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1 **Deep fine roots in forest ecosystems: why dig deeper?**

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12

## **Abstract**

13 While the number of studies dealing with fine root dynamics in deep soils layers (depth > 1  
14 m) has increased sharply recently, the phenology, the morphology, the anatomy and the role  
15 of deep fine roots are still poorly known in forest ecosystems. This review summarizes the  
16 current knowledge on fine root production, mortality and longevity in deep soil layers,  
17 mycorrhizal association with deep roots, and the role of deep fine roots on carbon, water and  
18 nutrient cycling in forest ecosystems. Plant species are known to be more deeply rooted in  
19 tropical ecosystems than in temperate and boreal ecosystems, but deep-rooted species are  
20 common in a wide range of climates. Deep fine roots are highly plastic in response to changes  
21 in environmental conditions and soil resources. Recent studies show that functional traits can  
22 be different for deep and shallow roots, with a possible functional specialization of deep fine  
23 roots to take up nutrients. With higher vessel diameter and larger tracheid, the anatomy of  
24 deep fine roots is also oriented toward water acquisition and transport by increasing the  
25 hydraulic conductivity. Deep fine roots can have a great impact on the biogeochemical cycles  
26 in many forests (in particular in tropical areas where highly weathered soils are commonly  
27 very deep), making it possible to take up water and nutrients over dry periods and  
28 contributing to store carbon in the soil. The biogeochemical models in forest ecosystems need  
29 to consider the specificity of deep root functioning to better predict carbon, water and nutrient  
30 cycling as well as net ecosystem productivity.

31

32 **Key words:** deep rooting, root growth, root traits, carbon sequestration, water uptake, nutrient  
33 uptake, deep mycorrhizas

## 34 **Introduction**

35 Roots have an essential role in forest ecosystems through the mechanical function of tree  
36 anchorage and the physiological function of absorbing and transporting the amounts of water  
37 and nutrients needed for plant development (Pregitzer *et al.*, 2002; McCormack and Guo,  
38 2014). The anchorage function is mainly enabled by physical interactions between the roots  
39 and the soil. The absorptive function is more complex as it involves biogeochemical  
40 interactions between fine roots, soil particles and soil biota, with sometimes symbioses  
41 between fine roots and soil bacteria or fungi. Fine roots, commonly considered as root with a  
42 diameter lower than 2 mm (McCormack *et al.*, 2015), have the ability to adapt to changing  
43 environments to facilitate plant development. Fine root activity can modify physical, chemical  
44 and biological soil properties, which can have repercussions at the plant level but also at the  
45 ecosystem level (McCormack *et al.*, 2015). Indeed, fine roots play a major role in carbon (C)  
46 cycling in forest ecosystems, with large C inputs into the soil through root exudates and  
47 necromass production, as well as large C returns to the atmosphere through root respiration  
48 and decomposition processes (Balesdent and Balabane, 1996; Strand *et al.*, 2008). The great  
49 plasticity of root systems, both architecturally and functionally, can be strongly influenced by  
50 plant phenology, soil properties and climatic conditions (Hodge *et al.*, 2009). Fine root  
51 dynamics have been studied quantifying production and mortality (Hendrick and Pregitzer,  
52 1993; McCormack and Guo, 2014), turnover and survivorship (Anderson *et al.*, 2003),  
53 senescence (Huck *et al.*, 1987) and elongation rates (Germon *et al.*, 2016; Lambais *et al.*,  
54 2017). Fine root dynamics are driven by exogenous factors like soil temperature and water  
55 content (Coll *et al.*, 2012) and endogenous factors like hormone productions (McAdam *et al.*,  
56 2016) and photosynthate and nutrient allocations within the plant (Tierney and Fahey, 2002;  
57 Sloan *et al.*, 2016).

58 Binkley (2015) pointed out the critical need to include depth and timescale of ecological  
59 processes below the soil surface in a modern conceptualization of forest ecosystems. The full  
60 'critical zone' concept from Earth science should be included in conventional thinking about  
61 ecosystems and deep roots can be a key functional element of the Critical Zone (Richter and  
62 Billings, 2015; Pierret *et al.*, 2016). Shrub and tree roots have the ability to explore huge  
63 volumes of soil and can be found at great depths in xeric environments (Canadell *et al.*, 1996;  
64 Schenk and Jackson, 2002). Deep roots improve tree tolerance to drought (McDowell *et al.*,  
65 2008; Nardini *et al.*, 2016) and store C in deep soil layers (Balesdent *et al.*, 2018).  
66 Understanding the spatial and temporal variability of fine root functioning in deep soil layers  
67 is needed to improve our understanding of biosphere-atmosphere interactions (Zeng *et al.*,  
68 1998; Kleidon and Heimann, 2000), and the accuracy of terrestrial biosphere models (Saleska  
69 *et al.*, 2007; Christoffersen *et al.*, 2014). Even though the importance of deep root systems has  
70 been highlighted in several reviews focused on trees (Canadell *et al.*, 1996; Maeght *et al.*,  
71 2013; Pierret *et al.*, 2016) or on crops (Thorup-Kristensen *et al.*, 2020), the functional  
72 significance of deep fine root dynamics, and their contribution to biogeochemical cycles are  
73 still poorly documented. Maeght *et al.* (2013) proposed to consider as deep roots the roots  
74 growing at a depth of more than 1 m. Even though fine root densities are low at great depths,  
75 deep roots are likely to play a key role in many processes of plant physiology, community  
76 ecology and biogeochemistry in forest ecosystems. Deep roots are found in many biomes  
77 where drought periods can occur (Nepstad *et al.*, 1994; Canadell *et al.*, 1996; Jackson *et al.*,  
78 2000; Schenk and Jackson, 2002). However, the maximum rooting depth reported in the  
79 scientific literature is commonly underestimated because most studies did not sample soils  
80 down to the root front, which artificially truncated root distributions (Freycon *et al.*, 2015). In  
81 a review paper, Stone and Kalisz (1991) reported 37 examples of root systems observed  
82 between 10 and 60 m below the soil surface, indicating that the maximum rooting depth can

83 vary considerably with climatic and soil conditions as well as between tree species. In another  
84 review paper, Canadell *et al.* (1996) estimated that roots extend in deep horizons down to 9.5  
85  $\pm 2.4$  m in deserts,  $7.3 \pm 2.8$  m in tropical evergreen forest and  $15.0 \pm 5.4$  m in tropical  
86 grassland and savannah, with a maximum rooting depth of 68 m reported for *Boscia*  
87 *albitrunca* trees in Botswana. Schenk and Jackson (2002) showed in a meta-analysis that the  
88 maximum rooting depth increased for plants growth forms as their size and life span  
89 increased, with the highest values for trees and shrubs (Figure 1).

90 Distributions and dynamics of deep roots are still poorly documented relative to shallow roots  
91 (Richter and Billings, 2015; Pierret *et al.*, 2016). Despite recent technical innovations, the  
92 observation of deep roots remains difficult, time-consuming, expensive and requires a  
93 combination of methods to obtain reliable results (Maeght *et al.*, 2013). Direct and indirect  
94 techniques can be used for monitoring deep roots depending on the research aim (Vogt *et al.*,  
95 1998; Hendricks *et al.*, 2006). Deep root functioning at considerable soil depths has been  
96 indirectly studied by quantifying water, nitrogen and carbon budgets of the ecosystem (Vogt  
97 *et al.*, 1998). Direct methods based on soil excavation, trenches, sequential coring, ingrowth  
98 cores, and rhizotron observations have been used to monitor root dynamics *in situ* (Maeght *et*  
99 *al.*, 2013). Both indirect and direct approaches can have potential biases leading to  
100 overestimate or underestimate root growth and root decomposition. There is no consensus on  
101 the most effective and reliable method that should be used to quantify fine root dynamics.

102 Several attempts in plant root architecture and development modelling were performed so far  
103 without considering deep rooting patterns. Some models were based on a continuous  
104 formalism through partial derivative equations that simulate root apex density and root  
105 interaction through time and space (Bastian *et al.*, 2008; Dupuy *et al.*, 2010; Bonneau *et al.*,  
106 2012). These types of models enabled direct coupling with water transport models (Doussan  
107 *et al.*, 1998), or nutrient uptake competition models (Bonneau *et al.*, 2012; Mayer *et al.*, 2012;

108 Gérard *et al.*, 2017). Other models were based on a discrete and/or random formalism that  
109 simulates root architecture, growth, branching and death processes. Some of them were based  
110 on mathematical processes such as L-systems (Leitner *et al.*, 2010) or fractals (van Noordwijk  
111 *et al.*, 1994; Ozier-Lafontaine *et al.*, 1999), or using combinations of the two (Shibusawa,  
112 1994), others were derived from direct measurements performed on real plants taking into  
113 account root-soil interaction functions (Diggle, 1988; Jourdan and Rey, 1997a, b; Lynch *et*  
114 *al.*, 1997; Pagès *et al.*, 2004; Dunbabin *et al.*, 2013; Pagès *et al.*, 2014; Barczi *et al.*, 2018),  
115 with water and nutrient uptake (Wu *et al.*, 2007; Javaux *et al.*, 2008; Leitner *et al.*, 2010;  
116 Postma *et al.*, 2017). Most of these models, with the exception of some of them (Jourdan and  
117 Rey, 1997a, b; Pagès *et al.*, 2014; Barczi *et al.*, 2018), are mainly designed for annual and  
118 herbaceous plants, with a short lifespan and a limited rooting depth. For perennial crops,  
119 shrubs and trees with longer lifespans and deeper rooting strategies, previous models do not  
120 consider possible changes in root architecture, diameter, growth, mortality, or functioning  
121 processes depending on (great) soil depth. A first attempt was made with the DigR model,  
122 which manages parameter values that may change depending on the position along roots of  
123 each type, changing with soil depth or not (Barczi *et al.*, 2018).

124 Our paper provides an up-to-date literature review on morphological and phenological traits  
125 of fine roots along deep soil profiles in forest ecosystems. The production, mortality rates and  
126 longevity of deep fine roots, as well as symbiosis with mycorrhizas, their role in water and  
127 nutrient uptake and their influence on belowground C sequestration are reviewed. We  
128 addressed the following questions: 1) How can environmental conditions, soil resources and  
129 symbiotic association along deep soil profiles influence the functioning of fine roots and their  
130 main functional traits? 2) Do we need to take into consideration the specificity of deep fine  
131 roots to improve current predictions of C, water and nutrient cycling in forest ecosystems? We

132 proposed a conceptual scheme summarizing how root traits vary between the topsoil and deep  
133 soil layers (Figure 2).



134

## 1. Morphology and anatomy of deep fine roots

135 The morphology and architecture of root systems vary greatly between plant species but also  
136 within individual species (Cannon, 1949; Nibau *et al.*, 2008). Biogeochemical processes in  
137 forest ecosystems are strongly influenced by root architecture (Addo-Danso *et al.*, 2020), as  
138 well as the ability of plants to survive under stressful conditions (Penuelas *et al.*, 2013).  
139 Functional traits of fine roots vary with environmental conditions and resource distribution  
140 (Ostonen *et al.*, 2007). Fine roots have been classified depending on their main functions and  
141 metabolic activity either in absorptive roots involved in the capture and uptake of soil  
142 resources that are extremely fine and are the most distal roots, or in roots involved in the  
143 transport of water and nutrients that are larger roots, higher in the branching order, and  
144 constitute most of the structural part of the root system (McCormack *et al.*, 2015). The high  
145 variability of environmental conditions such as soil moisture and temperature or resource  
146 (water and nutrients) availability along soil profiles result in contrasting fine root functional  
147 traits with soil depth.

148 Fine roots have been commonly considered as a coherent “pool” of an arbitrary 0-2 mm root  
149 diameter class with the same dynamics, turnover rates, respiration costs and the same rates of  
150 water and nutrient uptake (Persson, 1980; Jackson *et al.*, 1997). However, an increasing  
151 number of recent studies suggest that fine root functions can vary depending on the root order  
152 of the branching root system (Pregitzer *et al.*, 1997; Majdi *et al.*, 2001; Pregitzer *et al.*, 2002;  
153 Guo *et al.*, 2004; Wang *et al.*, 2006; Hishi, 2007; Wang *et al.*, 2007; Pregitzer, 2008;  
154 Valenzuela Estrada *et al.*, 2008; Comas and Eissenstat, 2009; Fan and Guo, 2010; Rewald *et al.*,  
155 2011; Beyer *et al.*, 2013; Rewald *et al.*, 2018; Wada *et al.*, 2019). These studies have  
156 clearly shown that several fine root traits such as diameter (D), length (L), specific root length  
157 (SRL), specific root area (SRA), root length density (RLD), branching density but also  
158 number of xylem vessels, tissue density, C/N ratios, phenolic, lignin and suberin contents,

159 mycorrhizal colonization and median lifespans varied depending on the root order. The  
160 highest fine root order number, the coarsest root diameter, the highest median lifespan, tissue  
161 density, xylem vessel number, lignin and suberin content, and the lowest length, branching  
162 density, RLD, SRL, SRA, C/N ratios, and mycorrhizal colonization.

163 Fine root exploration in deep soil layers represents a high metabolic cost for plants (Iversen,  
164 2010), which may influence fine root traits (Prieto *et al.*, 2015). Specific root length (SRL)  
165 and specific root area (SRA) can be affected by soil depth (Maurice *et al.*, 2010; Prieto *et al.*,  
166 2015; Pinheiro *et al.*, 2016), while other functional traits (concentrations of C, N, cellulose,  
167 lignin,...) seem less sensitive (Prieto *et al.*, 2015). SRL and SRA values are positively  
168 correlated with the soil volume in contact with fine roots, which influences the plant capacity  
169 to take up limited soil resources (Addo-Danso *et al.*, 2020). Changes in specific root length  
170 and specific root area with soil depth have been little investigated and the trends are not clear  
171 (Makita *et al.*, 2011; Prieto *et al.*, 2015; Pinheiro *et al.*, 2016). Pinheiro *et al.* (2016) showed a  
172 slight increase in SRL and SRA with soil depth down to 13.5 m for 4 genotypes of several  
173 *Eucalyptus* species in Brazil. Maurice *et al.* (2010) also found that SRL increased with soil  
174 depth (down to 3 m) in *Eucalyptus* plantations of different ages. On the contrary, SRL  
175 decreased with soil depth down to 1.2 m in *Pinus pinaster* plantations in France (Bakker *et*  
176 *al.*, 2009). Adriano *et al.* (2017) found no significant changes in SRL with soil depth down to  
177 8 m in *Citrus sinensis* plantations, but they observed a tendency toward an increase in mean  
178 fine root diameters. Gwenzi *et al.* (2011) also found that fine root thickness tended to increase  
179 with soil depth (down to 1.4 m) in *Acacia rostellifera* and *Melaleuca nesophila* plantations in  
180 Western Australia. Prieto *et al.* (2015) measured fine root functional traits in 20 plant  
181 communities under tropical climate, montane climate, and sub-humid Mediterranean climate.  
182 They showed that fine roots were thicker in deep soil layers (down to 1.6 m) compared to the  
183 topsoil. On the contrary, Sochacki *et al.* (2017) observed that root diameter decreased with

184 depth down to 6 m in *Eucalyptus globulus* plantations in southwest Australia. Mixing tree  
185 species can also greatly influence SRL and SLA but studies comparing fine root traits in  
186 mixture with the monospecific stands along deep soil profiles are scarce. Germon *et al.* (2018)  
187 showed that SRL and SRA values in mixed-species stands of *Acacia mangium* and *Eucalyptus*  
188 *grandis* were 110–150% and 34% higher, respectively, than in their monoculture, and the  
189 same pattern was observed between the topsoil and a depth of 6 m. Fast-growing species  
190 require a rapid and efficient acquisition of resources above and belowground, which generally  
191 translate into higher SRA and SRL values compared to slow-growing species, in particular in  
192 deep soil layers (Ryser, 2006; Reich, 2014; Jo *et al.*, 2015). High SRL and thin roots are often  
193 associated with a better capacity to capture soil resources (Hodge, 2004). Establishing a deep  
194 root system with a high area of contact between soil and fine roots (through high fine root  
195 density and SRA values) makes it possible to withdraw water from a large soil volume  
196 (Jackson *et al.*, 2000).

197 Deep roots are mainly oriented toward water acquisition and transport. McElrone *et al.* (2004)  
198 showed that deep roots of *Juniperus ashei*, *Bumelia lanuginosa*, *Quercus fusiformis* and  
199 *Quercus sinuate* had higher vessel diameter and larger tracheid than shallow roots in deep soil  
200 layers, down to a depth of 18-20 m, with higher hydraulic conductivity (Figure 3). Similar  
201 results were found for eucalypt fine roots in Brazil, where xylem vessels were less abundant  
202 but with a larger diameter at depth > 10 m than shallow roots of the same diameter class  
203 (Perron-Gomide *et al.*, Com. Pers. 2020). In line with those results, Pate *et al.* (1995) showed  
204 that roots at a depth of 2 m had larger xylem conduits, higher SRL and SRA values, as well as  
205 hydraulic conductivities up to 15 times higher than roots in shallow layers for tree and shrub  
206 species of *Proteaceae* (*Banksia prionotes*, *Banksia ilicifolia* and *Adenanthos cygnorum*) in  
207 Australia. Physiological and anatomical adjustments of fine roots in deep soil layers might be  
208 an adaptation of plants to maximize their hydraulic efficiency (McElrone *et al.*, 2007). Even

209 those promising results suggesting that very deep roots, despite their scarcity, could have a  
210 key role to take up water during drought periods, studies dealing with fine root morphology  
211 and anatomy at great depth are still scarce.

## 212 **2. Phenology of deep fine roots**

213 Fine roots in deep and shallow soil layers exhibit contrasting phenology with an asynchrony  
214 of growth. Maeght *et al.* (2015) showed that shallow fine root growth of *Hevea brasiliensis*  
215 was synchronized with rainfall events and ceased during the dry season. On the contrary, fine  
216 root growth occurred at the end of the wet season and continued over the dry season at a depth  
217 of more than 2.5 m. Germon *et al.* (2016) also observed an asynchrony between the growth of  
218 shallow and deep roots in an agroforestry system with walnut and durum wheat in the south of  
219 France. While the growth of tree roots in the topsoil occurred mainly in summer, root growth  
220 during the rainy period (in winter) was mainly observed at a depth of more than 2.5 m. The  
221 same behavior has been shown in tropical *Eucalyptus* plantations growing in very deep soils  
222 in Brazil. An asynchrony between shallow and deep root growth was observed, with fine root  
223 growth occurring in the topsoil over the rainy summer while it peaked deeper than 3 m at the  
224 end of the dry season (Lambais *et al.*, 2017). In another *Eucalyptus grandis* stand, Germon *et*  
225 *al.* (2019) showed a negative correlation between the amount of extractable water in the  
226 topsoil and the flushes of fine root growth in very deep soil layers. In those plantations, fine  
227 root growth in deep soil layers seems to be related to the overall water demand of the whole  
228 tree and controlled by the need to use increasingly deeper water resources when water  
229 becomes scarce in the topsoil, which is consistent with modeling studies (Christina *et al.*,  
230 2017; Christina *et al.*, 2018). Vertical growth rates of trees were almost symmetrical above-  
231 and below-ground in *Eucalyptus* plantations, reaching 10.4 and 19.2 m in height and a  
232 maximum rooting depth of 9.2 and 15.8 m at 1.5 and 3.5 years after planting, respectively  
233 (Christina *et al.*, 2011). Other studies using different methodologies (deep drilling,

234 observations on trench walls, injection of  $^{15}\text{N}$  tracer) in the same area confirmed this velocity  
235 of root front displacement (Laclau *et al.*, 2013b; Pinheiro *et al.*, 2016; Pinheiro *et al.*, 2019).  
236 The growth rates of *Eucalyptus* roots observed on minirhizotrons by Lambais *et al.* (2017) are  
237 consistent with this downward speed of exploration, with mean elongation rates increasing  
238 with soil depth up to a maximum value of  $3.6 \text{ cm day}^{-1}$  over a short period below 3 m. In  
239 another *Eucalyptus grandis* stand, minirhizotron observations confirmed higher fine root  
240 elongation rates in deep soil layers than in the topsoil (Figure 4), reaching a maximum of 4.3  
241 cm per day over a short period at depths below 5 m (Laclau *et al.*, 2013b; Germon *et al.*,  
242 2016; Lambais *et al.*, 2017; Germon *et al.*, 2019).

243 Increasing root growth rates with soil depth could be an adaptation to drought (Annerose and  
244 Cornaire, 1994), providing a rapid access to large amounts of water stored in deep soil layers  
245 (Christina *et al.*, 2017). This pattern suggests a positive feedback from root growth downward  
246 to shoot growth (Friend *et al.*, 1994). Environmental conditions and plant growth regulators  
247 may control root exploration of deep soil layers (López-Bucio *et al.*, 2003). Soil water  
248 contents are commonly higher in deep soil layers and variations of temperature are lower than  
249 in the topsoil (Du and Fang, 2014; Radville *et al.*, 2016). Climatic factors are buffered in deep  
250 soil layers, fluctuating less throughout the day and the seasons than in the upper layers, which  
251 influences differentially root phenology along deep soil profiles. Changes in fine root  
252 phenology with soil depth might also be controlled by other factors. As deep roots are more  
253 distant from the shoot than shallow roots, photosynthates might take more time to reach deep  
254 roots.

255 The longevity of fine roots generally increases with soil depth (Hendrick and Pregitzer, 1996;  
256 Baddeley and Watson, 2005) but root behavior at depth may be different in some situations.  
257 Wells *et al.* (2002) showed that root longevity of *Prunus persica* significantly increased with  
258 soil depth down to 1.6 m. Germon *et al.* (2016) showed that the mortality of walnut roots was

259 higher in the topsoil than in deep soil layers with a median life span of 167 days within the  
260 first soil meter and 208 days in the 2.5-4.7 m layer in an agroforestry system in the south of  
261 France. On the contrary, Maeght *et al.* (2015) found that root lifespan decreased with soil  
262 depth in a rubber tree plantation in Thailand, from 180-250 days between the depth of 1 and  
263 2.5 m to 120 days between 3 and 4.5 m. Lambais *et al.* (2017) found no significant differences  
264 in the lifespan of *Eucalyptus* fine roots between the topsoil and a depth of 6 m in Brazil. The  
265 relationship between depth and fine root longevity is therefore probably dependent on the  
266 ecophysiology of tree species as well as on local environmental parameters (e.g., temperature,  
267 water content, N availability, CO<sub>2</sub> and probably O<sub>2</sub> partial pressure) (Vogt *et al.*, 1995). There  
268 are still major uncertainties about the mechanisms controlling fine root phenology in deep soil  
269 layers (Radville *et al.*, 2016).

### 270 **3. Fine root biomass and carbon sequestration in deep soil layers**

271 Soil C storage may be strongly underestimated because most studies have focused on the  
272 topsoil (Harrison *et al.*, 2011; Callesen *et al.*, 2016). While fine roots play a major role in the  
273 global carbon cycle, their contribution on soil C storage in very deep soil layers remains little  
274 understood (Fontaine *et al.*, 2007; Balesdent *et al.*, 2018). Fine root biomass deeper than 1 m  
275 is generally a small proportion of the total biomass in forest ecosystems (Schenk and Jackson,  
276 2002; Pierret *et al.*, 2016). However, the huge C stocks in deep soil layers worldwide suggest  
277 that fine root dynamics could have a strong impact, on the long-term (Rumpel and Kögel-  
278 Knabner, 2011; Stahl *et al.*, 2016). Fine roots account for large C inputs to the soil through the  
279 release of exudates and root necromass and large amounts of C return to the atmosphere  
280 through root respiration and decomposition processes (Balesdent and Balabane, 1996; Strand  
281 *et al.*, 2008). Estimating fine root production and turnover throughout the entire soil profile is  
282 needed to predict more accurately the potential role of forest ecosystems to mitigate climate  
283 change.

284 Even though fine root densities sharply decrease with soil depth, the root biomass at a depth  
285 of more than 1 m depth has probably been underestimated. Maeght *et al.* (2015) showed that  
286 more than 50% of the total fine root biomass was below 1 m depth in a rubber plantation in  
287 Thailand. Fine root biomass between the depths of 1.0 and 4.0 m was 5.8 t ha<sup>-1</sup> while it  
288 amounted to only 4.8 t ha<sup>-1</sup> in the 0-1 m soil layer. Soil coring and measurements of fine root  
289 intersects on deep soil trenches showed a similar pattern in Brazil for several *Eucalyptus*  
290 species with about 50% of the total fine root length at a depth of more than 1 m, from 1 to 6  
291 years after planting (Laclau *et al.*, 2013b; Pinheiro *et al.*, 2016). In an agroforestry system in  
292 the south of France, Cardinael *et al.* (2015) showed that 35% of the total fine root intersects of  
293 walnut trees on trench walls were deeper than 2 m. At the same site, using the minirhizotron  
294 technique, Germon *et al.* (2016) measured 25% of the total fine root production deeper than 4  
295 m. Germon *et al.* (2018) showed that the proportion of fine root biomass in the 0-1 m layer  
296 relative to the total fine root biomass down to 17 m was 31% in *Eucalyptus grandis* stands,  
297 52% in *Acacia mangium* stands and 37% in a mixture with 50% of the two species, at 4 years  
298 after planting. The proportion of deep roots increases with stand age in young stands. Fine  
299 roots below 1 m represented 10 %, 30% and 42% of the total fine root biomass in 2-, 4- and  
300 12-year-old *Ziziphus jujube* plantations in China (Ma *et al.*, 2013). Fine root intersects on  
301 trench walls at a depth of more than 4 m represented 5%, 10% and 15% of total fine roots in  
302 1-, 3.5- and 6-year-old *Eucalyptus* plantation in Brazil (Laclau *et al.*, 2013b). The rooting  
303 depth also increased with stand age down to a maximum of 23.2 m at age 22 years in apple  
304 orchards in a sub-humid region of China, and roots deeper than 1 m accounted for 49% of the  
305 total fine root biomass at 22 years (Li *et al.*, 2019). However, the increase of root biomass in  
306 deep soil layers can decrease water availability in sub-humid or arid climates (Figure 5).

307 A recent meta-analysis of changes in stable carbon isotope signatures across different climatic  
308 zones (at 112 sites) showed that the proportion of carbon allocated deeper than 30 cm was

309 much higher than the proportion of root biomass documented in meta-analyses (Balesdent *et*  
310 *al.*, 2018). This pattern could be explained by the contribution of root exudates in addition to  
311 root mortality as well as by reduced decay rates at depth. Several interacting processes could  
312 contribute to slow down decay rates at depth: scattered microbial biomass, stabilization of soil  
313 organic matter by minerals, as well as a reduced stimulation of SOC decomposition by the  
314 supply of fresh carbon (priming effect) (Fontaine *et al.*, 2007). Fine root decomposition rates  
315 influence the ability of forest ecosystems to store C and act as a sink for CO<sub>2</sub>. When roots are  
316 decomposed, parts of root tissues are incorporated into the soil organic matter (Strand *et al.*,  
317 2008). De Camargo *et al.* (1999) showed that fine roots can be decomposed at least down to a  
318 depth of 5 m in eastern Amazon. Nepstad *et al.* (1994) estimated that C stocks deeper than 1  
319 m exceeded SOC in the 0-1 m layer and the above-ground organic C in an Amazonian  
320 tropical forest. The deep root system of this Amazonian forest probably released large  
321 amounts of organic C into the soil through root exudation, mycorrhizal associations and fine  
322 root mortality (Nepstad *et al.*, 1994). Moreover, the microbial biomass is much lower in deep  
323 soil layers than in the topsoil, which in combination with oxygen limitations could enhance  
324 organic C sequestration as a result of low mineralization rates (Taylor *et al.*, 2002; Rumpel  
325 and Kögel-Knabner, 2011). Organic C derived from roots is generally more sequestered in the  
326 soil than organic C coming from the aboveground litter, which is more affected by  
327 physicochemical processes and has a different structural composition (Rasse *et al.*, 2005;  
328 Schmidt *et al.*, 2011; Menichetti *et al.*, 2015). Further studies investigating the relationships  
329 between fine root dynamics, microbial communities and soil environment throughout very  
330 deep soil profiles in contrasting pedo-climatic conditions are needed to improve the  
331 predictions of soil C storage in deep soil layers under climate change.

#### 332 **4. Mycorrhizal association with deep roots**



333 Symbiotic association with root systems involving mycorrhizal fungi are common in forest  
334 ecosystems (Högberg and Högberg, 2002; Churchland and Grayston, 2014), with beneficial  
335 effects both for plants and fungi. Plants provide carbon to mycorrhizal fungi and in exchange,  
336 mycorrhizas greatly increase the volume of soil explored, which makes it possible to increase  
337 the amounts of water and nutrients taken up in the soil and transferred to the plants (Johnson  
338 and Gehring, 2007). Symbiotic associations between deep roots and mycorrhizal fungi are  
339 poorly documented and until recently, it was commonly believed that mycorrhizal  
340 associations were limited to shallow soil layers. Nevertheless, recent researches on microbial  
341 communities have highlighted the value of studying deep soil layers and showed unexpected  
342 abundant and diverse microbial communities in subsoils (Li *et al.*, 2014; Gocke *et al.*, 2017;  
343 Zheng *et al.*, 2017; Pereira *et al.*, 2018).

344 Most of research about arbuscular mycorrhizal (AM) fungi depending on soil depth has been  
345 carried out in agricultural systems down to a maximum depth of 1 meter. The results were  
346 mainly focused on the abundance and diversity of AM spores, with few studies taking into  
347 account AM fungi root colonization (Kabir *et al.*, 1998; Oehl *et al.*, 2005; Cuenca and Lovera,  
348 2010; Yang *et al.*, 2010; Taniguchi *et al.*, 2012; Shukla *et al.*, 2013; Becerra *et al.*, 2014; Gai  
349 *et al.*, 2015). Nevertheless, some older studies report observations of mycorrhizal associations  
350 more deeply, down to a depth of 4 m (Virginia *et al.*, 1986; Zajicek *et al.*, 1986). In tropical  
351 agroforests with *Faidherbia albida* trees, Dalpé *et al.* (2000) showed that AM propagules  
352 were viable in cores taken down to a depth of 34 m, which highlights the importance of  
353 improving our knowledge of deep mycorrhizal symbioses. A recent survey showed the  
354 presence of AMF fungal spores in deep soil layers down to a depth of 8 m in pure and mixed-  
355 species plantations of *Eucalyptus grandis* and *Acacia mangium* in Brazil (Pereira *et al.*, 2018),  
356 with root colonization rates between 6 and 25% for the 0-100 cm soil, and a decrease to about  
357 10% below 1 meter and 5% - 6% below 3 m. This weak AMF colonization could be partly

358 due to the age of the trees (over 1 year old) because the symbiosis with AM fungi is  
359 commonly known to be substituted gradually by ectomycorrhizal fungi in trees plantations  
360 (Read, 1991; Bellei *et al.*, 1992; Boerner *et al.*, 1996).

361 A vertical structuration of ectomycorrhizal (ECM) symbioses has been shown in numerous  
362 studies, with different ECM fungal communities between organic and mineral soil layers  
363 (Moyersoen *et al.*, 1998; Dickie *et al.*, 2002; Rosling *et al.*, 2003; Genney *et al.*, 2006).  
364 Unfortunately, most of the studies do not exceed the depth of 2 m (Bakker *et al.*, 2006;  
365 Clemmensen *et al.*, 2015; Rocha *et al.*, 2016). ECM root tips have been observed down to a  
366 depth of 4 m in bedrock fissures (Bornyasz *et al.*, 2005; Querejeta *et al.*, 2007). As for AM  
367 fungi, the presence of ECM fungi propagules has been shown in very deep soil layers, down  
368 to 10 m (Santana *et al.*, 2016). Robin *et al.* (2019) demonstrated for the first time using  
369 molecular sequencing that ECM symbioses occurred with *Eucalyptus grandis* roots at a depth  
370 of 4 m in Brazil (Figure 6). The intraspecific diversity of the fungus *Pisolithus* in this study  
371 was strongly impacted by the depth, suggesting the presence of a reservoir of biodiversity  
372 associated with the deepest roots.

373 The occurrence of mycorrhizal associations (with both AM and ECM fungi) in deep soil  
374 layers can contribute to increasing the volume of soil explored by scarce roots, which can  
375 greatly enhance water and nutrient capture during drought periods (Lehto and Zwiazek, 2011;  
376 Begum *et al.*, 2019). Moreover, mycorrhizal fungi have a strong impact on carbon cycling  
377 (Rillig *et al.*, 2001; Tedersoo and Bahram, 2019), with possible consequences on C  
378 sequestration in deep soil layers. For example, the symbiosis with ECM fungi increases the  
379 lifespan of fine roots (King *et al.*, 2002; Guo *et al.*, 2008; McCormack and Guo, 2014;  
380 Lambais *et al.*, 2017), and the fungal biomass of both AM and ECM fungi can represent a  
381 significant C sink in forest ecosystems (Rillig *et al.*, 2001; Wilson *et al.*, 2009; Cairney, 2012;  
382 Clemmensen *et al.*, 2015). The turnover of fungal biomass in deep soil layers can be lower

383 than in the topsoil as a result of the low abundance of predatory organisms (Fernandez *et al.*,  
384 2016), which suggests that the contribution of fungi to C storage in the subsoil could be  
385 important.

386 There are serious technical and methodological difficulties to study mycorrhizal associations  
387 with deep roots, which explains that mycorrhizal symbioses in deep soil layers are still very  
388 little documented. The difficulty to sample a sufficient weight of mycorrhizal fungi in  
389 undisturbed soil at large depth is a major challenge. Some authors speculated that they did not  
390 sample deeply enough to determine the limits of ECM fine roots (Bakker *et al.*, 2006). The  
391 minirhizotron method is well suited for root observations and has already been used to study  
392 the dynamics of ECM fungi (Allen and Kitajima, 2013; McCormack *et al.*, 2017). A recent  
393 study using minirhizotrons showed typical ECM structures associated with deep roots down  
394 to 6 m in a Brazilian eucalypt plantation (Lambais *et al.*, 2017). However, the method itself  
395 could affect mycorrhization, especially in deep soil layers (transport of spores, modification  
396 of the environment near the tube...) and might create a favorable environment for fungi  
397 growth. These interesting observations, despite their limitations, suggest the urgent need to  
398 combine several methods making it possible to study *in situ* simultaneously the dynamics of  
399 roots and mycorrhizal symbioses. We also need to go beyond diversity approaches and to  
400 study more the functional aspects of these symbioses. Although a growing body of evidence  
401 suggests that biological activity in deep soil layers is a major scientific lock poorly  
402 investigated and important to resolve to improve our understanding of the biogeochemistry of  
403 forest ecosystems, it remains a major methodological and technical challenge (Gocke *et al.*,  
404 2017).

## 405 **5. Water and nutrient uptake in deep soil layers**

406 The role of deep roots on water uptake by trees is well documented (Phillips *et al.*, 2016).  
407 Deep roots are essential to sustain high tree transpiration over dry seasons, which strongly  
408 influences the Amazonian climate (Kleidon and Heimann, 2000; Saleska *et al.*, 2007). Soil  
409 water content monitoring throughout soil profiles as well as studies using hydrogen and  
410 oxygen isotopes at specific dates make it possible to estimate at which depth water is taken up  
411 by tree roots (Guderle and Hildebrandt, 2015; Beyer *et al.*, 2016; Koeniger *et al.*, 2016;  
412 Trogisch *et al.*, 2016; Beyer *et al.*, 2018). Stahl *et al.* (2013) showed that 46% of the trees  
413 were extracting water at a depth of at least 1.2 m in a tropical rainforest. Trees have developed  
414 efficient strategies for the acquisition of water resources in deep soil layers, which can also  
415 help sustain shallow root functioning during drought through hydraulic redistribution  
416 (Burgess *et al.*, 1998; Domec *et al.*, 2004; Bleby *et al.*, 2010). Burgess *et al.* (2001) have  
417 demonstrated that *Eucalyptus* species have the capacity to redistribute water from wetter deep  
418 layers into shallow soil layers through vertical and horizontal roots. Hydraulic redistribution  
419 has now been demonstrated for many tree species and modeling approaches showed that this  
420 process can strongly influence the evapotranspiration and the net carbon exchange of the  
421 ecosystem (Domec *et al.*, 2010). Water uptake in very deep soil layers is highly dynamic in  
422 response to changes in atmospheric demand and soil water contents in the upper layers  
423 (Christina *et al.*, 2017). A modeling approach showed that the occurrence of rainfall events,  
424 changing from a week to another, had a strong impact on which depth water uptake occurs  
425 (Figure 7). It has also been shown that tree nutrition can greatly influence water withdrawal  
426 by roots in very deep soil layers (Christina *et al.*, 2018). Recently, Li *et al.* (2019) showed that  
427 the extraction of water in deep soil layers by the root system of apple stands between 15 and  
428 22 years of age was mainly occurring at depths below 12 m in a sub-humid region of China.  
429 They also suggested that roots in the 1-12 m layer remained alive to transport the water taken  
430 up below 12 m as they were probably unable to extract additional water in the upper 12 m.

431 The access of roots to a very deep water table can dramatically change tree functioning and  
432 the net C exchanges in forest ecosystems (Roupsard *et al.*, 1999; Carter and White, 2009;  
433 Zolfaghar *et al.*, 2017). To improve soil-vegetation-atmosphere transfer models in tropical  
434 forest ecosystems, we need a better understanding of the potential of very deep roots to  
435 withdraw water stored in the subsoil (Akkermans *et al.*, 2012).

436 The contribution of deep roots to supply tree requirements has been much less studied for  
437 nutrients than for water. A safety net of tree roots reducing the losses of nutrients by deep  
438 leaching is well known in agroforestry systems (Allen *et al.*, 2004). Monitoring soil solution  
439 chemistry throughout very deep soil profiles showed that *Eucalyptus* roots take up most of the  
440 nutrients dissolved in the gravitational solutions before leaching at great depth (Laclau *et al.*,  
441 2010; Mareschal *et al.*, 2013), with a very quick uptake by a root mat during the  
442 decomposition processes in the forest floor (Laclau *et al.*, 2004). Sr and Ca cycling were also  
443 very conservative in a tropical rainforest in French Guyana, with very little Sr contribution  
444 from deep soil layers for tree species differing by their rooting depth, which supported the  
445 theory that Sr and Ca uptake and cycling are mostly superficial in tropical rainforests (Poszwa  
446 *et al.*, 2002). Recent studies using markers suggest that a functional specialization of fine  
447 roots could also influence their ability to take up nutrients depending on the depth. Comparing  
448 oak, European beech and Norway spruce monocultures in Denmark, Göransson *et al.* (2006)  
449 showed that the distribution of roots and mycelia was not a reliable indicator of nutrient  
450 uptake capacity by tree roots at different soil depths. The uptake capacity from deep soil  
451 layers was higher than expected from the root distribution for most of the markers compared  
452 with the topsoil, which might be explained by an overlap of the uptake zones around the roots  
453 and mycorrhizal hyphae in the topsoil (Göransson *et al.*, 2006). Injection of  $^{15}\text{NO}_3^-$ ,  $\text{Rb}^+$  ( $\text{K}^+$   
454 analog) and  $\text{Sr}^{2+}$  ( $\text{Ca}^{2+}$  analog) markers at the depths of 10, 50, 150 and 300 cm in Brazilian  
455 Ferralsol soils also suggested a functional specialization of fine roots with a higher capacity to

456 take up cations in deep soil layers, in 2- and 6-year-old *Eucalyptus grandis* plantations (Da  
457 Silva *et al.*, 2011; Bordron *et al.*, 2019). Trees exhibit a great flexibility in their capability to  
458 adjust their root development and the uptake of soil resource in the layers where they are  
459 available (Jackson *et al.*, 1990; Hutchings and de Kroon, 1994; Robinson, 1996). A recent  
460 study in a rainfall exclusion experiment showed that eucalypt fine root functioning can be  
461 considerably altered as a response to drought in deep soil profiles (Pradier *et al.*, 2017).  
462 Whereas  $\text{H}_3\text{O}^+$  and exchangeable  $\text{K}^+$  concentrations were not influenced by the drought  
463 treatment (37% of rainfall exclusion) in the bulk soil, they were significantly higher in the  
464 rhizosphere than in the bulk soil in plots with reduced rainfall, notably at a depth of more than  
465 2 m. This study suggested that root-induced weathering of K-bearing minerals contributed to  
466 increasing rhizosphere acidification and K bioavailability at great depth.

## 467 **6. Influence of soil environment and resource availability**

468 Deep roots are highly plastic in response to heterogeneous resource distributions (Hodge *et*  
469 *al.*, 2009). Plants have the ability to adapt their root system to changing soil water contents,  
470 nutrient availabilities, soil physical properties, and soil atmosphere composition. The  
471 variability of environmental factors affecting root growth are buffered in deep soil layers  
472 compared to the topsoil (Voroney, 2007). Changes in fine root structure, architecture, and  
473 production with soil depth can be influenced by the spatial heterogeneity of soil resources and  
474 soil microclimate (Addo-Danso *et al.*, 2020). Root ingrowth bags installed down to a depth of  
475 6 m in mixed-species plantations of *Acacia mangium* and *Eucalyptus grandis* showed a  
476 remarkable capacity of very deep roots to explore resource-rich soil patches despite their low  
477 density in the soil (Germon *et al.*, 2018). A high plasticity of fine roots has also been shown  
478 through a vertical segregation of fine roots in mixed-species forests making it possible to  
479 explore more intensively deep soil profiles than monospecific stands (Schenk *et al.*, 1999).  
480 Some studies in agroforestry systems and forest ecosystems suggest that fine roots of the

481 weakest competitor can be partially excluded from soil horizons where the resources limiting  
482 tree growth are concentrated (Schmid and Kazda, 2002; Mulia and Dupraz, 2006; Laclau *et*  
483 *al.*, 2013a).

484 Plant species use a large range of rooting patterns to cope with periodic drought, from  
485 "drought tolerant strategies" with fine roots surviving in periodically dry soil to "drought  
486 avoiding strategies" shedding fine roots from dry soil horizons while rapidly developing roots  
487 in moister areas (Brunner *et al.*, 2015; Vries *et al.*, 2016; Bristiel *et al.*, 2018). Soil water  
488 content is a major driver of root growth and production in deep soil layers. Adriano *et al.*  
489 (2017) showed that fine root mass of *Citrus sinensis* were higher in deep soil layers (between  
490 the depths of 5 m and 8 m) for rainfed trees than for irrigated trees. However, changes in SRL  
491 and SRA along soil profiles were unclear in those *Citrus* plantations, whatever the water  
492 supply regime. Schenk and Jackson (2002) showed that the maximum rooting depth in  
493 tropical ecosystems was positively correlated with the length of the dry season and negatively  
494 correlated with the annual precipitation. Wang *et al.* (2015) also found a highly negative  
495 correlation between root mass and soil water content down to a depth of 21 m in grasslands  
496 and shrublands in China. Drought periods commonly increase the proportion of fine roots in  
497 deep soil layers as well as specific root areas (Markesteyn and Poorter, 2009; Ma *et al.*, 2018;  
498 Zhou *et al.*, 2018). In a survey of 62 tropical tree species, Markesteyn and Poorter (2009)  
499 showed that trees increase the belowground biomass and the proportion of deep roots in  
500 response to dry conditions. Germon *et al.* (2019) showed an increase in SRL and SRA down  
501 to a depth of 16 m in response to throughfall exclusion for *Eucalyptus* trees in Brazil.

502 Fine root dynamics can also be influenced by the depth of the water table. Li *et al.* (2015)  
503 showed that the displacement of the root front of *Alhagi sparsifolia* was 0.66 cm d<sup>-1</sup> when the  
504 water table was at a depth of 0.8 m and 1.5 cm d<sup>-1</sup> when the water table was at a depth of 2.2  
505 m. Canham *et al.* (2012) showed a seasonal distribution of fine root biomass in deep soil

506 layers in response to the fluctuations of the depth of the water table in southwest Australia.  
507 Although the physiological mechanisms remain little understood, some studies investigating  
508 the relationships between changes in water table depth and fine root dynamics suggest that an  
509 increase in water table depth could promote an increase in root elongation rates downwards  
510 (Stave *et al.*, 2005; Canham, 2011).

511 The influence of soil texture on fine root distributions remains unclear. Fine root distributions  
512 were shallower in sandy soils than in clayey soils in a tropical evergreen forest (Schenk and  
513 Jackson (2002). However, roots of *Haloxylon ammodendron* reached a depth of 10 m in a  
514 sandy soil and only 3 m in a heavy soil (Xu and Li, 2009). Comparing root distributions for  
515 *Entandrophragma cylindricum* Sprague (Meliaceae) in African semi-deciduous rainforests,  
516 Freycon *et al.* (2015) showed that fine root densities down to a depth of 6 m were lower in a  
517 coarse-textured Arenosol soil than in a fine-textured Ferralsol soil. The same pattern was  
518 showed by Laclau *et al.* (2013b) comparing fine root densities down to a depth of 10 m in  
519 sandy and clayey Ferralsol soils in the same *Eucalyptus* stand. Similarly, Robinson *et al.*  
520 (2006) in Australia reported that eucalypt species can reach 8-10 m deep and withdraw deep  
521 soil water (Figure 8) despite a high bulk density (up to  $2.0 \text{ g cm}^{-3}$ ) in clayey subsoil. Canadell  
522 *et al.* (1996) cited some examples of roots reaching great depths in rocky soils, using cracks  
523 and macropores at the vicinity of rocks to grow with low mechanical constraints.

524 Nutrient availability can also influence fine root traits throughout deep soil profiles. Studying  
525 fine roots and nutrient distributions down to a depth of 10 m in five semi-arid and arid forests  
526 in the southwestern USA, McCulley *et al.* (2004) showed morphological and physiological  
527 adjustments of fine roots in response to nutrient availability. The fate of tracers injected at  
528 various depth in a Ferralsol soil suggested that NPK fertilization increased the capacity of  
529 *Eucalyptus grandis* fine roots to take up nutrients down to a depth of 3 m (Bordron *et al.*,  
530 2019). Moreover, NPK fertilization increased fine root density, specific root length and



531 specific root area throughout the soil profile. However, N fertilization did not influence the  
532 fine root biomass down to a depth of 3 m in another *E. grandis* stand at the same site in Brazil  
533 (Jourdan *et al.*, 2008). The relationships between nutrient availability throughout deep soil  
534 profiles, fine root dynamics and fine root traits are difficult to disentangle from changes in  
535 environmental conditions and further studies are needed to gain insight into the specific effect  
536 of soil nutrient contents.

537 Even though the consequences of elevated CO<sub>2</sub> concentrations in the atmosphere on plant  
538 growth has been studied in many FACE experiments, fine root responses are still little  
539 documented for trees. In a review paper, Iversen (2010) showed that high atmospheric CO<sub>2</sub>  
540 concentrations tend to increase root depth in forest ecosystems. However, most of the studies  
541 dealing with fine roots in FACE experiments were carried out in the upper soil layers. Fine  
542 root traits influence tree functioning (Prieto *et al.*, 2015; Addo-Danso *et al.*, 2020) but the  
543 scarcity of information on the influence of the rise of atmospheric CO<sub>2</sub> concentrations on fine  
544 roots traits at depths of more than 30 cm limits our understanding of the response of forests to  
545 climate change on huge areas. Studies dealing with the influence of elevated CO<sub>2</sub>  
546 concentrations on root distributions and fine root traits in deep soil layers are therefore  
547 urgently needed for tree species.

## 548 **7. Modeling approaches to gain insight into the functioning of deep fine** 549 **roots**

550 Modeling architecture development and dynamics of the deep fine roots is hindered by the  
551 limited data available in the literature, yet necessary to parametrize and evaluate the models.  
552 Root number, root diameter, root volume, and root radial distances are the main parameters of  
553 root system biomechanics (Nicoll and Ray, 1996; Danquechin Dorval *et al.*, 2016), varying  
554 considerably with soil layers. Soil depth strongly influences the root system architecture due

555 to the heterogeneity of its environment. Root architectural models could simulate accurately  
556 spatial and temporal dynamics through a simulation of the root system in 3D. Integrating a  
557 vertically discretized soil into a model is particularly important as shallow and deep roots  
558 present different spatial and temporal dynamics. Model parametrization needs to consider  
559 shallow and deep-rooted systems behaving differently according to the environmental factors  
560 and soil conditions. These models can be parametrized according to the definition of root  
561 types (e.g. RootTyp from Pagès *et al.* (2004); or DigR (Figure 9) from Barczi *et al.* (2018)) or  
562 by branching order (e.g. OpenSimRoot from Postma *et al.* (2017)) or through parametric L-  
563 system modeling (Leitner *et al.*, 2010), which also might vary with soil layers. Such a model  
564 without discretized processes by soil layers is not capable to simulate accurately the impact of  
565 environmental conditions and soil resources on root development. Models devoted to  
566 simulating water and nutrient uptake dynamics need to integrate the functional specialization  
567 of deep roots and root growth plasticity in response to environmental conditions, in particular  
568 in deep soil layers. However, most root functioning rules are still not completely understood,  
569 especially at great depth as a result of the difficulty of measuring those processes *in situ*.  
570 Therefore, model calibration must cope with this knowledge and experimental limits.  
571 Architectural models can also be coupled with models simulating nutrient uptake (Mayer,  
572 1999; Bonneau *et al.*, 2012; Mayer *et al.*, 2012), water transport (Doussan *et al.*, 1998),  
573 rhizospheric processes (Kim and Silk, 1999), or even reactive transport models (Mayer, 1999;  
574 Mayer *et al.*, 2012; Gérard *et al.*, 2017). Nevertheless, it can be convenient to simulate  
575 accurately the overall architecture and any specialized functions of deep roots compared to  
576 shallow roots.

577 Furthermore, deep roots have a strong influence on deep carbon stocks, which accounts for a  
578 significant amount of carbon (Jobbágy and Jackson, 2004) and can be partially renewed at the  
579 10-year scale (Baisden and Parfitt, 2007; Koarashi *et al.*, 2012). Models predicting soil

580 organic carbon stocks through a single soil layer modeling approach (Hansen *et al.*, 1991;  
581 Sallih and Pansu, 1993; Petersen *et al.*, 2005; Pansu *et al.*, 2010; Oelbermann and Voroney,  
582 2011) are therefore not considering adequately deep roots that play an active role in carbon  
583 cycling. In recent years, an awareness of the importance of deep carbon stocks by the  
584 modeling community has led to the development of different discretized models depending on  
585 the soil depth (Braakhekke *et al.*, 2011; Braakhekke *et al.*, 2013; Guenet *et al.*, 2013;  
586 Taghizadeh-Toosi *et al.*, 2014). However, modeling accurately deep root dynamics and their  
587 active role in C fluxes in forest ecosystems, as well as nutrient and water uptake throughout  
588 tree growth remains a major challenge for the next decades.

## 589 **Conclusion**

590 Deep roots are a major component of forest ecosystems that can greatly influence the  
591 biogeochemistry of the Critical Zone. Their anatomical, morphological and functional root  
592 traits may be different from those of shallow roots (Figure 2; Appendix 1), with a major  
593 orientation towards the acquisition and transport of water. Climatic factors affect root  
594 phenology throughout deep soil profiles differently, as the soil environment is buffered in the  
595 deep soil layers. More research is needed to gain insight into the relationships between fine  
596 root dynamics and their anatomical, architectural and functional characteristics along deep  
597 soil profiles for a wide range of species, climates and soil properties. A high plasticity of fine  
598 roots has been shown in response to changing soil conditions from topsoil to deep soil layers  
599 (Appendix 1) but the control of fine root dynamics in very deep soil layers remains little  
600 understood despite their crucial role during dry periods on huge areas of forest worldwide.  
601 Research efforts should be directed to understanding the deep-root dynamics and associated  
602 functions that could have an important influence on climate change mitigation.

603

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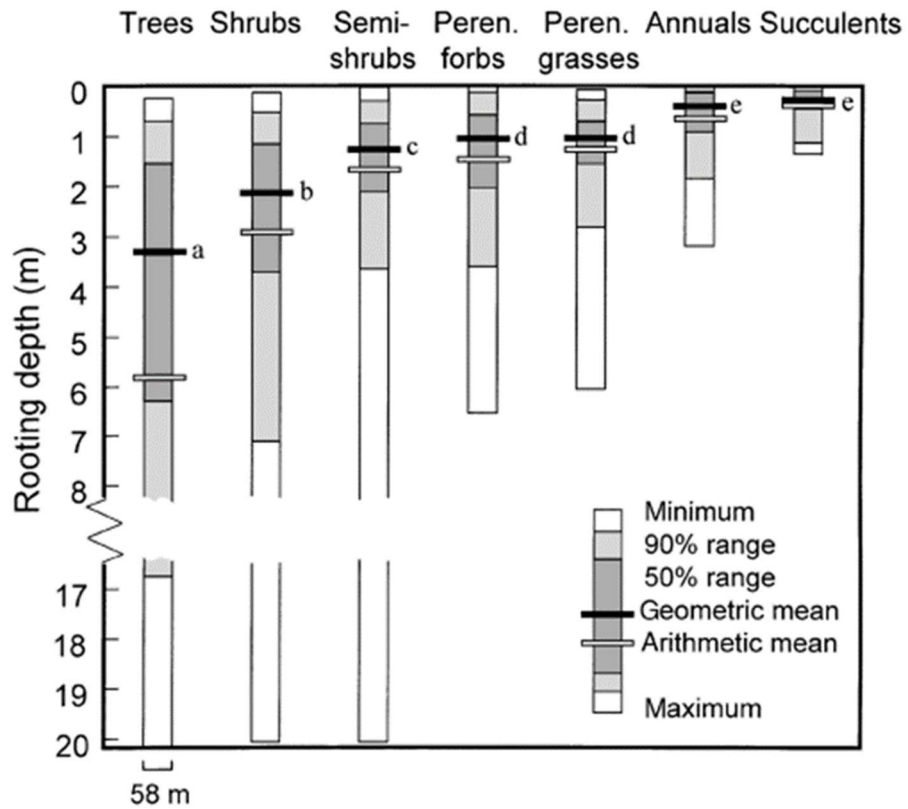
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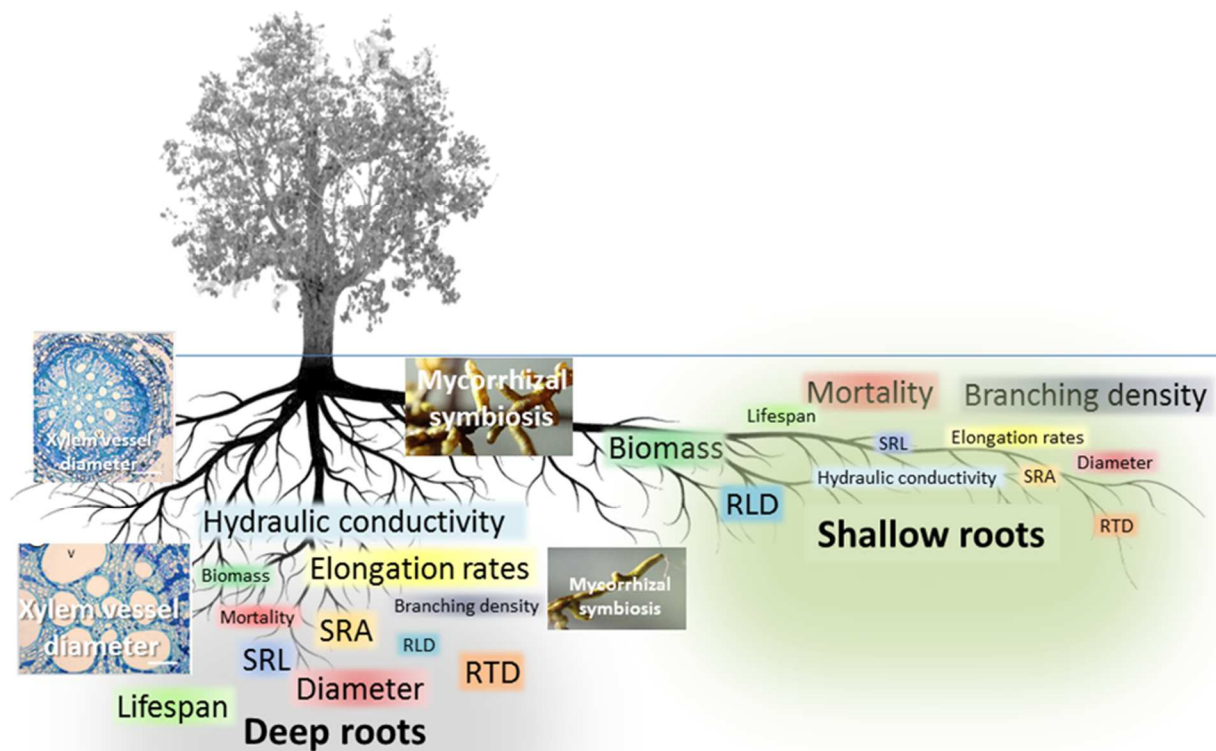


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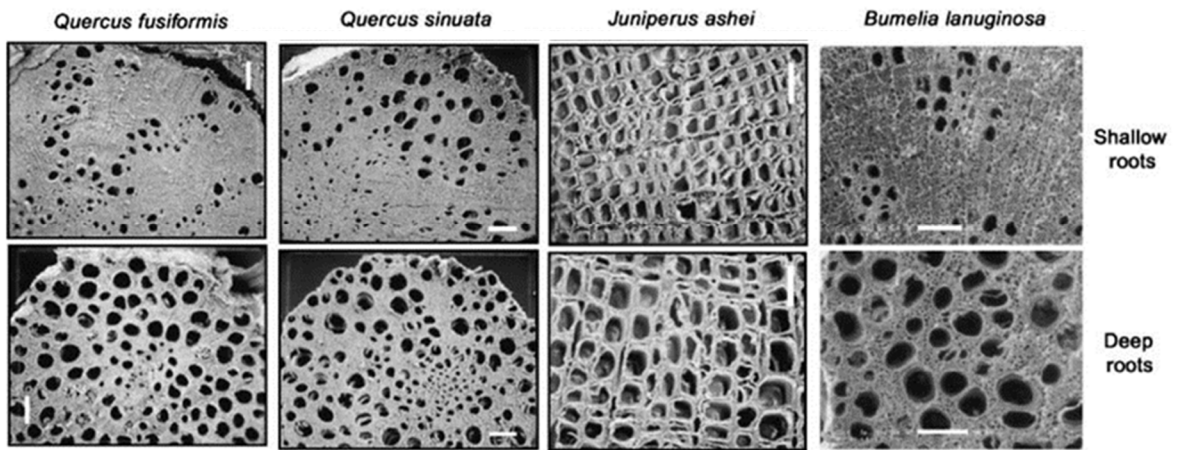
1263 **Figure 1.** Maximum rooting depths of plant growth forms. Geometric means marked by  
 1264 different letters were significantly different according to one-way ANOVAs. Source: Schenk  
 1265 and Jackson (2002), used by permission.

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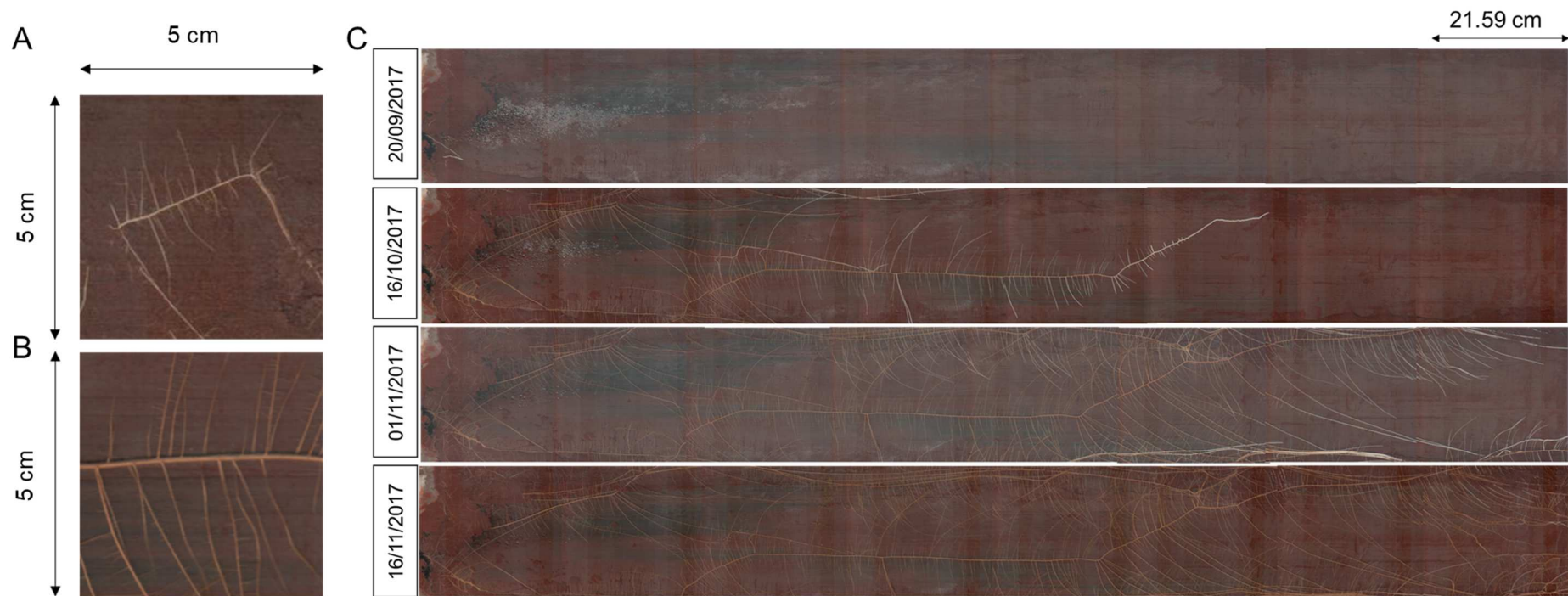
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1268 **Figure 2.** Conceptual scheme of root trait variations between the topsoil and deep soil layers.  
 1269 The larger the size of the text, the higher the value of the root trait considered. The main  
 1270 tendencies in the literature (indicated in Appendix 1) are shown here, but the behavior of  
 1271 certain plant species can be different. RLD for root length density, SRL for specific root  
 1272 length, SRA for specific root density and RTD for root tissue density. Images of root anatomy  
 1273 and ectomycorrhizal symbiosis were adapted from Perron-Gomide *et al.* (Com. Pers. 2020)  
 1274 and Robin *et al.* (2019), respectively.  
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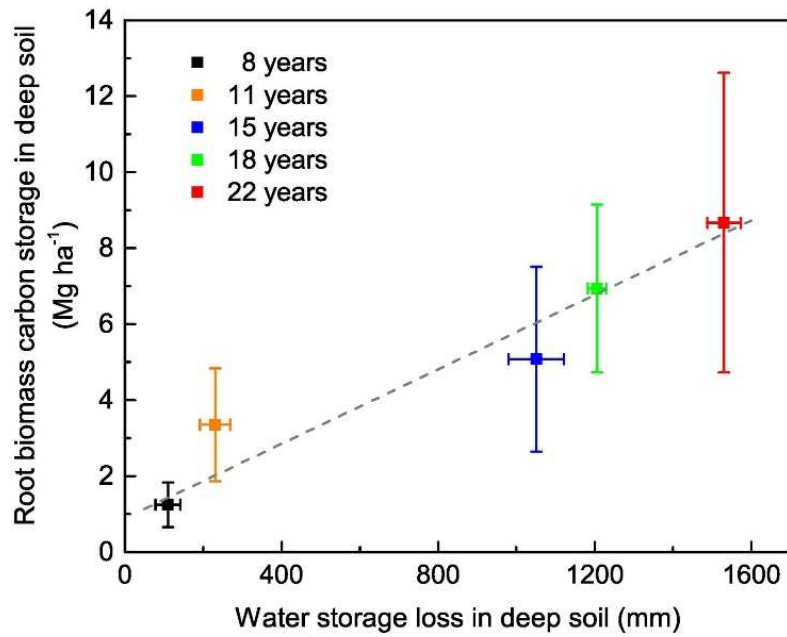
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1277 **Figure 3.** Scanning electron micrographs of shallow roots (top row) and deep roots (bottom  
 1278 row, depth of 18-20 m) for *Quercus fusiformis*, *Juniperus ashei*, *Quercus sinuata* and *Bumelia*  
 1279 *lanuginosa* tree species from the Edward's Plateau region of central Texas. The white line in  
 1280 each sub-figure shows the scale for a length of 50  $\mu\text{m}$  for *Juniperus ashei*, 300  $\mu\text{m}$  for  
 1281 *Quercus sinuata* and *Quercus fusiformis*, and 200  $\mu\text{m}$  for *Bumelia lanuginosa*. Adapted from  
 1282 McElrone *et al.* (2004), used by permission.



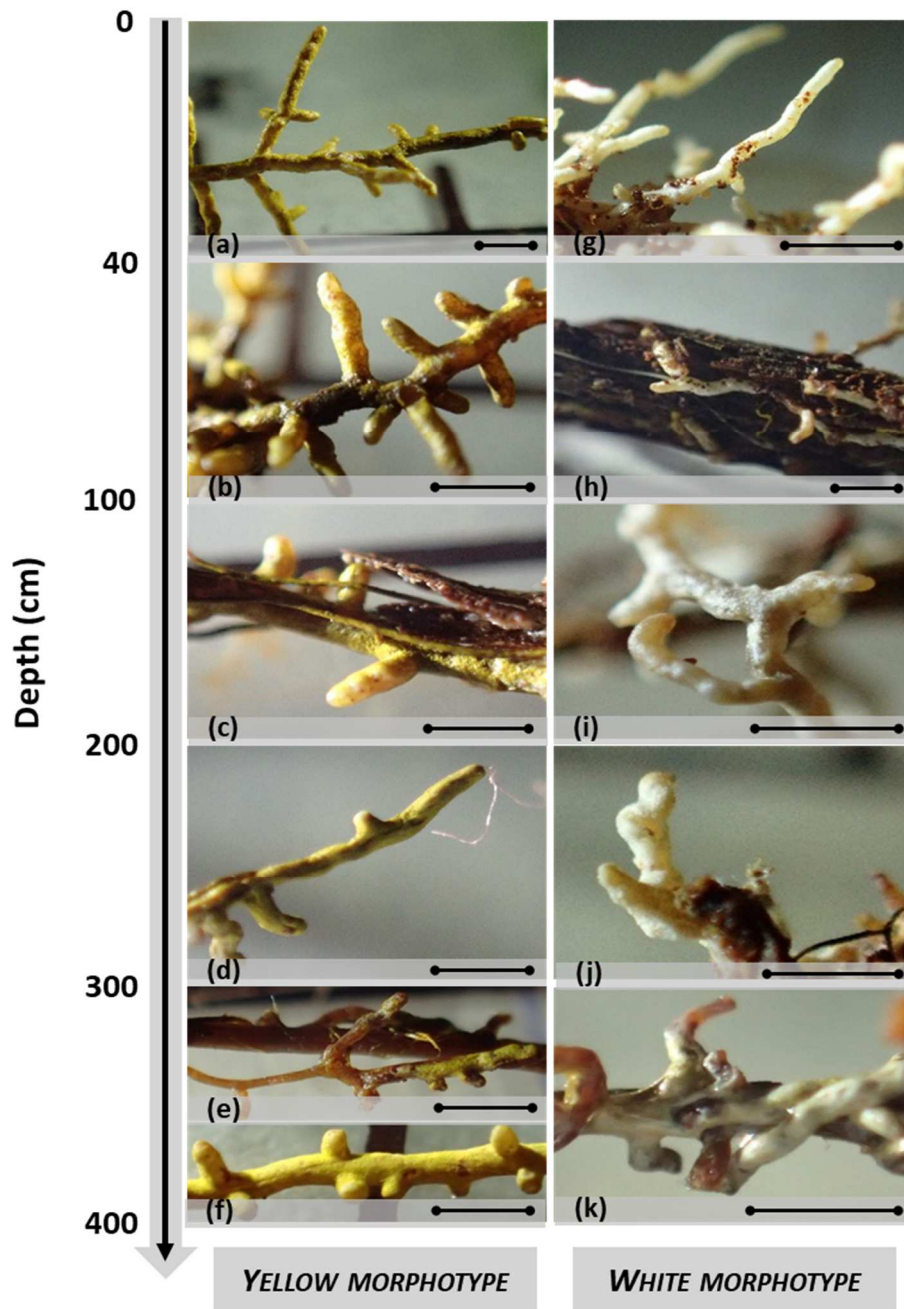
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1284 **Figure 4.** Images of *Eucalyptus* fine roots in the topsoil (A), and at depth of 11.5 m (B) in minirhizotron tubes installed in deep permanent pits in  
 1285 Brazil showing great differences in branching density of very fine roots. The velocity of exploration of deep soil layer in this stand (C) is shown  
 1286 scanning the same 1.8-m long minirhizotron tube inserted at a depth of 11.5 m from September 20, 2017 to November 16, 2017. Adapted from  
 1287 Germon (2019).



1288

1289 **Figure 5.** Relationship between root biomass carbon storage and water storage loss relative to  
 1290 long-term cultivated farmlands between the depths of 1m and 23.2 m in a chronosequence of  
 1291 8-, 11-, 15-, 18-, and 22-year-old afforested apple (*Malus pumila* Mill.) orchard stands in a  
 1292 sub-humid region of the Chinese Loess Plateau. The standard deviations are indicated (n = 3).  
 1293 Adapted from Li *et al.* (2019), used by permission.

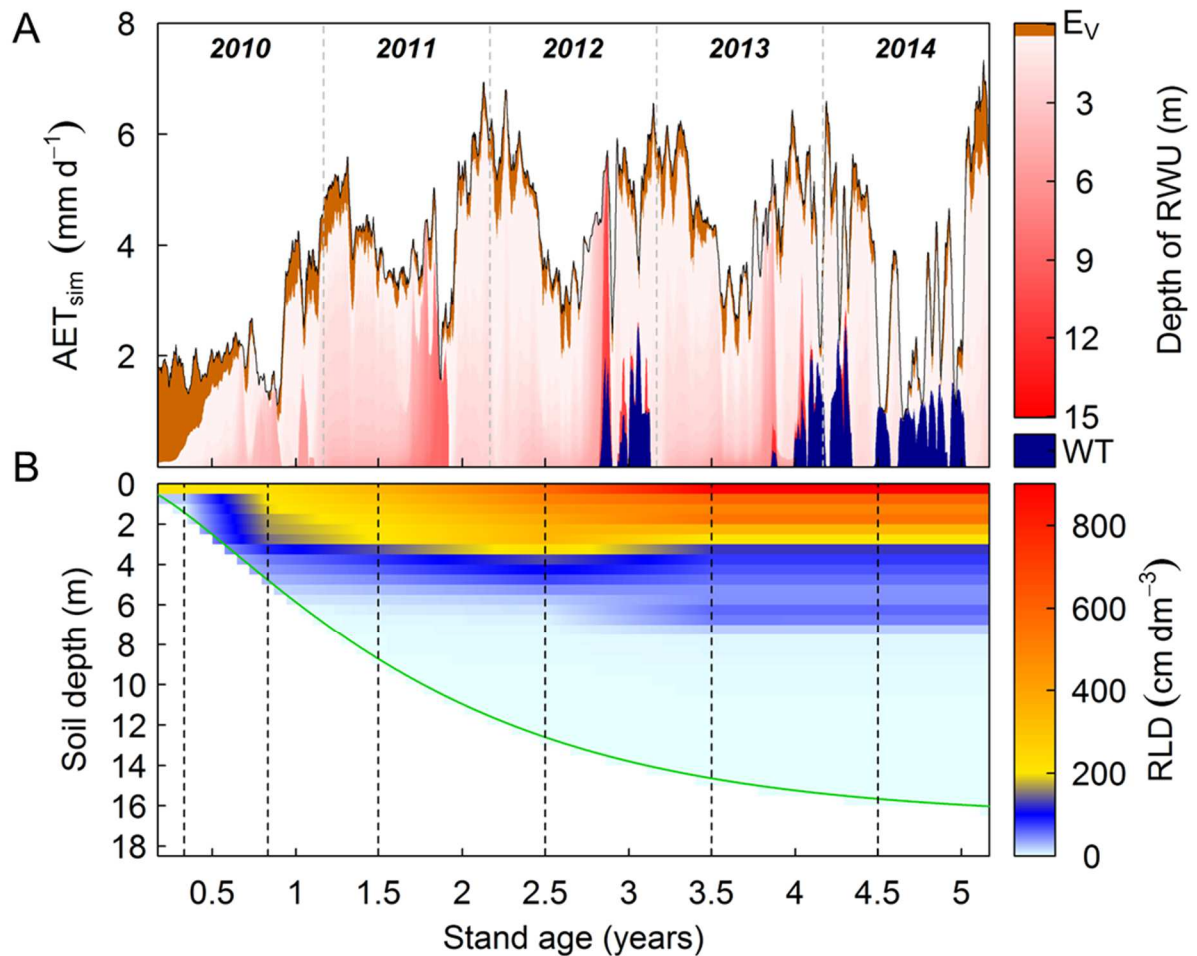


1294

1295 **Figure 6.** Ectomycorrhizal root tips originated from 4-m deep pits in a *Eucalyptus grandis*  
 1296 plantation in Brazil. The yellow morphotype (a–f) was identified molecularly as *Pisolithus*  
 1297 *spp.* and the white morphotype (g–k) as *Scleroderma spp.* In each image, the scale bar  
 1298 corresponds to 1 mm. Adapted from Robin *et al.* (2019), used by permission.

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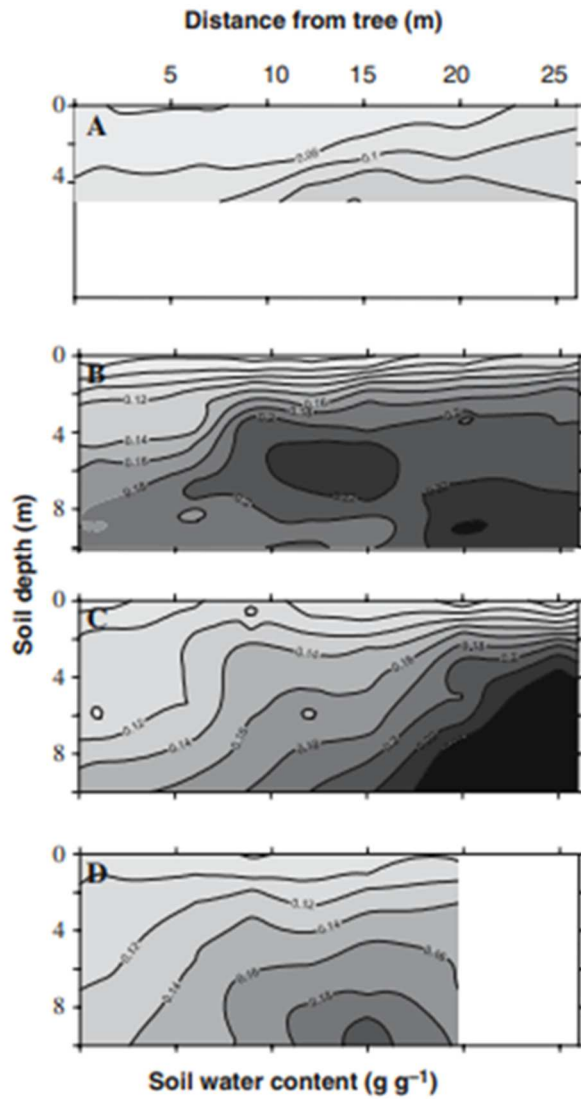




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1301 **Figure 7.** Daily simulated actual evapotranspiration ( $AET_{sim}$ ) using MAESPA model (A) and  
 1302 time series of root length density (RLD,  $cm\ dm^{-3}$ ) (B) over 5 years after planting *Eucalyptus*  
 1303 trees in Brazil. The  $AET_{sim}$  (A) is represented as a function of the depth of root water uptake  
 1304 ( $RWU_{sim}$ , red gradient) or uptake from the capillary fringe above the water table (WT, blue),  
 1305 and the evaporation from the soil surface and from the wet canopy is represented in brown.  
 1306 Vertical lines (B) indicate the days when root profiles were measured, and the green line is the  
 1307 maximum measured rooting depth. Adapted from Christina *et al.* (2017), used by permission.

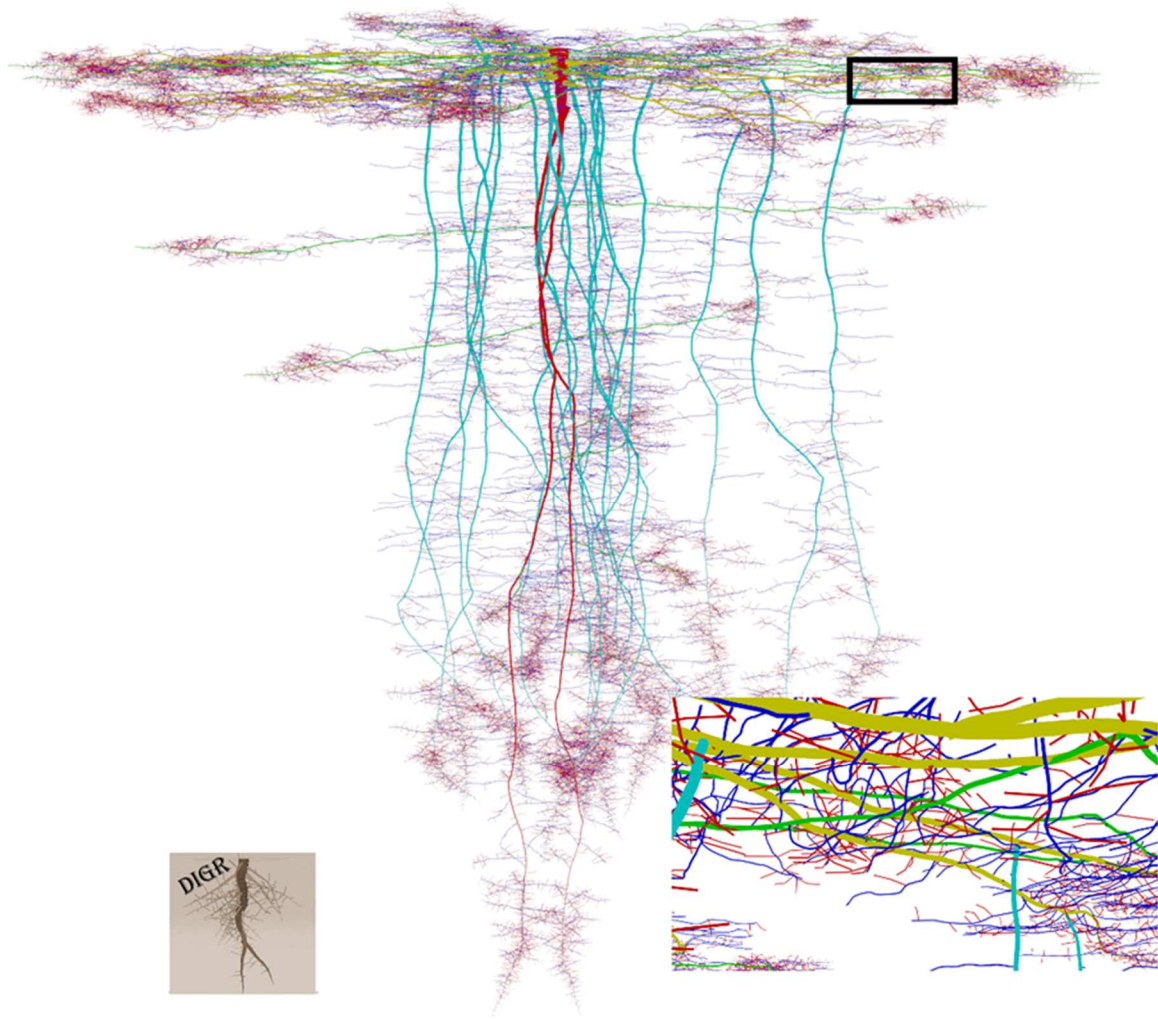
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1310 **Figure 8.** Soil water content ( $\text{g g}^{-1}$ ) of transects drilled to depths of up to 10 m perpendicular  
 1311 to eucalypt tree belts at 4 locations across south-west Western Australia (A-D). Dry areas  
 1312 show indirectly where eucalypt roots take up water. Adapted from Robinson *et al.* (2006),  
 1313 used by permission.




1314









1315

1316 **Figure 9.** Simulation of *Eucalyptus* root system by DigR model. Side view of a 5-year-old  
 1317 seedling (main) and detail (black rectangle) of shallow roots (bottom right). Different root  
 1318 types are shown: taproot (red), distal secondary taproot (light blue), plagiotropic secondary  
 1319 root (blue), cable-like root (yellow), long fine root (blue), medium fine root (purple), short  
 1320 fine root (red). DigR logo represents  $2 \times 2$  m scale for the whole root system. Adapted from  
 1321 Barczy *et al.* (2018), used by permission.

1322

1323 Appendix 1: Main changes in fine root traits in deep soil layers compared to the topsoil.  indicates an upward trend,  indicates a downward  
 1324 trend and  indicates predominantly no effect. Categories of root traits and individual root traits are adapted from Brunner *et al.* (2015), Brunner  
 1325 *et al.* (2009), McCormack *et al.* (2012) and Prieto *et al.* (2015).

Root traits categories	Fine root traits	Trend as depth increases	Annual rainfall (Mean Temperature)	Soil type	Forest type	Topsoil		Deepest horizon		References
						Depth (cm)	Mean value	Depth (cm)	Mean value	
Growth and life span	Root length density (cm cm <sup>-3</sup> )		740 mm	Sandy soil	Woody evergreen species	10	6.3	130	0.2	Gwenzi <i>et al.</i> (2011)
	Root density (roots m <sup>-2</sup> )		1740 mm (24.9 °C)	Arenosol	Tropical semi deciduous forest with many evergreen taxa	0-10	3427	290-300	33	Freycon <i>et al.</i> (2015)
			1740 mm (24.9 °C)	Ferralsol	Tropical semi-deciduous forest	0-10	1293	290-300	353	Freycon <i>et al.</i> (2015)
	Fine root lifespan (days)		873 mm (15.4 °C)	Alluvial fluvisol	Silvoarable Agroforestry system with Walnut trees	0-170	167	250-470	208	Germon <i>et al.</i> (2016)
	Root half-life (months)		1077 mm (range from 8.3 to 40.3°C)	Deep loamy sand	Rubber plantation	40-60	16	290-310	4	Maeght <i>et al.</i> (2015)
	Cumulative dead		1360 mm	Deep Ferralsols	<i>Eucalyptus</i>	0-30	4.3	300-400	0.4	Lambais <i>et al.</i> (2017)

	root length production (m m <sup>-2</sup> )		(20°C)		plantation over 2 years of measurements					
	Cumulative dead root length loss (cm m <sup>-2</sup> )	✘	873 mm (15.4 °C)	Alluvial fluvisol	Silvoarable Agroforestry system with Walnut trees	0-70	162	400-470	19	Germon <i>et al.</i> (2016)
	Max root elongation rates (cm day <sup>-1</sup> )	✔	1390 mm (20°C)	Deep Ferralsols	<i>Eucalyptus</i> plantation	0-100	1.16	1100-1200	4.25	Germon <i>et al.</i> (2019)
	Mean root elongation rate (cm day <sup>-1</sup> )	✔	1360 mm (20°C)	Deep Ferralsols	<i>Eucalyptus</i> plantation over 2 years of measurements	0-30	0.08	200-600	0.17-0.29	Lambais <i>et al.</i> (2017)
	Daily root elongation rate (cm m <sup>-2</sup> day <sup>-1</sup> )	✔	1390 mm (20°C)	Deep Ferralsols	<i>Eucalyptus</i> plantation	0-100	1.5	1100-1200	94.7	Germon <i>et al.</i> (2019)
Architecture	Root area index (m <sup>2</sup> m <sup>-2</sup> )	✘	1390 mm (20°C)	Deep Ferralsols	<i>Eucalyptus</i> plantation	0-100	11	500-1000	2.8	Germon <i>et al.</i> (2019)
		✘	1758 mm (19.5°C)	Deep Ferralsols	Clones and seedling of <i>Eucalyptus</i>	0-100	2	500-1200	1.5	Pinheiro <i>et al.</i> (2016)
	Root area density (cm <sup>2</sup> cm <sup>-3</sup> )	✘	1360 mm (20°C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	0-30	> 0.2	280-320	< 0.05	Bordron <i>et al.</i> (2019)
	Root tissue density (g cm <sup>-3</sup> )	✘	1360 mm (20°C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	0-30	0.62	280-320	0.4	Bordron <i>et al.</i> (2019)

	Root length density (cm cm <sup>-3</sup> )	✘	1360 mm (20°C)	Deep Ferrasols	<i>Eucalyptus grandis</i> plantation	0-30	> 2.4	280-320	< 0.5	Bordron <i>et al.</i> (2019)
	Root length density (mm cm <sup>-3</sup> )	✘	1077 mm (range from 8.3 to 40.3°C)	Deep loamy sand	Rubber plantation	0-10	28	4.0	0.2	Maeght <i>et al.</i> (2015)
	Specific root length (m g <sup>-1</sup> )	✔	1390 mm (19°C)	Deep Ferrasols	<i>Eucalyptus grandis</i> plantation	5-15	12	285-295	32	Maurice <i>et al.</i> (2010)
	Specific root length (m g <sup>-1</sup> )	✔	1758 mm (19.5°C)	Deep Ferrasols	Clones and seedling of <i>Eucalyptus</i>	0-100	21.3	1100-1200	36.9	Pinheiro <i>et al.</i> (2016)
	Specific root length (m g <sup>-1</sup> )	➡	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0-100	12.9	100-150	12.74	Prieto <i>et al.</i> (2015)
	Specific root area (cm <sup>2</sup> g <sup>-1</sup> )	✔	1758 mm (19.5°C)	Deep Ferrasols	Clones and seedling of <i>Eucalyptus</i>	0-100	267.5	1100-1200	360.2	Pinheiro <i>et al.</i> (2016)
	Mean root diameter (mm)	✔	1360 mm (20 °C)	Deep Ferralic Arenosol	<i>Citrus sinensis</i> (L.) Osbeck plantation	0-50	0.55	700-750	0.7	Adriano <i>et al.</i> (2017)
	Mean root diameter (mm)	✔	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0-20	0.7	100-150	0.8	Prieto <i>et al.</i> (2015)

	Mean root diameter (mm)	➡	1360 mm (20°C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	0-30	0.26	280-320	0.38	Bordron <i>et al.</i> (2019)
Anatomy	Mean conduits diameter (µm)	➡	Ranges from 600 mm to 800 mm (from 7.9°C in January to 27.4°C in July)	Shallow soil on top of fractured Cretaceous limestone	<i>Juniperus ashei</i> <i>Quercus Fusiformis</i> <i>Quercus sinuata</i> <i>Brumelia lanuginosa</i>	5-10 5-10 5-10 5-10	5 42 40 30	~ 700 ~ 700 1800-2000 1800-2000	20 90 90 50	McElrone <i>et al.</i> (2004)
	Mean vessel diameter (µm)	➡	1390 mm (20°C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0-50	22.8	1200-1600	51.6	Perron-Gomide <i>et al.</i> (Com. Pers. 2020)
	Mean vessel number	➡	1390 mm (20°C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0-50	61.9	1200-1600	10.5	Perron-Gomide <i>et al.</i> (Com. Pers. 2020)
	Total xylem area (cm <sup>2</sup> )	➡	1390 mm (20°C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0-50	23	1200-1600	7.8	Perron-Gomide <i>et al.</i> (Com. Pers. 2020)
Biotic traits	<i>Pisolithus</i> spp. diversity indice (Shannon)	➡	1360 mm (19°C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0-20	1.11	350-400	1.08	Robin <i>et al.</i> (2019)
	<i>Pisolithus</i> spp. Richness indice (Sobs)	➡	1360 mm (19°C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0-20	23	350-400	20	Robin <i>et al.</i> (2019)
Chemical traits	Carbon concentration (mg g <sup>-1</sup> )	➡	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols,	agricultural, agro-ecosystems and forestry	0-20	446	100-150	445.4	Prieto <i>et al.</i> (2015)

				Fluvisols	systems					
	Nitrogen concentration (mg g <sup>-1</sup> )	↘	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0-20	11.3	100-150	9.7	Prieto <i>et al.</i> (2015)
	Soluble carbohydrate concentrations (mg g <sup>-1</sup> )	→	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0-20	292.2	100-150	297.5	Prieto <i>et al.</i> (2015)
Biochemical traits	Cellulose concentration (mg g <sup>-1</sup> )	→	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0-20	270	100-150	275.8	Prieto <i>et al.</i> (2015)
	Lignin concentration (mg g <sup>-1</sup> )	↗	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0-20	216.67	100-150	221.69	Prieto <i>et al.</i> (2015)
Physiological traits	Sap velocity (cm h <sup>-1</sup> )	↗	630 mm (from 8° in January to 27°C in July)	calcareous soils	deciduous <i>Bumelia lanuginosa</i> (gum bumelia) in savannah and woodland region	0-50 cm	< 0	in a cave at ~2000	> 10	Bleby <i>et al.</i> (2010)
	Hydraulic conductivity (kg m <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	↗	Ranges from 600 mm to 800 mm	Shallow soil on top of fractured Cretaceous	<i>Buemia lanuginosa</i>	5-10 5-10	9 14	1800-2000 1800-2000	22 43	McElrone <i>et al.</i> (2004)



			(from 7.9°C in January to 27.4°C in July)	limestone	<i>Quercus fusiformis</i>					
Hydraulic conductivity (kg m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	➡		Ranges from 600 mm to 800 mm (from 7.9°C in January to 27.4°C in July)	calcareous soils	<i>Quercus fusiformis</i> Small (Texas live oak)	0-50	2e <sup>-6</sup>	1000-2000	4e <sup>-5</sup>	Johnson <i>et al.</i> (2014)
Specific relative uptake potential of cations (Rb <sup>+</sup> and SR <sup>2+</sup> in % cm <sup>-1</sup> cm <sup>3</sup> )	➡		1360 mm (19°C)	Clayey soil	<i>Eucalyptus grandis</i> plantation	0-20	> 30	280-320	< 20	Da Silva <i>et al.</i> (2011)
Specific relative uptake potential of cations (Rb <sup>+</sup> and SR <sup>2+</sup> in % cm <sup>-1</sup> cm <sup>3</sup> )	➡		1360 mm (19°C)	Sandy soil	<i>Eucalyptus grandis</i> plantation	0.20	> 30	280-320	< 20	Da Silva <i>et al.</i> (2011)
Specific relative uptake potential of cations (Rb <sup>+</sup> and SR <sup>2+</sup> in % cm <sup>-1</sup> cm <sup>3</sup> )	➡		1360 mm (20°C)	Deep Ferrasols	<i>Eucalyptus grandis</i> plantation	0-20	<20	280-320	>100	Bordron <i>et al.</i> (2019)
Specific relative uptake of NO <sub>3</sub> <sup>-</sup> (% cm <sup>-1</sup> cm <sup>3</sup> )	➡		1360 mm (19°C)	Clayey soil	<i>Eucalyptus grandis</i> plantation	0-20	> 60	280-320	< 10	Da Silva <i>et al.</i> (2011)
Specific relative uptake of NO <sub>3</sub> <sup>-</sup>	➡		1360 mm (19°C)	Sandy soil	<i>Eucalyptus grandis</i>	0-20	> 60	280-320	< 10	Da Silva <i>et al.</i> (2011)

	(% cm <sup>-1</sup> cm <sup>3</sup> )				plantation					
	Specific relative uptake of NO <sub>3</sub> <sup>-</sup> (% cm <sup>-1</sup> cm <sup>3</sup> )	✘	1360 mm (20°C)	Deep Ferrasols	<i>Eucalyptus grandis</i> plantation	0-20	20	280-320	40	Bordron <i>et al.</i> (2019)

1326