vulnerability (shrinkage or distortion) of root hairs under water stress limits their potential role
126 in water uptake in drying soils. Duddek et al. (2022) demonstrated that, in maize, root hair
127 shrinkage (i.e. reduction of root hair length and volume) was initiated at relatively high soil
128 matric potentials (between -10 and -310 kPa). Hence, recent evidence converges towards a
129 predominant role for longer and denser root hairs in buffering the drop in matrix potential within
130 the rhizosphere by maintaining the root-soil hydraulic continuum in drying soils (Carminati et
131 al., 2017; Marin et al., 2021).

132 Beyond root hair formation, roots can influence the chemical and physical characteristics of
133 their surrounding soil by releasing carbon compounds - a mechanism called rhizodeposition
134 that includes root exudation and dead cell release from the root (Barber, 1995). Root exudates
135 include high molecular weight compounds such as proteins and polysaccharides and lower
136 molecular weight compounds that are mainly composed of primary and secondary metabolites
137 (amino acids, sugars, carboxylates, flavonoids, etc). Root exudates can account for 20 to 40 %
138 of the plant photosynthate depending upon species and varieties within species and are highly
139 controlled by environmental factors (Chen et al., 2022; de la Fuente Cantó et al., 2020).
140 Quantitative and qualitative changes in rhizodeposition have been reported in response to
141 drought (Preece and Peñuelas, 2016; Williams and Vries, 2020; Wang et al., 2021). Drought
142 often leads to a decrease in absolute rhizodeposition due to decrease in photosynthesis and in
143 carbon availability for exudation. However, several studies suggest that there is an increase in
144 relative C allocated to rhizodeposition relative to plant biomass in water stress conditions,
145 highlighting the importance of this trait in response to drought (Williams and Vries, 2020;
146 Wang et al., 2021). Indeed, rhizodeposits can contribute to water stress tolerance directly by

147 changing the physico-chemical properties of the rhizosphere or indirectly as a source of
148 nutrients and signals for soil microbes.

149 Among rhizodeposits, mucilages are polysaccharides produced by active secretory cells of
150 the root cap representing roughly 50% of the root exudates (Ropitiaux et al., 2020). Mucilages
151 have high water retention capability thus enhancing water content around the root and possibly
152 attenuating the drops in soil hydraulic conductivity during drying (Benard et al. 2019). In
153 addition, mucilages can bind soil particles together and thus stabilise soil aggregates (Morel et
154 al., 1991) and affect the physical stability of the rhizosphere (Brax et al., 2020). Mucilage
155 deposition around the root tip might be particularly important to alleviate the drop in soil matric
156 potential in this region of high water uptake (Carminati and Vetterlein, 2013; Carminati et al.,
157 2016). However, the impact of mucilage on water retention and hydraulic conductivity varies
158 between species and is dependent on soil textures (Kroener et al., 2018). For instance,
159 modelling showed that coarse soils require higher mucilage concentration to increase soil water
160 content (Kroener et al., 2018). Their impact also depends on the severity and frequency of
161 drying episodes (Carminati and Vetterlein, 2013). Upon extreme soil drying, mucilage may
162 create a protective layer preventing water loss from the root to the soil as it becomes water
163 repellent when dried (Moradi et al. 2011; Moradi et al., 2012; Ahmed et al., 2016a; Zickenrott
164 et al., 2016). Therefore, rhizodeposition of mucilage may play important roles in delaying soil
165 drying of the rhizosphere and prevent root-soil loss of contact.

166 Altogether, these alterations of the soil by the plant can culminate in some species with the
167 formation of a layer of soil adhering tightly to the root system, called the rhizosheath (George
168 et al., 2014; Mccully., 1999; Ndour et al., 2020; Aslam et al., 2022). Rhizosheath formation is
169 found in many plant families across the plant kingdom and depends mostly on root hair and
170 rhizodeposition (Ndour et al., 2020; Aslam et al., 2022). In dry soils, rhizosheath has higher
171 water content than bulk soil, and may substantially contribute to water uptake (North & Nobel,

172 1997). Accordingly, larger rhizosheath has been associated with improved resistance to water
173 stress in chickpea, foxtail millet and wheat (Rabbi et al., 2018b; Liu et al., 2019; James et al.,
174 2016). Interestingly, rhizosheath formation is largely controlled by the plant genotype and could
175 therefore be targeted by breeding programmes (George et al., 2014; de la Fuente Cantó et al.,
176 2022).

177 **The interplay between root and soil microbiome contributes to shape the hydraulic** 178 **properties of the rhizosphere**

179 Roots interact with many organisms in the soil to shape the rhizosphere microbial
180 communities (de la Fuente Cantó et al., 2020). This in turn has a large impact on soil structure
181 and hydraulic properties. In response to droughts, photosynthesis is reduced and therefore limits
182 carbon availability. In those conditions, there is a trade-off for C allocation between root
183 development (root growth, branching, root hair development, etc) and C invested in the soil
184 compartment (rhizodeposition and symbiosis with soil microbe - chiefly arbuscular mycorrhizal
185 fungi) leading to different strategies to deal with water stress (Wang et al., 2021).

186 Rhizodeposition is a major source of energy, carbon and nitrogen for soil microbes and has
187 therefore a very strong effect on the rhizosphere microbiota, both quantitatively (microbial
188 biomass is positively correlated to the amount of rhizodeposits) and qualitatively (the structure
189 of the microbial population influenced by the nature of the exudates - Preece and Peñuelas,
190 2016). Rhizodeposition varies both quantitatively and qualitatively along the root, between
191 genotypes (species and varieties) and in response to environmental parameters such as water
192 stress (Preece and Peñuelas, 2016; Williams and Vries, 2020; Wang et al., 2021). Changes in
193 rhizodeposition in response to water stress depend on the intensity of drought with a positive
194 impact of mild stress, which decreases as stress intensity increases (Preece and Peñuelas, 2016).
195 Crops seem to have more stable root exudation in response to drought stress than their wild
196 relatives (Preece and Peñuelas, 2016).

197 The reduction in water availability within the soil as well as the changes in rhizodeposition
198 brought about by water stress influence the rhizosphere microbiota (Preece and Peñuelas,
199 2016). Interestingly, the soil microbiota seems to be more resilient (i.e. its structure is less
200 affected) to water stress than plants and resilient microbiota that were subjected to previous
201 water stress may improve plant resilience (Preece and Peñuelas, 2016). In some cases, changes
202 in rhizodeposition and microbiota upon water stress are associated with improved plant drought
203 tolerance (see Preece and Peñuelas, 2016; Williams and Vries, 2020 for review). Soil microbes
204 shape the rhizosphere physico-chemical properties in many ways (de la Fuente Cantó et al.,
205 2020). Microbes produce extracellular polymeric substances (EPS) mainly composed of
206 polysaccharides that are primarily involved in biofilm formation (Flemming and Wigender,
207 2010). Like mucilages, EPS bind soil particles together and change the hydraulic properties of
208 the soil, improving water retention and maintaining the connectivity of the liquid phase around
209 the root (Nazari et al., 2022; Benard et al., 2019). This delays desiccation of the rhizosphere
210 and helps to maintain a flow of water and nutrients during soil drying. Besides, microbial
211 exopolysaccharides contribute to rhizosheath formation (Ndour et al., 2020). It has been shown
212 that bacteria from the root microbiota can modulate (either increase or decrease depending on
213 the strain) suberin deposition in the root endodermis in the context of mineral nutrient
214 homeostasis (Salas-Gonzales et al 2021). This would also have an effect on root hydraulics as
215 it creates a barrier for apoplastic water flow. The microbiome can also change root architecture
216 for instance by inducing root branching (Gonin et al 2023). This would also change root and
217 rhizosphere hydraulics as larger root surface area attenuates water potential gradients in the
218 rhizosphere. However, these effects of the root microbiome have not been studied in the context
219 of water stress.

220 Arbuscular mycorrhizal fungi (AMF) have been shown to be the most important component
221 of the root microbiome for drought tolerance in trees (Allsup et al 2023). The arbuscular

222 mycorrhizal symbiosis is a mutualistic association between most angiosperms and AMF- from
223 the Glomeromycota phylum (Redecker et al., 2013). The fungus develops specific structures,
224 called arbuscules, in root cortical cells to exchange resources with the plant and a network of
225 hyphae that forage the soil for water and nutrients (Smith and Smith, 2011). Association with
226 AMF has been known for a long time to improve plant resistance to water stress (Augé, 2001).
227 Part of this effect is indirect via improved plant mineral nutrition and osmoregulation, reduced
228 drought-induced oxidative stress and increased root hydraulic conductivity (Quiroga et al.,
229 2019; Zulfiqar and Ashraf, 2021; Mbodj et al., 2018). Moreover, the hyphal network binds soil
230 particles together, stabilises aggregates, impacts soil porosity (Hallett et al., 2009; Miller et al.,
231 2000) and link roots to the surrounding soil, limiting hydraulic continuity loss and the formation
232 of air gaps during drying (Augé, 2001). However, the effect of AMF on soil water retention and
233 hydraulic conductivity is very dependent on the soil texture with opposite effects reported for
234 loam and sand (Pauwels et al., 2023).

235 Recently, direct contribution of AMF to water transfer from the soil to plant roots via fungal
236 hyphae was observed (Kakouridis et al., 2022). AMF hyphae can transport water across air gaps
237 in the soil (Kakouridis et al., 2022) and extract water from small pores that are inaccessible to
238 roots, two properties that can be advantageous for the water scavenging in dry soils. Under
239 edaphic stress, AMF maintained the hydraulic continuity between root and soil in drying soils,
240 thereby reducing the drop in soil matric potential near the root surface and sustaining root water
241 uptake in dry soils (Abdalla and Ahmed, 2021). Altogether, this indicates that AMF act as an
242 extension of the root and increase access to soil resources including water.

243 **Conclusion and outlook**

244 The root-soil interface is an important hydraulic resistance upon soil drying affecting whole
245 plant hydraulics and response to drought stress. Accordingly, plants have evolved different
246 mechanisms to shape the physico-chemical properties of the rhizosphere to maintain the soil-

247 root hydraulic continuum and water acquisition. This includes root hair development,
248 rhizodeposition and symbioses with arbuscular mycorrhizal fungi. Interestingly, all these traits
249 are under plant genetic control and could therefore represent new breeding targets to improve
250 plant water use and drought tolerance. Indeed, as recently demonstrated for maize, most of the
251 past selection for drought tolerance was based on traits like phenology and architecture but did
252 not exploit mechanistic traits that contribute to environmental adaptation such as rhizosphere
253 traits (Welcker et al., 2022). More work is needed to better characterise the genetic and
254 physiological mechanisms controlling rhizosphere hydraulics and to evaluate how these impact
255 drought tolerance in a breeding context. As roots influence the hydraulic properties of the
256 rhizosphere, root positioning in the soil column (i.e. root system architecture) defines which
257 regions of the soil exhibit root-induced alterations to their hydraulic properties and therefore
258 the flow of water through the soil. Root system architecture and rhizospheric traits need
259 therefore to be integrated to optimise water uptake by the plant.

260 Hydraulic properties of the soil-root interface can impact plant transpiration and eventually
261 plant water use efficiency. In the actual and future context of water scarcity, agriculture needs
262 to be more water efficient. Developing more efficient crops requires a holistic understanding
263 of water use efficiency that involves a complex regulation of parameters related to soil
264 properties, root traits, transpiration and photosynthesis (Vadez et al., 2023). For having an
265 impact, these properties have to be regarded in the context of specific varieties used in different
266 agrosystems prone to different stress patterns. Models combining soil-plant-atmosphere
267 interactions at the plot level are needed to identify strategies better suited to different types of
268 stress under variable agronomic contexts.

269

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275

276 **Authors contribution**

277 All authors contributed to the first version of the text and revised the manuscript. P.A., A.G.
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287

288 **Conflict of interest**

289 The authors have no conflicts to declare.

290

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Boxes and Figure Legends

Figure 1: The soil - plant - atmosphere continuum. Water movement is driven by differences in water potentials.

Box 1: Recent developments in our understanding of the role of the rhizosphere properties in drought tolerance.

(A) Cai et al. (2022) showed that, during soil drying, root water uptake is constrained within a wide range of soil water potential (-6 to -1000 kPa), depending on both soil and root hydraulic properties.

(B) Dominguez-Rodriguez and Brodribb (2020) demonstrate that upon soil drying, the hydraulic resistance of the root-soil interface increases to ca. 90% of the total soil-plant hydraulic resistance and thus represents the main constraint to transpiration. The resistance of each component was measured in olive trees by following the rehydration rate of plants/organs submitted to different drought stress intensities

(C) Abdalla et al. (2021) illustrated that stomatal closure under drought is driven by an increase in soil-root hydraulic resistance.

(D) Müllers et al. (2023) estimated the vertical distribution of conductance and reported that, under drought, maize plants locally increase root conductivity in wetter soil layers hereby compensating for a reduced root conductance in upper, drier layers.

Box 2: Key developments in our understanding of the role of the root traits that contribute to building up the rhizosphere.

(A) Burak et al. (2021) highlighted that both root hairs length and density promote rhizosheath formation in barley and maize.

(B) Brax et al. (2020) studied the influence of the physico-chemical properties of root mucilage on the microstructural stability of sand.

(C) Galloway et al. (2022) showed altered properties and structures of polysaccharides exuded by the root in a root hairless mutant of barley. This highlighted the role of root hairs in rhizodeposition.

(D) Duddek et al. (2022) demonstrated that, in maize, root hair shrinkage during soil drying, was initiated at relatively high soil matric potentials (between -10 and -310 kPa). This highlights the important role of root hairs in maintaining root-soil continuity.

Box 3: Recent developments in our understanding of the role of the microbiome in shaping the root-soil hydraulic continuum.

(A) Nazari et al. (2022) reported a meta-analysis of more than 80 studies showing the role of mucilages in shaping the rhizosphere microbial habitat. Mucilages are degraded by microbes that produce exopolysaccharides (EPS) with similar properties. Altogether, plant mucilage and bacterial exopolysaccharides form a mucigel that binds soil particles together and changes the hydraulic properties of the soil.

(B) Kakouridis et al. (2022) showed that AMF hyphae can directly transport water from the soil to the root and that this transport can occur across air gaps in the soil. Part of the transport occurs in hyphae through an extracytoplasmic pathway.

(C) Pauwels et al. (2023) demonstrated that colonisation by AMF hyphae changes water retention and hydraulic conductivity in root-free soil. However, the response was opposite in soils with very contrasted texture (loam and sand).

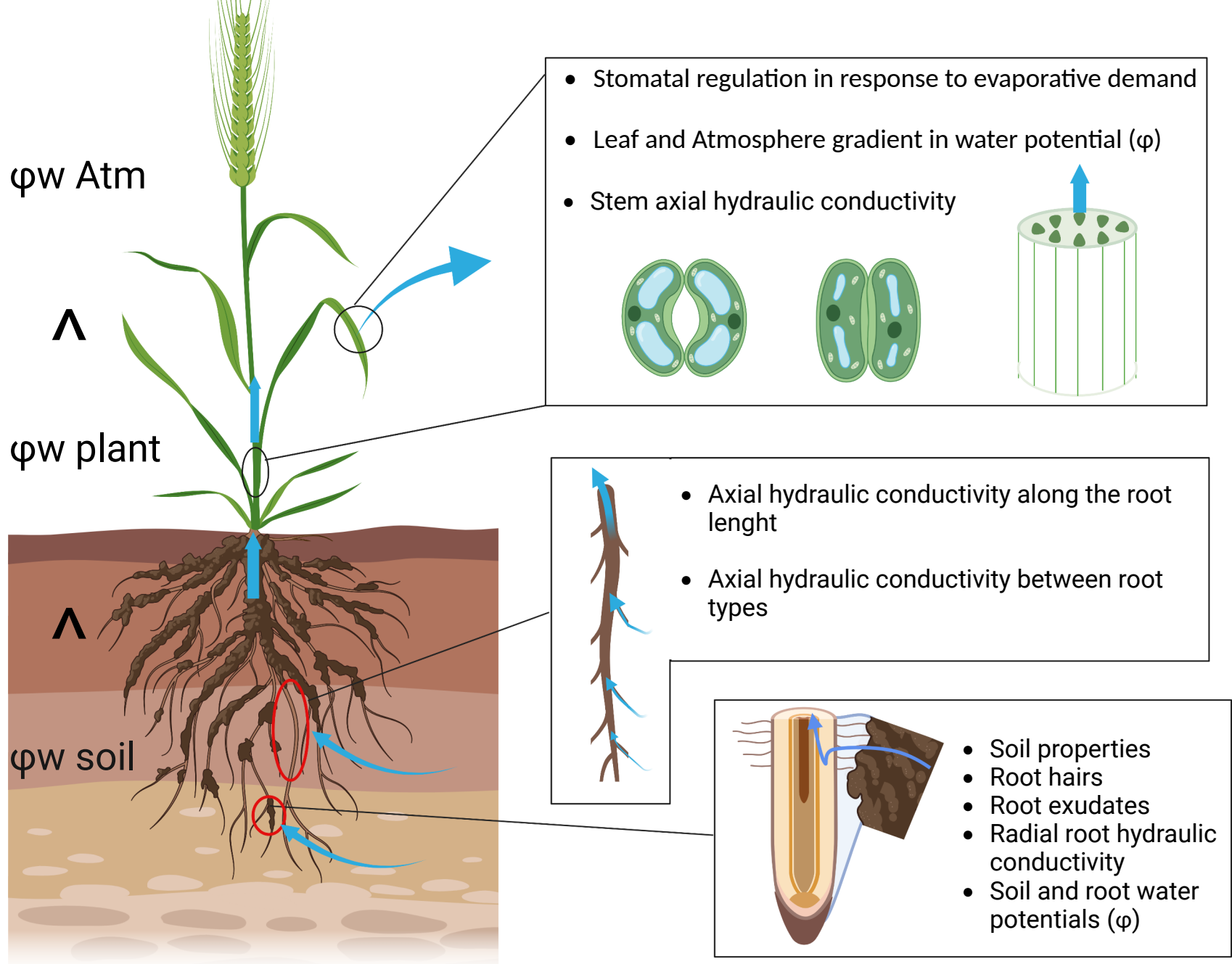


Figure 1: The soil - plant - atmosphere continuum. Water movement is driven by differences in water potentials. Figure produced with BioRender.com.

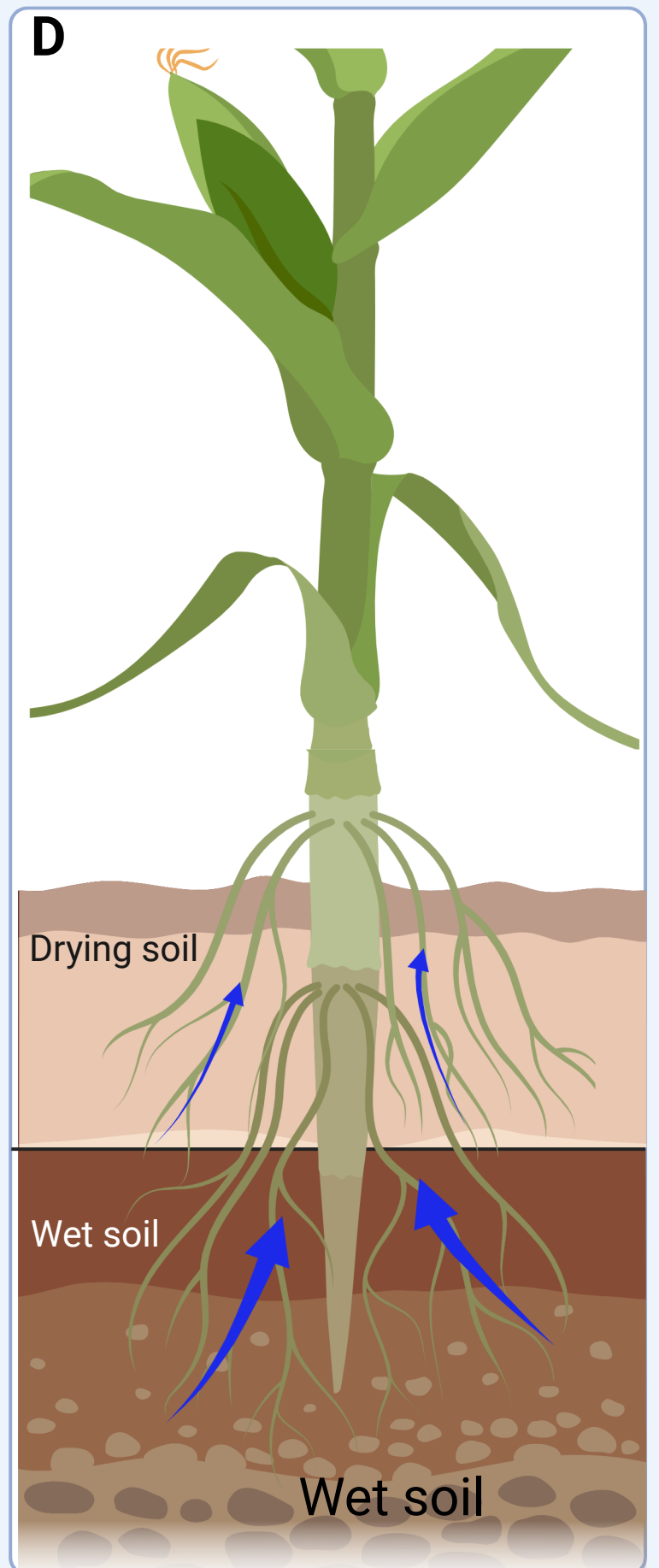
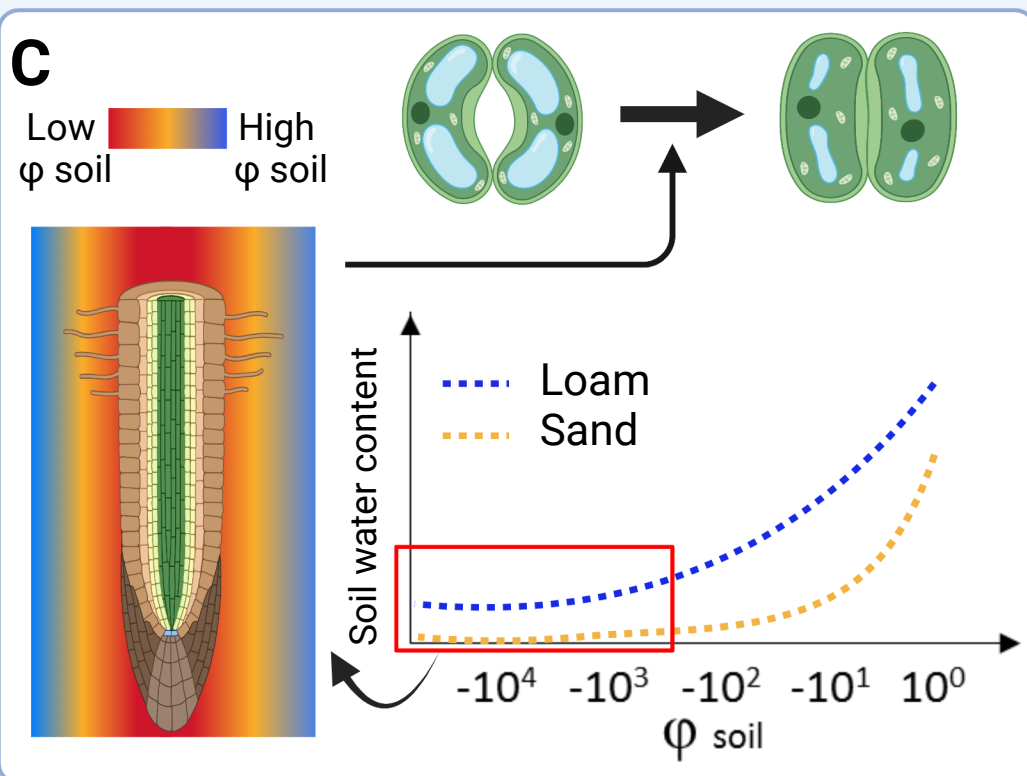
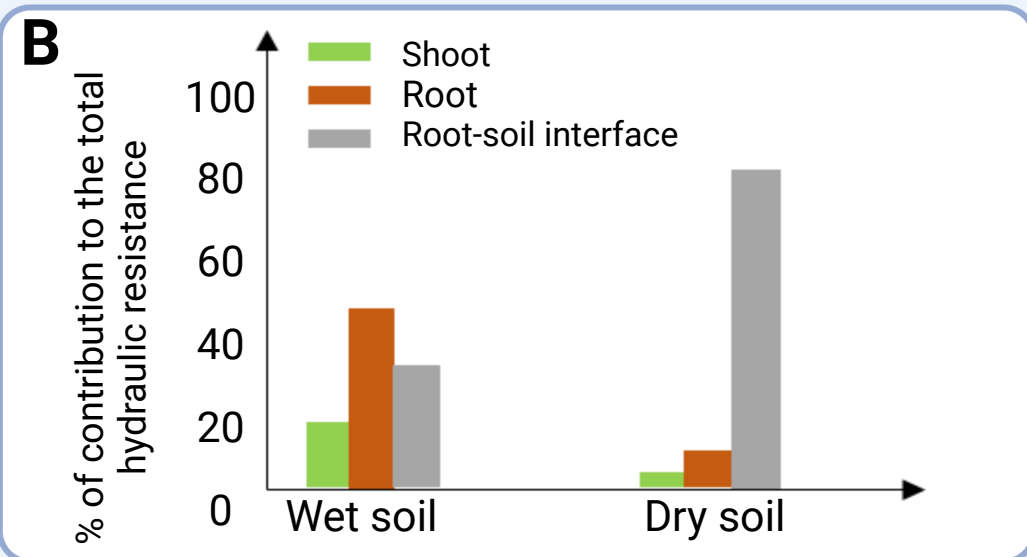
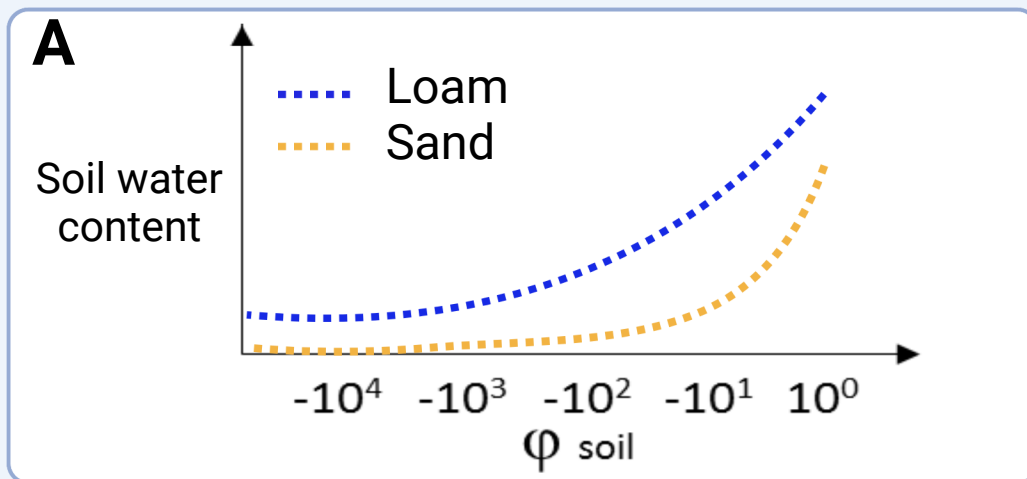
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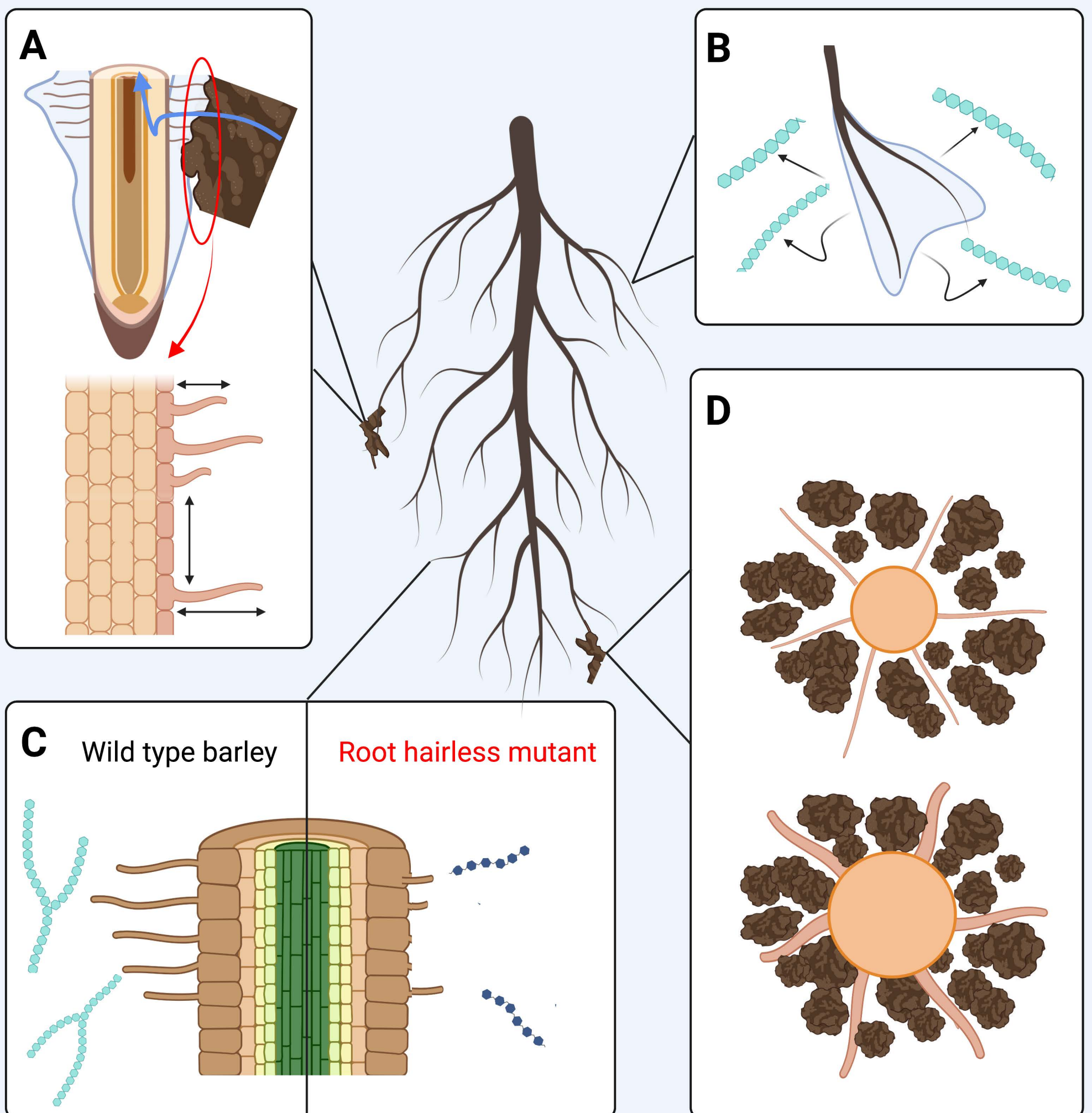
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