Consequences of clear-cutting and drought on fine root dynamics down to 17 m in coppice-managed eucalypt plantations

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Abstract

Improving our understanding of the spatiotemporal dynamics of fine roots in deep soil layers is of utter importance to manage tropical planted forests in a context of climate change. Our study aimed to assess the effect of clear-cutting and drought on fine-root dynamics down to the water table in Brazilian ferralsol under eucalypt plantations conducted in coppice. Fine roots (i.e. diameter < 2 mm) were sampled down to 17 m deep in a throughfall exclusion experiment comparing stands with 37% of throughfall excluded by plastic sheets (-W) and stands without rain exclusion (+W). Root dynamics were studied using minirhizotron in two permanent pits down to 17 m deep, over 1 year before clear-cutting, then over 2 years in coppice, as well as down to 4 m deep in a non-harvested plot (NH) serving as a control. After harvesting, a spectacular fine root growth of trees conducted in coppice occurred in very deep soil layers (> 13 m) and, surprisingly, root mortality remained extremely low whatever the depth and the treatment. Total fine-root biomass in coppice down to 17 m depth was 1,266 and 1,017 g m^{-2} in +W and -W, respectively, at 1.5 year after the clear-cut and was 1,078 g m^{-2} in NH 7.5 years after planting. Specific root length and specific root area were about 15% higher in -W than in +W. Proliferation of fine roots at great depths could be an adaptive mechanism for tree survival, enhancing the access to water stored in the subsoil. The root system established before clear-cutting provides access to water stored in very deep layers that probably contribute to mitigate the risk of tree mortality during prolonged drought periods when the eucalypt plantations is conducted in coppice after the clear-cut.

Key words: Brazil, coppice, deep ferralsol profile, deep root growth, *Eucalyptus grandis*, minirhizotron, throughfall exclusion

1. Introduction

Future climate projections predict longer and more severe dry periods in tropical and subtropical regions (Solomon *et al.*, 2009; Dai, 2011; He and Soden, 2017). Extensive tree mortality triggered by drought and changes in rainfall patterns has been reported worldwide (Allen, 2009; Williams *et al.*, 2013; McDowell *et al.*, 2018). Tree survival greatly depends on rooting system behavior and functioning (Nepstad *et al.*, 1994; Markewitz *et al.*, 2010; Pierik and Testerink, 2014; Christina *et al.*, 2017), as plant growth is highly dependent on the absorptive function of fine roots for water and nutrients (Hinsinger, 2001). Fine roots also play a major role in the global carbon (C) cycle, representing significant C input into the soil by the incorporation of exudates and root necromass, and also generating a return of C to the atmosphere through respiration and decomposition processes (Balesdent and Balabane, 1996; Strand *et al.*, 2008). Improving our understanding of how root systems respond to drought is therefore crucial for terrestrial biosphere models to predict the effect of climate change on tree survival and carbon sequestration in forest and tree-based ecosystems.

Plant species use a large range of rooting patterns to cope with periodic drought, from "drought tolerant strategies" with fine roots surviving in periodically dry soil, to "drought avoiding strategies" shedding fine roots from dry soil horizons while rapidly developing roots in moister areas (Brunner *et al.*, 2015; Vries *et al.*, 2016; Bristiel *et al.*, 2018). Drought can increase the root-to-shoot ratio, the root area or root length-to-leaf area ratio, as well as the proportion of fine roots in deep soil layers and/or the specific root area (Markesteijn and Poorter, 2009; Ma *et al.*, 2018; Zhou *et al.*, 2018). Root growth peaks have been shown in deep soil layers during dry periods for eucalypt and rubber trees in tropical soils (Maeght *et al.*, 2015; Lambais *et al.*, 2017). Drought tolerance strategies are common for herbaceous plants, while drought avoiding strategies are often adopted by trees in evergreen tropical forests (Brunner *et al.*, 2015). Despite

67   the crucial role of fine roots in coping with drought, root phenology remains poorly understood

68   in comparison to leaf ecophysiology (Radville *et al.*, 2016).

69   Deep roots commonly reported as roots growing beyond 1 m in depth can play an important

70   role in supplying water to trees (Kell, 2012; Pierret *et al.*, 2016). Trees can be deeply rooted

71   (Canadell *et al.*, 1996; Schenk and Jackson, 2002), and some studies suggest that very deep

72   roots (at depths > 10 m) are common in highly weathered tropical soils (Nepstad *et al.*, 1994;

73   Saleska *et al.*, 2007; Broedel *et al.*, 2017). Even though low fine root densities are generally

74   found at great depth (Pierret *et al.*, 2016), they can take up substantial amounts of water needed

75   for tree survival during drought periods (McDowell *et al.*, 2008; Nardini *et al.*, 2016). Deep

76   roots can also contribute to closing the biogeochemical cycles in tropical forests through

77   nutrient uptake in deep soil layers (Lehmann, 2003; Jobbágy and Jackson, 2004; Da Silva *et*

78   *al.*, 2011; Bordron *et al.*, 2018), which reduces nutrient losses by deep leaching (Lehmann and

79   Schroth, 2003; Laclau *et al.*, 2010). While many studies show that the role of very deep roots

80   in tropical forest functioning and productivity has been greatly underestimated (Jackson *et al.*,

81   2000; Markewitz *et al.*, 2010; Freycon *et al.*, 2015), as far as we are aware, fine root dynamics

82   and mortality have never been studied at depths > 10 m.

83   *Eucalyptus* plantations cover more than 20 million hectares and account for around 8% of forest

84   plantations in the world (Booth, 2013). The diversity of *Eucalyptus* species planted in tropical

85   regions has led to a wide range of products and management practices (Gonçalves *et al.*, 2013).

86   Although many *Eucalyptus* plantations are intensively managed to produce raw materials for

87   industry (mainly pulp and paper, but also solid-wood products, fiberboards and charcoal for

88   steel production), used as a domestic source of energy and also contributes to alleviating

89   poverty in developing countries (Cossalter and Pye-Smith, 2003). Most eucalypt plantations are

90   located in areas with low soil fertility and prolonged drought periods (Keenan *et al.*, 2015).

91   Coppice management could be an adaptive solution to cope with water deficit in these

92 plantations, because the sprouts growing on stumps are likely to benefit from the pre-existing

93 root system that explores deep soil layers where water availability is generally higher than in

94 the topsoil. The effects of clear-cutting on fine root dynamics in coppiced-managed forest

95 plantations are poorly documented and tendencies are not clear. Sequential coring in Brazilian

96 coppiced-managed eucalypt plantations showed that fine root density decreased in the 0-1 m

97 soil layer in the first 60 days after harvesting, while fine root decomposition was accelerated

98 (Mello *et al.*, 2007). Fine root mortality exceeded fine root production after clear-cutting in

99 *Populus* stands (Berhongaray *et al.*, 2015). In contrast, Dickmann *et al.* (1996) observed little

100 change in fine root production and mortality in the 0-1 m soil layer after clear-cutting in other

101 *Populus* stands. While 50% of fine root biomass can be found below a depth of 1 m in tropical

102 eucalypt plantations (Christina *et al.*, 2011; Laclau *et al.*, 2013), fine root dynamics in coppice-

103 managed forests have only been studied in the upper meter of the soil profile.

104 Our study was carried out in *Eucalyptus grandis* (Hill ex. Maid) stands planted in a throughfall

105 exclusion experiment in Brazil (Battie-Laclau *et al.*, 2014). We aimed to gain insight into the

106 effects of contrasting rainfall regimes on fine root dynamics in coppice-managed eucalypt

107 plantations after tree clear-cutting in very deep tropical soils. We put forward the hypothesis

108 that trees invest in belowground biomass in response to throughfall exclusion, in order to

109 increase the exploration of fine roots in deep soil layers (H1), and that they adjust fine root traits

110 to increase the specific root area, in order to capture more resources per gram of C invested in

111 fine roots (H2). In addition, we put forward the hypothesis that *Eucalyptus grandis* stands with

112 clear-cutting and tree regrowth in coppices would increase fine root turnover throughout the

113 soil profile (H3).

114   **2. Materials and methods**

115   a. Study site

116   The experiments were conducted at the research station owned by the Luiz de Queiroz College

117   of Agriculture (ESALQ) near Itatinga (São Paulo, Brazil, 23°02′S 48°38′W). The study area,

118   located 300 km from the sea, has a relief typical of the São Paulo Western Plateau, with a

119   topography varying from flat to hilly (slopes < 3%). The altitude is 850 m, and the climate is

120   humid subtropical with a dry winter (Cwa) according to the Köppen classification. Over the 15

121   years prior to this study, the mean annual rainfall was 1390 mm (with 74% between October

122   and May), and the mean air temperature and relative humidity were 20°C and 77%,

123   respectively. A dry and cool (15°C) season occurs between June and September. The total

124   rainfall over the study period (from May 2015 to July 2018) was 5,629 mm. The annual rainfall

125   was 1,557 mm and 2,303 mm in 2016 and 2017, respectively. The soils are very deep Ferralsols

126   (IUSS Working Group WRB, 2015) developed on Cretaceous sandstone. Clay content ranges

127   from 160 mg g^{-1} soil in the topsoil to about 250 mg g^{-1} soil at a depth of 15 m, and clay minerals

128   are mainly kaolinite (Christina *et al.*, 2015).

129   b. Experimental layout

130   A split-plot experimental design was set up in June 2010 with a *Eucalyptus grandis* clone used

131   in commercial plantations by the Suzano Company (São Paulo, Brazil). The experimental

132   layout with 6 treatments and 3 blocks was described in detail by Battie-Laclau et al. (2014). We

133   studied two treatments out of all those available in the experimental design: one treatment with

134   undisturbed rainfall (+W) and one treatment with throughfall exclusion (-W), which was

135   equipped with plastic sheets installed since September 2010, allowing the exclusion of 37% of

136   throughfall (Battie-Laclau *et al.*, 2014). Treatments -W and +W were used to determine the

137   water deficit effect. The trees were planted in June 2010 at a spacing of 3 m x 2 m with a

138   stocking density of 1666 trees per hectare. The plots received a standard commercial fertilizer

139   (at planting: 3.3 g P m^{-2}, 200 g m^{-2} of dolomitic lime and trace elements; at 3 months of age: 12

140   g N m^{-2}, 0.45 mol K m^{-2} applied as KCl) and herbicides were applied to avoid the presence of

141 other understory species. In +W and -W, the eucalypt stands were harvested six years after

142 planting, in June 2016, and the plantation was coppice-managed thereafter. Several new shoots

143 were regenerated from the stumps after the clear-cut and 1 or 2 shoots per stump were selected

144 to maintain the same stocking density and prevent the growth of additional new shoots. A third

145 treatment served as a control, with undisturbed rainfall and no harvest (NH), to assess the clear-

146 cutting effect. Tree height and circumference at breast height were recorded each year after the

147 clear-cut on 36 central trees per plot during the first rotation (May 2010 - June 2016) and during

148 the second rotation in coppice (starting in June 2016).

149   c.   Soil water monitoring

150 The volumetric soil water content (SWC) was monitored in the +W and -W treatments

151 throughout the study period at half-hourly intervals using CS616 probes (Campbell Scientific

152 Inc., Logan, UT, USA) installed at the following depths: 0.15, 0.5, 1, 2, 3, 4, 6, 8, 10, 12, 14

153 and 16 m, with 3 probes at each depth in block 1. Extractable water (mm) was calculated as the

154 difference between the current soil water stock (mm) and the minimum soil water stock (i.e.

155 lower limit of soil water content in mm) (Granier *et al.*, 1999).

156   d.   Deep permanent pits for root phenology observations

157 Between February and March 2014, two deep permanent pits were excavated in +W and -W in

158 block 1 to gain access to the complete soil profile from the top soil down to the water table. The

159 pits were 1.5 m in diameter and reached a depth of 17 m and were located between four

160 *Eucalyptus* trees (Figure 1) at a distance of 90 cm, 90 cm, 130 cm and 130 cm from each four

161 trees respectively. The pit walls were made of concrete rings in direct contact with the soil.

162 Clear-colored roofs of the same diameter as the pits were used to prevent light and rain entering

163 the pits. Platforms were set up at two-meter intervals in the pits, equipped with artificial lighting

164 and fans used during working sessions, allowing access and safe work down to the water table

165   (Figure 1). The high cost of opening up and securing these pits prevented further replications

166   in the other two blocks. However, other measurements, including deep fine root sampling and

167   tree growth were carried out in all three blocks, making it possible to extrapolate some of the

168   observations made in the two deep pits. In October 2015, a third pit was excavated in the non-

169   harvested treatment (NH) down to 3.5 m to determine the clear-cut effect.

170   e.   Minirhizotrons

171   Fine root dynamics were studied through transparent polyvinyl chloride tubes (length:180 cm;

172   inner diameter: 6.5 cm), commonly called minirhizotrons (Maeght *et al.*, 2013). In October

173   2014, twenty-four transparent minirhizotrons were installed using a powerhead drill in the +W

174   and -W treatments of block 1. Outside the pits, three minirhizotrons were inserted into the soil

175   surface in the same plots a minimum of 10 m apart and at a distance of 90 cm from the trunk

176   (Figure 1). Nine tubes were inserted into the pit walls down to a depth of 17 m: two tubes at a

177   depth of 1 m and one tube at depths of 3.5, 5.5, 7.5, 9.5, 11.5, 13.5, 15.5 m (Figure 1). The tubes

178   were inserted at a 45-degree angle and allowed an observation depth of 1.3 m below the depth

179   at which they were inserted into the soil profile. In October 2015, 3 additional tubes were

180   installed at the soil surface in the +W and -W treatments of blocks 2 and 3 (12 tubes in total) to

181   increase the number of replications in the top meter. In October 2015, seven tubes were installed

182   in the NH treatments (3 into the soil surface, 2 tubes inserted at depths of 1 m and 3.5 m into

183   the pit walls).

184   Root dynamics were recorded using a circular scanner system (CI-600 Root Growth Monitoring

185   System, CID, USA). This scanner was selected for the quality of the images it produces, an

186   essential element for the analysis (Graefe *et al.*, 2008). In order to have a significant

187   stabilization period after soil disturbance from the installation, fine root monitoring began eight

188   months after minirhizotron installation (Graefe *et al.*, 2008; Germon *et al.*, 2016). Eight images

189   (21.59 x 19.56 cm, 100 dpi) per tube (43 tubes in total) were taken every two weeks for more

190   than three consecutive years from May 2015 to July 2018: over one year before the clear-cut

191   and two years after harvesting, in a coppice. Images were taken at a resolution of 100 dpi, as

192   we obtained the same root lengths and diameter compared to images of 300 dpi and 600 dpi,

193   and it was less time-consuming in the field than with a higher resolution.

194   f.   Root image processing

195   WinRhizoTron™ software (Régent Instrument Inc., Quebec, Canada) was used to analyze more

196   than 24,000 root images taken in the minirhizotrons. This software was chosen as it allowed the

197   analysis of large number of images and overlayed the images to visualize the time evolution of

198   the roots throughout the tubes. This manual root measurement program estimated the length

199   and diameter of each root observed and stored each data item in a text file. By comparing two

200   consecutive images chronologically, it was possible to estimate changes in root length and

201   phenology features. Root mortality was evaluated based on the absence of growth over the

202   entire study period up to the last images, when roots turned black and presented clear signs of

203   decomposition (Germon *et al.*, 2016; Lambais *et al.*, 2017). For each fine root (diameter < 2

204   mm) we recorded the time of the first appearance, the diameter, the length over time, and the

205   time of disappearance. In this study, we considered only root appearing during the study period.

206   g.   Root length calculations

207   As described in Germon et al. (2016) and Lambais et al. (2017) the following metrics were used

208   to estimate root production and the root elongation rate: living and dead root length production

209   (LP, cm m^{-2}) was calculated for each root as the individual root length (living or dead) at time

210   t divided by the observed soil area of each image. The cumulative living or dead root length

211   production (CLP, cm m^{-2}) was calculated summing, at each time t, the individual length of all

212   the roots observed, divided by the observed soil area of each image. The individual root

213 elongation rate (RER, cm day^{-1}) was calculated as the difference in individual root length

214 observed between two consecutive sessions (t and t$_{-1}$) divided by the time in days between t and

215 t$_{-1}$. The daily root elongation rate (DRER, cm m^{-2} day^{-1}) was calculated by summing, at each

216 time t, each individual root elongation rate of all the roots observed, divided by the observed

217 soil area of each image. The mean root elongation rate (MeanRER, cm day^{-1}) and the maximum

218 root elongation rate (MaxRER, cm day^{-1}) were calculated as the mean and the maximum of

219 individual root elongation rates considering all the roots growing during the study period. LLP,

220 CLP, RER, DRER, MeanRER and MaxRER were estimated for each treatment (+W, -W and

221 NH), each soil layer and between consecutive image sessions over the entire study period.

h. Root sampling

223 In order to check the consistency of fine root dynamics in deep soil layers observed by the

224 minirhizotron method, total fine root biomass, fine root length and fine root area down to the

225 water table were measured in October 2017, i.e. 1.5 years after the clear-cut in the coppices

226 (+W and -W) and 7.5 years after planting in NH. Fine roots (diameter < 2 mm) were sampled

227 down to 17 m in the two treatments (+W and -W) inside the three blocks and in the non-

228 harvested (NH) treatment inside one block. Four trees were randomly selected in each plot and

229 soil samples were collected around each tree between the topsoil and a depth of 2 m and around

230 2 other trees between depths of 2 and 17 m (i.e. 12 sampling points down to a depth of 2 m and

231 6 further down to a depth of 17 m in the +W and -W treatments and 4 sampling points down to

232 a depth of 2 m and 2 down to a depth of 17 m in the NH treatment). At each sampling position,

233 soil layers at 0-0.2, 0.2-0.5, 0.5-1, 1-1.5, 1.5-2 m were collected using a cylindrical auger with

234 an inner diameter of 4.5 cm. The Brazilian "cavadeira" tool, a cylindrical auger with an inner

235 diameter of 9 cm and a length of 30 cm, was used to collect soil cores every 50 cm from 2 m

236 down to a depth of 17 m. From each soil core, about 1.5 and 2 kg of soil was collected using

237 the same methodology as described in Germon et al. (2018) and Christina et al. (2011). To

238   avoid contamination of the collected soil samples, only soil blocks from the inner part of the

239   auger were considered. Total fresh soil mass was measured, and a sub-sample of 5 g was

240   weighed in the laboratory to estimate the soil water content by drying the sample at 105°C for

241   72 h. Each soil sample was identified and stored at 4°C before being processed a maximum of

242   1 week after sampling. Living roots (i.e. living stele, bright color and elasticity) and dead roots

243   (i.e. by sight, touch and flotation) > 1 cm long were carefully separated by hand after gentle

244   washing away of the soil with tap water on a sieve with a mesh size of 0.5 mm. For the 0-0.2,

245   0.2-0.5 and 0.5-1 m soil layers, 10 % of the weight of each soil sample was used to estimate the

246   mass of extremely fine roots (i.e. length < 1 cm). For the other soil layers 100% of the weight

247   was considered. Living and dead roots more than 1 cm in length were scanned using a double-

248   sided scanning procedure at a resolution of 800 dpi. Then, living roots and dead roots over > 1

249   cm in length and fragments of living and dead roots less than 1 cm in length were dried for 72h

250   at 65° C and weighed (±0.1 mg). For the upper layers where only 10% of the weight of the soil

251   was screened for living and dead roots < 1 cm in length, the mass of fragments was multiplied

252   by 10 to estimate the mass of fragments of the whole soil sample. Root weight was then obtained

253   for each soil layer, sampling position, treatment and block.

254   i.   Root trait calculations

255   The fine root scans obtained where analyzed using WinRhizo Version Pro V. 2009c software

256   (Régent Instruments Inc., Quebec, Canada) to estimate root lengths and areas per soil layer,

257   sampling position, treatments (+W, -W and NH) and blocks. As described in Germon et al.

258   (2018) the following metrics were used to estimate fine root traits. The specific root length

259   (SRL, m g^{-1}, i.e. total length of scanned roots divided by their dry mass) and specific root area

260   (SRA, cm^2 g^{-1}, i.e. total area of scanned roots divided by their dry mass) were calculated for

261   each soil sample. Fine root mass density (g kg^{-1} soil) was calculated as the total root dry mass

262   divided by the dry weight of the soil used for root separation. Fine root density (FRD, g dm^{-3}

263   soil) was obtained by multiplying fine root mass density by the soil bulk densities (measured

264   by the standard core method down to a depth of 17 m in each treatment). Fine root biomasses

265   (FRB, g m^{-2}) were calculated in each soil layer multiplying the mean fine root density by the

266   soil layer volume (dm^3). The root area index (RAI, m^2 m^{-2}) was calculated as the surface area

267   and length of fine roots divided by the sampled soil area respectively. FRD, FRB, SRL, SRA,

268   and RAI were obtained for each soil layer from the soil surface down to a depth of 17 m, for

269   the sampling position, +W, -W and NH treatments, and blocks.

270   j.   Statistical analyses

271   Linear mixed-effect models were used to test the effect of soil depth, treatment and the

272   interaction between depth and treatment on cumulative length production (CLP), root

273   elongation rate (RER), daily root elongation rate (DRER), mean root elongation rate

274   (MeanRER), maximum root elongation rate (MaxRER), fine root density (FRD), fine root

275   biomass (FRB), specific root length (SRL), specific root area (SRA), root area index (RAI) and

276   root diameter for the whole soil profile. Blocks were considered as fixed effects and residues

277   were modeled by a first-order autoregressive correlation model to account for the correlations

278   between soil depths. Two-way analyses of variance (ANOVAs) were used to assess the effect

279   of treatments and blocks for individual soil layers on CLP, RER, DRER, MeanRER, MaxRER,

280   FRD, FRB, SRL, SRA, RAI and root diameter. Measurements within a given soil layer were

281   considered independent, since the sampling positions were located near different trees in each

282   treatment and plot. The homogeneity of variances was verified, and log-transformations were

283   used when the residuals did not follow a normal distribution. Tukey's post-hoc Honest

284   Significant Difference (HSD) was used to determine the significant differences between

285   treatments. R software version 3.4.4 (Team R 2013) was used for all the calculations and

286   statistical analyses with a 5% significance level. The "lmerTest" package was used to perform

287   the linear mixed-effect models (Kuznetsova *et al.*, 2017).

288 ### 3. Results

289   a. Tree growth

290 Initial vertical growth was faster in the coppices than in the replanting: nine months after

291 harvesting (in February 2011 for the replanting, and February 2017 for the coppices), mean tree

292 height was 1.3 m and 1.5 m in the +W and -W replanted plots and was 2.7 m and 3.1 m in the

293 +W and -W coppice plots, respectively (Figure 2). There were no significant differences in

294 vertical growth between the +W and -W treatments for either replanting or coppice in the first

295 3 years after harvesting.

296   b. Volumetric soil water contents (SWCs)

297 In both the +W and -W treatments, rainfall events led to large variations in SWC (Figure 3). At

298 a depth of 0.5 m, SWC ranged from 5.9% to 15.8% in -W and from 7% to 19.4% in +W. At a

299 depth of 14 m, SWC ranged from 9.9% to 10.9% in -W and from 11.3% to 18.1% in +W. Over

300 the study period, throughfall reduction led to a sharp decrease in SWC, on average, by 12.9 ±

301 4.9% from the topsoil to a depth of 16 m. At the end of the rainy season, the mean SWC values

302 of the soil profile in April 2016, i.e. 2 months before the clear-cut, were 12.5% and 14.0% in -

303 W and +W, respectively and in April 2017, i.e. 10 months after the clear-cut, there were 14.4%

304 and 16.2% in -W and +W, respectively. After clear-cutting, the soil profiles were recharged

305 with water due to the interruption of tree transpiration. In +W, the gravitational soil solutions

306 reached a depth of 16 m only 10 months after clear-cutting, while in -W they reached a

307 maximum depth of only 12 m 13 months after clear-cutting. Gravitational soil solutions did not

308 reach the water table in -W over the study period (one year before the clear-cut and the first 2

309 years of coppice management).

310   c. Fine root length production

311   The highest cumulative root length production (CLP) over the study period was at depths > 4

312   m, in both +W and -W (Figure 4). In –W, CLP reached about 19 m m^{-2} at a depth of 13.5-14.8

313   m, and only 3.9 m m^{-2} in the upper 2.3 m of the soil profile. In +W, the highest CLP was found

314   in an intermediate soil layer (5.5-6.8 m deep) with a CLP of 18.9 m m^{-2}. CLP reached about 12

315   m m^{-2} in very deep soil layers (13.5-14.8 m deep) and only about 2 m m^{-2} in the upper 2.3 m of

316   the soil profile in +W.

317   d.   Fine root elongation rates

318   Daily root elongation rates (DRERs) were highly variable between the soil layer and the season,

319   in both +W and -W (Figure 5). Fine root growth started in the top soil after the clear-cut and

320   occurred more and more deeply over time in +W and -W. The intensity (measured as the

321   maximum DRER) and the period of fine root growth differed depending on soil depth. DRER

322   measured during flushes of root growth was much lower in the topsoil than at great depth in

323   +W, -W and NH (no observation below 4.8 m in NH). At a depth of 3.5-4.8 m, flushes of DRER

324   in NH came earlier than in clear-cut plots. In the coppices, the first flush of DRER occurred

325   about 6 months after clear-cutting in the topsoil, 12 months after clear-cutting in the 3.5-4.8 m

326   soil layer and 16 months after clear-cutting in the 13.5-14.8 m soil layer, in both +W and -W.

327   Moreover, DRER sharply increased in the 15.5-16.8 m layer of +W 18 months after clear-

328   cutting.

329   DRER peaks ranged from 1.5 cm m^{-2} day^{-1} in the topsoil to 94.7 cm m^{-2} day^{-1} at a depth of

330   about 12 m in +W, and from 3.5 cm m^{-2} day^{-1} in the topsoil to 83.7 cm m^{-2} day^{-1} at a depth of

331   about 14 m in -W. The maximum elongation rate of individual roots (MaxRER) reached 4.3 cm

332   day^{-1} in -W and 3.0 cm day^{-1} in +W (Table 1) and was much higher at great depths than in the

333   topsoil (data not shown). DRER values peaked at the end of the dry season in all the soil layers

334   at depths > 6 m when SWC decreased in the upper soil layers (Figure 3, Figure 5). Thus, DRER

335   values were not necessarily correlated with soil water contents for a given soil layer. A

336   synchrony between the decrease in cumulated extractable water in the topsoil and DRER peaks

337   was observed in -W (Figure 6) after the clear-cut. Successive DRER peaks appeared more and

338   more deeply at the end of the dry season when the extractable water stocks in the 0-2 m layer

339   fell below about 80 mm.

340   e.   Fine root distributions

341   Auger sampling carried out on the same date in the NH plot and in the +W and -W coppices

342   1.5 years after clear-cutting showed a similar pattern of deep rooting, whatever the treatment

343   (Figure 7). Fine root densities dropped below a depth of 20 cm, then decreased gradually down

344   to the water table in NH, +W and -W. Fine roots where found down to 17 m in all treatments.

345   Total fine root biomass down to a depth of 17 m was 1,078 g m^{-2} in NH, 1,017 ± 301 g m^{-2} in

346   +W and 1,266 ± 363 g m^{-2} in -W (Table 2). Fine root densities were about 25% higher in -W

347   than in +W and NH in most of the soil layers. At depths > 7 m, fine root densities were at least

348   twice as high in -W as in +W and NH.

349   f.   Fine root traits

350   The total root area index (RAI) was significantly ($F = 32.78$, $P < 0.001$) higher in –W (32.8 m^2

351   m^{-2}) than in +W (26.5 m^2 m^{-2}) (Figure 8). Similar RAI values in the NH stand (26.8 m^2 m^{-2})

352   and in the +W coppice suggested that the effect of clear-cutting on fine root dynamics was low,

353   in agreement with elongation and mortality rates observed in the upper 4 m on minirhizotron

354   tubes. RAI in the 0-1 m surface soil layer accounted for only one third of the total RAI down

355   to the water table in NH, +W and -W (about 11 m^2 m^{-2} on average). Significant differences

356   between +W and -W were found at depths > 5 m ($P < 0.001$, Figure 8). In the 5-10 m soil layers,

357   RAI was 5.0 m^2 m^{-2} in -W and 2.8 m^2 m^{-2} in +W. At depths > 10 m, RAI was 3.2 m^2 m^{-2} in -W

358   and only 0.4 m^2 m^{-2} in +W.

359   In the NH, +W and -W treatments, depth had little effect on specific root length (SRL), specific

360   root area (SRA) and fine root diameter (data not shown). SRL and SRA were significantly

361   higher in -W than in +W ($P < 0.001$), and similar values were observed in +W and NH, although

362   the sampling in NH (pseudo-replication on one block) did not allow a confirmation with

363   statistics (Table 2). Down to a depth of 17 m, mean SRL values were 28.8, 30.6 and 34.4 m g$^-$

364   ^{1}, mean SRA values were 258.8, 267.5 and 305.3 cm^2 g^{-1}, and mean fine root diameters were

365   0.31, 0.32 and 0.36 mm in NH, +W and -W, respectively (Table 2).

366   g. Fine root mortality

367   Cumulative dead root length in the minirhizotron images over the study period of 3 years across

368   all soil layers accounted for only 6-7% of cumulative root length production, in both +W and -

369   W (Table 1). Surprisingly, dead fine root length did not increase after clear-cutting and did not

370   differ between depths and between the +W and -W treatments. Dead fine root mass estimated

371   1.5 years after clear-cutting amounted to 163.2 g m^{-2} in +W and 167.9 g m^{-2} in -W (Table 2).

372   **4. Discussion**

373   The main novelty of our results lies in the first direct observation of fine root phenology at

374   depths of more than 10 m and derived knowledge raised from a comparison between the

375   treatments. The consequences of tree harvesting on fine root dynamics in coppice-managed

376   plantations raise specific questions never studied before along a deep tropical soil profile. Since

377   the 1980s, the minirhizotron technique has been widely used to study fine root dynamics and

378   turnover (Graefe *et al.*, 2008; Maeght *et al.*, 2013). Many studies have shown that the soil

379   environment close to minirhizotrons can be modified relative to undisturbed soil (Majdi and

380   Nylund, 1996), which is likely to influence fine root dynamics. However, in our study the very

381   low root mortality rates after clear-cutting revealed by minirhizotron monitoring was consistent

382   with the small amounts of dead fine roots measured by soil coring. Despite some unavoidable

383   limitations, direct observations from minirhizotron tubes or field rhizotrons is for now the most

384   accurate way of studying fine root phenology in situ (Dipesh and Schuler, 2013; Radville *et*

385   *al.*, 2016).

386   *Root behavior in response to drought*

387   The main purpose of our study was to investigate whether fine roots explore very deep soil

388   layers and do so more intensively when trees are subjected to prolonged drought periods. This

389   study, carried out in a throughfall exclusion experiment and including a non-harvested plot,

390   made it possible to assess the effect of clear-cutting under two contrasting rainfall regimes. In

391   agreement with our first hypothesis, *Eucalyptus* trees responded to drought by increasing fine

392   root densities at great depth. Previous studies in Brazil showed that *Eucalyptus* trees have the

393   ability to explore very deep layers in soils without hindrance to root growth (Christina *et al.*,

394   2011; Pinheiro *et al.*, 2016). In a survey of 62 tropical tree species, Markesteijn and Poorter

395   (2009) showed that trees increase belowground biomass and the proportion of deep roots in

396   response to dry conditions. Root growth in deep soil layers can increase the amount of water

397   available to sustain tree growth, which could be a key advantage for eucalypt trees in coping

398   with severe drought events (Christina *et al.*, 2017).

399   After clear-cutting, fine root growth at more than 4 m deep was spectacular at the end of the

400   dry season, whatever the water supply regime. Lambais et al. (2017) also showed flushes of

401   fine root growth down to a depth of 6 m at the end of dry periods in a Brazilian eucalypt

402   plantation. Fine root growth in deep soil layers was initiated when the extractable water content

403   in the 0-2 m soil layer fell below a threshold of about 80 mm, which suggests that soil water

404   content in a particular soil layer was not the main driver of fine root growth. Endogenous and

405   exogenous factors are major drivers of fine root phenology (Moroni *et al.*, 2003; Tierney *et al.*,

406   2003; Abramoff and Finzi, 2015), but are difficult to disentangle in deep soil layers. The

407   successive flushes of fine root growth from the topsoil to the deepest soil layers at the end of

408   the dry season and the first months after the onset of the rainy season in +W and -W might have

409   resulted from a rapid exhaustion of water resources in the topsoil, inducing tree roots to grow

410   deeper in the soil (Schenk and Jackson, 2002; Billings, 2015). Furthermore, a strong increase

411   in sugar sap concentration and sugar allocation belowground has been shown in forests during

412   dry periods (Pate and Arthur, 1998; Scartazza *et al.*, 2015), which could be a physiological

413   response to a rapid exhaustion of water in the top soil and could help to explain the root growth

414   in deep soil layers at the end of dry periods in our study.

415   In agreement with our second hypothesis, *Eucalyptus* trees facing drought adapted their root

416   morphology to maximize the root surface area to take up limited resources. SRL and SRA were

417   higher in –W than in +W, which in combination with higher fine root densities led to a much

418   higher root area index. Despite many uncertainties due to soil disturbance by the auger, the

419   results obtained are consistent with those of other studies in plantations of the same type

420   (Germon *et al.*, 2018) as well as with other methods based on excavations (Maurice *et al.*, 2010;

421   Laclau *et al.*, 2013). In a meta-analysis, Ostonen et al. (2007) showed that SRL response to

422   drought varies greatly between species. While Arend et al. (2011) did not observe any

423   significant change in SRL, root area index and root tissue density for oak trees (*Quercus sp.*)

424   exposed to drought, Olmo *et al.* (2014) showed an increase in SRL and root tissue density under

425   drought conditions for 10 tree species. *Eucalyptus grandis* trees coped with drought in our

426   experiment by increasing their capacity to take up soil resources for a relatively low investment

427   in belowground biomass. A large increase in SRL and SRA was recently shown throughout

428   deep soil profiles down to 17 m deep for *Acacia mangium* Wild and *E. grandis* roots in response

429   to the mixture relative to monospecific stands (Germon *et al.*, 2018). Our study showed that

430   *Eucalyptus* trees can modify fine root traits to enhance resource capture and the exploration of

431   very deep soil layers to survive in a context of climate change, which contributes to maintaining

432   water uptake during dry periods (Brunner *et al.*, 2015; Christina *et al.*, 2017).

433 *Key role of deep roots in coppice management*

434 Contrary to our third hypothesis, relatively few roots were lost by mortality (< 10% out of all

435 the roots observed over 3 years), which suggested that most of the root system remained

436 functional after clear-cutting. The effect of clear-cutting on fine root mortality remains unclear

437 in coppice-managed forest plantations. Unlike our observations, sequential coring in the 0-1 m

438 soil layer showed a decrease in fine root density after harvesting coppice-managed *E. grandis*

439 stands in Brazil (Mello *et al.*, 2007). Wildy and Pate (2002) also showed high fine root mortality

440 rates after cutting the trees in plantations of *Eucalyptus kochii* Maiden & Blakely subsp.

441 plenissima Gardner (Brooker), but the root system superstructure was sustained down to a depth

442 of at least 4 m. Teixeira et al. (2002) showed from sequential coring in the 0-0.6 m soil layer

443 that fine-, medium- and coarse-root biomasses increased over time after harvesting coppice-

444 managed *Eucalyptus urophylla* S. T. Blake trees. Using the minirhizotron technique, Dickmann

445 *et al.* (1996) showed an absence of root mortality for coppice-managed poplar clones. Our study

446 suggested that 6-year-old *Eucalyptus grandis* trees have enough reserves within the root system

447 and the appropriate edaphic surrounding conditions to maintain the fine root biomass

448 established down to the water table after clear-cutting, which probably contributed to promoting

449 early shoot growth (Drake *et al.*, 2013; Brunner *et al.*, 2015).

450 Fine root growth after clear-cutting started in the topsoil, then continued successively in deeper

451 and deeper soil layers, which confirmed our third hypothesis, even though the lapse of several

452 months after clear-cutting was not expected. This pattern might have resulted from high nutrient

453 and water availabilities in the upper layers after harvesting *Eucalyptus* stands due to an

454 interruption of tree water uptake and fertilizer application (Laclau *et al.*, 2010). The asynchrony

455 within the root system, delaying root growth in deep soil layers, might be a strategy for

456 maximizing the water and nutrient uptake needed to meet the high demand of these fast-growing

457 trees. The behavior observed in this study is original compared to what has been observed in

458   other types of coppice stands where repeated clear-cutting increased root growth in the top soil

459   and increased tree sensitivity to drought (Corcuera *et al.*, 2006; Zadworny *et al.*, 2014). In this

460   study, root growth occurred at a depth of 14 m less than one year after clear-cutting of coppice-

461   managed *E. grandis* trees, while the maximum depth reached by *E. grandis* roots one year after

462   planting is about 7 m in very deep soils (Christina *et al.*, 2011; Laclau *et al.*, 2013). Deep roots

463   can provide access to large amounts of water stored in the subsoil after clear-cutting and small

464   fine root densities in deep soil layers can be sufficient to take up substantial amounts of water

465   (Christina *et al.*, 2017). Low fine root mortality rates after clear-cutting suggest that coppice-

466   management of *Eucalyptus* plantations might be a promising option for coping with water

467   scarcity, since the pre-existing root system can provide access to water stored throughout deep

468   soil profiles.

469   *Carbon sequestration and implication for the management of eucalypt plantations*

470   Surprisingly, cutting the trees did not lead to an increase in root mortality throughout the soil

471   profile, whatever the water supply regime. Fine roots play an active role in carbon (C) cycling

472   in forest ecosystems, through respiratory processes, exudation and root mortality (Balesdent

473   and Balabane, 1996; Marsden *et al.*, 2008; Strand *et al.*, 2008). The consequences of deep

474   rooting on subsoil C stocks in tropical planted forests and other forest ecosystems remain poorly

475   known (Nepstad *et al.*, 1994; Harper and Tibbett, 2013; Gao *et al.*, 2018; Meyer *et al.*, 2018).

476   On the one hand, the supply of fresh carbon might promote the activity of microbes and affect

477   the stability of pre-existing organic matter through a "priming effect" (Kuzyakov *et al.*, 2000;

478   Fontaine *et al.*, 2007; Derrien *et al.*, 2014). Promoting the mineralization of ancient C would

479   result in high emissions of carbon dioxide (CO_2) under aerobic conditions and of methane (CH_4)

480   under anaerobic conditions. However, a complementary study in our plots showed that CO_2 and

481   CH_4 emissions did not increase significantly after clear-cutting in the coppice-managed stands

482   compared to the non-harvested stand (Germon et al. in prep.). Gas emission rates after clear-

483   cutting in our experiment were therefore consistent with the low rates of root mortality

484   observed. On the other hand, deep roots might also contribute to sequestrating large amounts

485   of C in soil. Total below-ground carbon allocations account for about 20-30% of gross primary

486   production in *Eucalyptus* plantations (Ryan *et al.*, 2010; Epron *et al.*, 2012; Nouvellon *et al.*,

487   2012). Fine root elongation rates were higher at great depth compared to the topsoil, with an

488   increase in fine root density after the clear-cut in very deep horizons. Moreover, microbial

489   biomass is lower in deep soil layers than in the topsoil, which in combination with oxygen

490   limitations could enhance C sequestration as a result of low mineralization rates (Taylor *et al.*,

491   2002; Rumpel and Kögel-Knabner, 2011). C from roots is generally retained more in the soil

492   than C from aboveground litter, which is more affected by physicochemical processes and also

493   due to structural composition differences between leaves and roots (Rasse *et al.*, 2005; Schmidt

494   *et al.*, 2011; Menichetti *et al.*, 2015). Further studies are needed to assess whether the

495   management of *Eucalyptus* plantations in very deep soils could be an effective option to help

496   mitigate the increase in CO_2 in the atmosphere.

497   **Conclusions**

498   The fine root phenology of coppice-managed *Eucalyptus* trees under contrasting water supply

499   regimes revealed unexpected low rates of root mortality. The early growth of the sprouts after

500   cutting the trees benefited from the root system established over the previous rotation cycle,

501   and the asynchrony of fine root growth depending on depth highlighted tree plasticity in

502   response to soil conditions. Establishing deep root systems in tropical planted forests could help

503   trees withstand the long drought periods expected under climate change in many tropical

504   regions. Our study suggested that coppice management might be an interesting option in

505   tropical *Eucalyptus* plantations, both to improve tree tolerance to drought and store carbon at

506   great depth in the soil.

507   **Acknowledgments**

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765 Table 1: Mean diameter (mm), maximum elongation rate of individual roots (cm day^{-1}), number
766 of roots observed and root mortality over 3 years in the minirhizotron images across all the soil
767 layers, from the surface to the water table at a depth of about 17 m, in the undisturbed rainfall
768 plot (+W) and the plot with 37% of throughfall excluded by plastic sheets (-W).

769

	+W	-W
Mean diameter (mm)	0.61 ± 0.31	0.52 ± 0.28
Maximum root elongation rate (cm day^{-1})	3.0	4.3
Number of roots observed	12,247	14,118
Mortality (%)	7.4	5.7

770

771

772

773 Table 2: Total living fine root biomass (g m^{-2}), total fine root necromass (g m^{-2}), mean specific
774 root length (m g^{-1}), mean specific root area (cm^2 g^{-1}) and mean root diameter down to a depth
775 of 17 m in the undisturbed rainfall plots +W, in the plot with 37% of throughfall excluded by
776 plastic sheets (-W), both in coppices and 1.5 years after the clear-cut, and in the non-harvested
777 plot (NH), i.e. a 7.5-year-old tree plantation. Standard deviations are indicated. Different lower-
778 case letters indicate significant differences between treatments +W and -W ($p < 0.05$). NH was
779 not included in statistical analyses because the three soil coring replicates were located in the
780 same plot.

781

|	+W	-W	NH
Fine root biomass (g m^{-2})	1,016.5 ± 362.8	1,265.8 ± 301.4	1,078.3 ± 83.9
Fine root necromass (g m^{-2})	163.2 ± 55.9	167.9 ± 31.3	139.1 ± 17.7
Specific root length (m g^{-1})	30.6 ± 6.9 b	34.4 ± 14.1 a	28.8 ± 7.6
Specific root area (cm^2 g^{-1})	267.5 ± 55.7 b	305.3 ± 150.1 a	258.9 ± 92.6
Root diameter (mm)	0.32 ± 0.08 b	0.36 ± 0.13 a	0.31± 0.08

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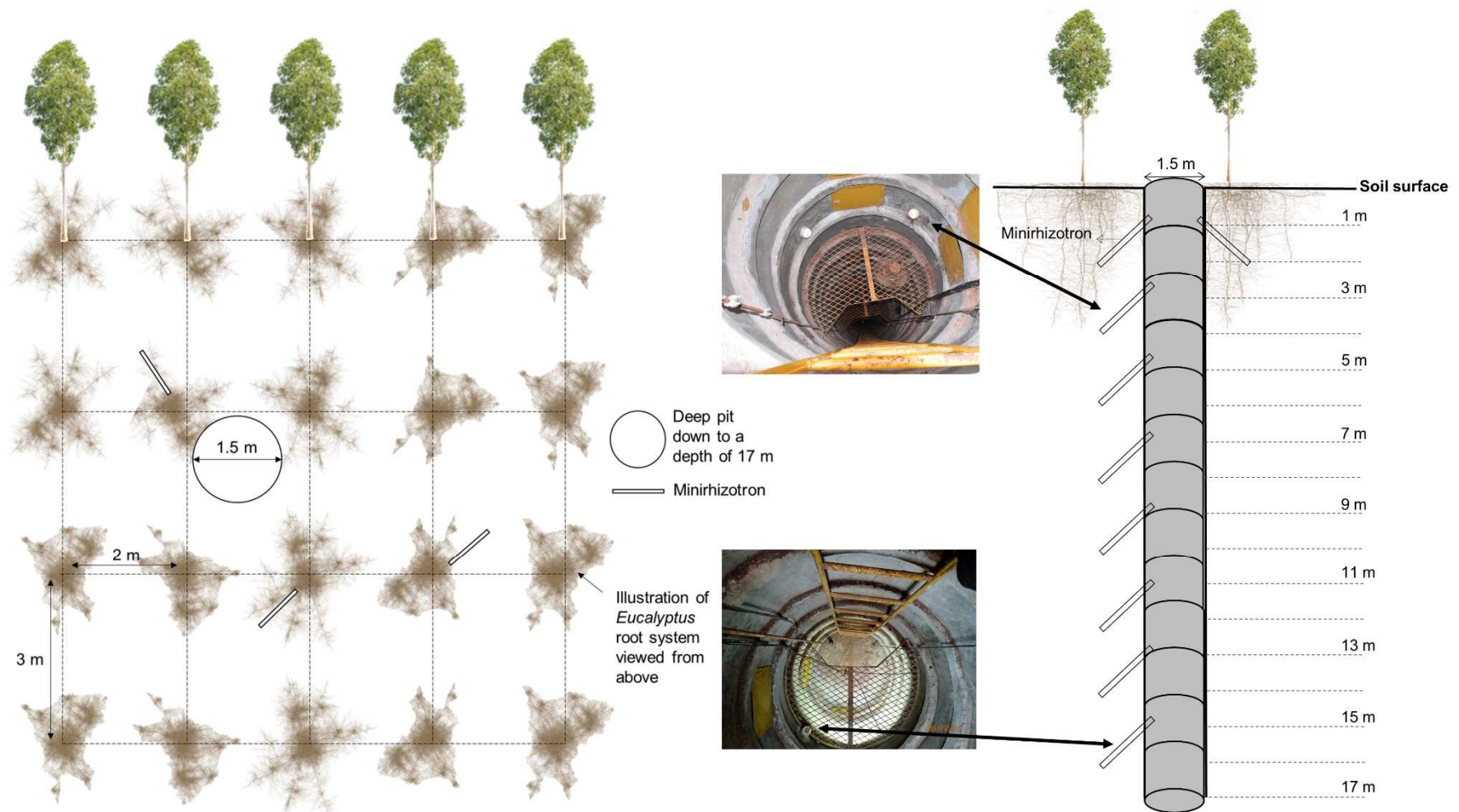
Figure 1: Layout of the position of the pit in the +W treatment of block 1 and distribution of minirhizotron tubes at the soil surface (n=3) and in the permanent pit from 1 m (n=2) down 17 m (n=1 per m in depth). The same set-up was used for the -W treatment.
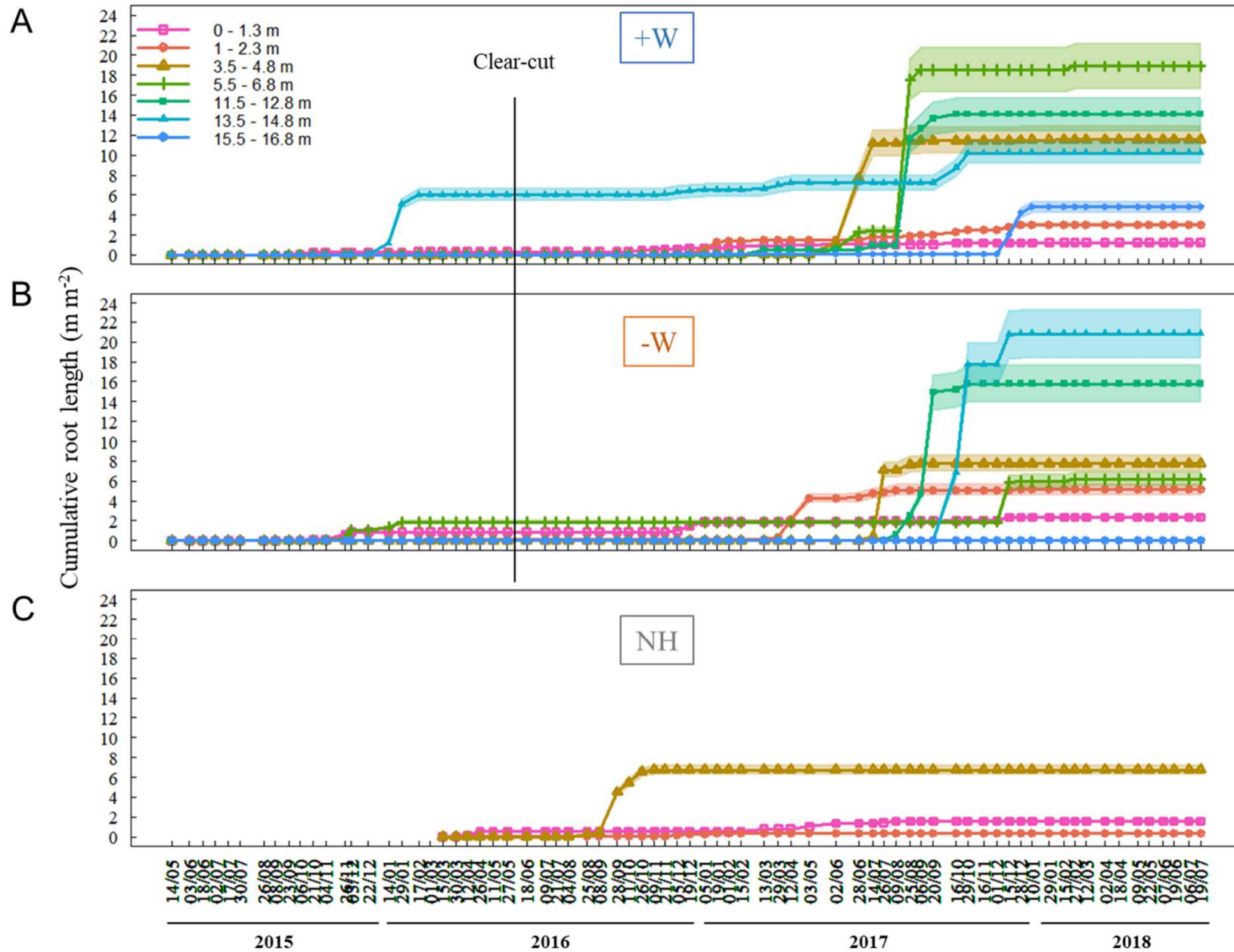
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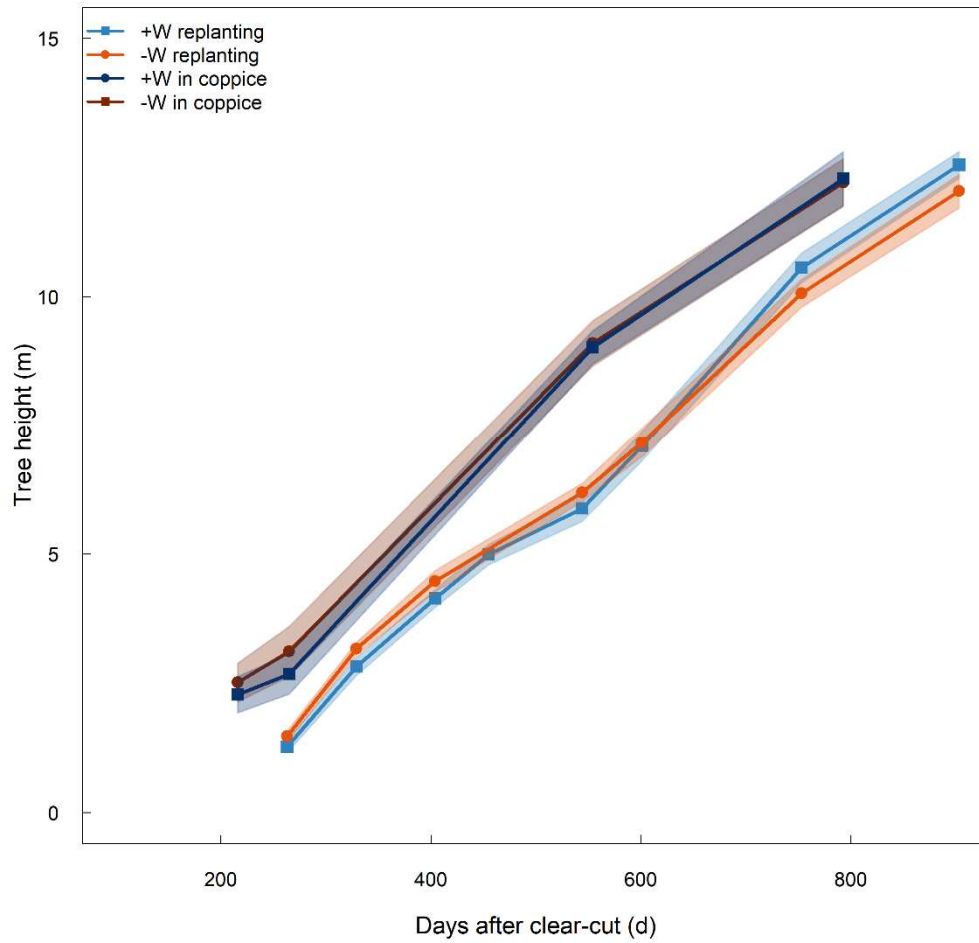
Figure 2: Vertical growth (m) over the first 2.5 years after harvesting of the previous stands for the replanting (June 2010-June 2016) and the coppice (from June 2016) in the undisturbed rainfall plots (+W, blue) and in the plots with 37% of throughfall excluded by plastic sheets (-W, orange). Standard errors are shown (shaded area).
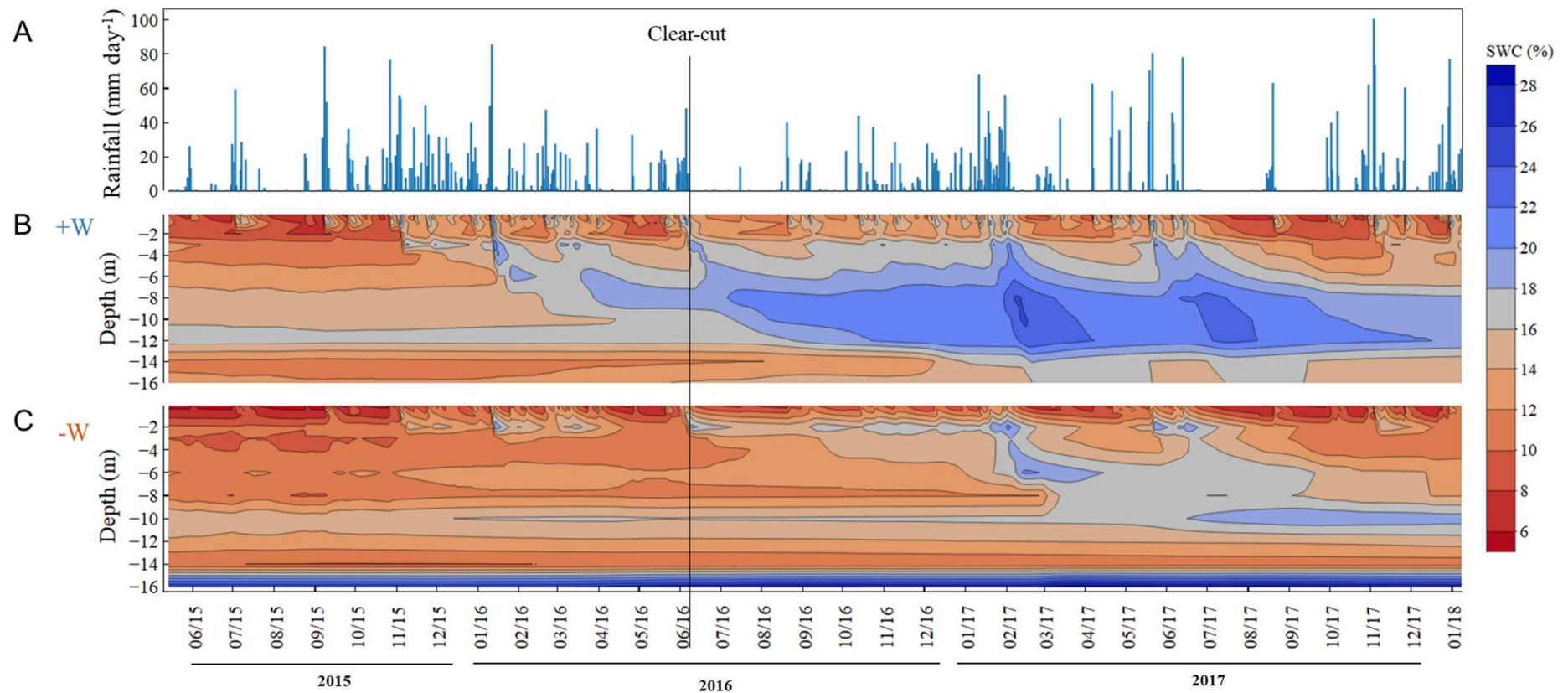
Figure 3: Daily rainfall (A) and soil water content (SWC, %) within the soil profiles down to a depth of 16 m in the undisturbed rainfall plots (+W, B) and in the plots with 37% of throughfall excluded by plastic sheets (-W, C) from May 2015 to January 2018. SWC graphical representation is a contour line interpolation obtained with a marching square algorithm. R software version 3.4.4 and the "plotly" package version 4.8.0 were used. The clear-cut date is indicated by a vertical line. The stand was coppice-managed after the clear-cut.

Cumulative root length (m m^{-2})

A +W
Clear-cut

0 – 1.3 m
1 – 2.3 m
3.5 – 4.8 m
5.5 – 6.8 m
11.5 – 12.8 m
13.5 – 14.8 m
15.5 – 16.8 m

B -W

C NH

2015   2016   2017   2018

798

Figure 4: Cumulated root length production (CLP) on minirhizotron tubes (m m^{-2} of minirhizotron area) measured every 14 days from May 2015 to July 2018 in soil layers 0–1.3 m, 1–2.3 m, 3.5-4.8 m, 5.5–6.8 m, 11.5-12.8 m, 13.5–14.8 m and 15.5-16.8 m in the undisturbed rainfall plot (+W, A), in the plot with 37% of throughfall excluded by plastic sheets (-W, B) and in the non-harvested plot (NH, C). Standard errors are shown (shaded area). The clear-cut date is indicated by a vertical line. The stands were coppice-managed after clear-cutting in +W and -W. The monitoring of CLP started in May 2015 in the +W and -W plots, and in March 2016 in the NH stand, where only the first three layers (0-1.3 m, 1-2.3 m and 3.5-4.5 m) were sampled.

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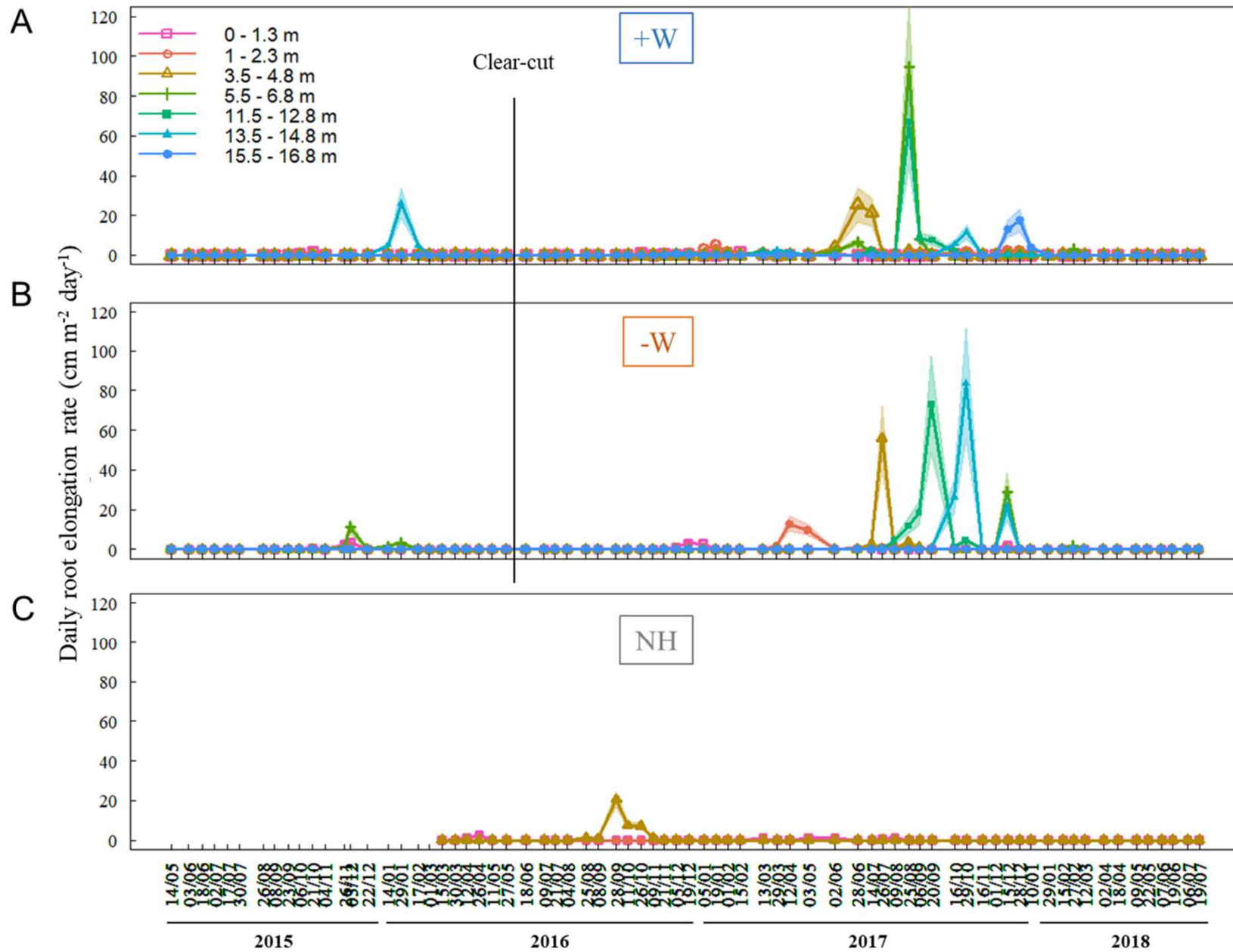
806 Figure 5: Daily living root elongation rate (DRER) on minirhizotron tubes (cm m^{-2} of minirhizotron area day^{-1}) estimated every 14 days from May
807 2015 to July 2018 in soil layers 0–1.3 m, 1–2.3 m, 3.5-4.8 m, 5.5–6.8 m, 11.5-12.8 m, 13.5–14.8 m and 15.5-16.8 m in the undisturbed rainfall plot
808 (+W, A), in the plot with 37% of throughfall excluded by plastic sheets (-W, B) and in the non-harvested plot (NH, C). Standard errors are shown
809 (shaded area). The clear-cut date is indicated by a vertical line. The stands were coppice-managed after clear-cutting in +W and -W. The monitoring
810 of DRER started in May 2015 in the +W and -W plots, and in March 2016 in the NH stand, where only the first three layers (0-1.3 m, 1-2.3 m and
811 3.5-4.5 m) were sampled.

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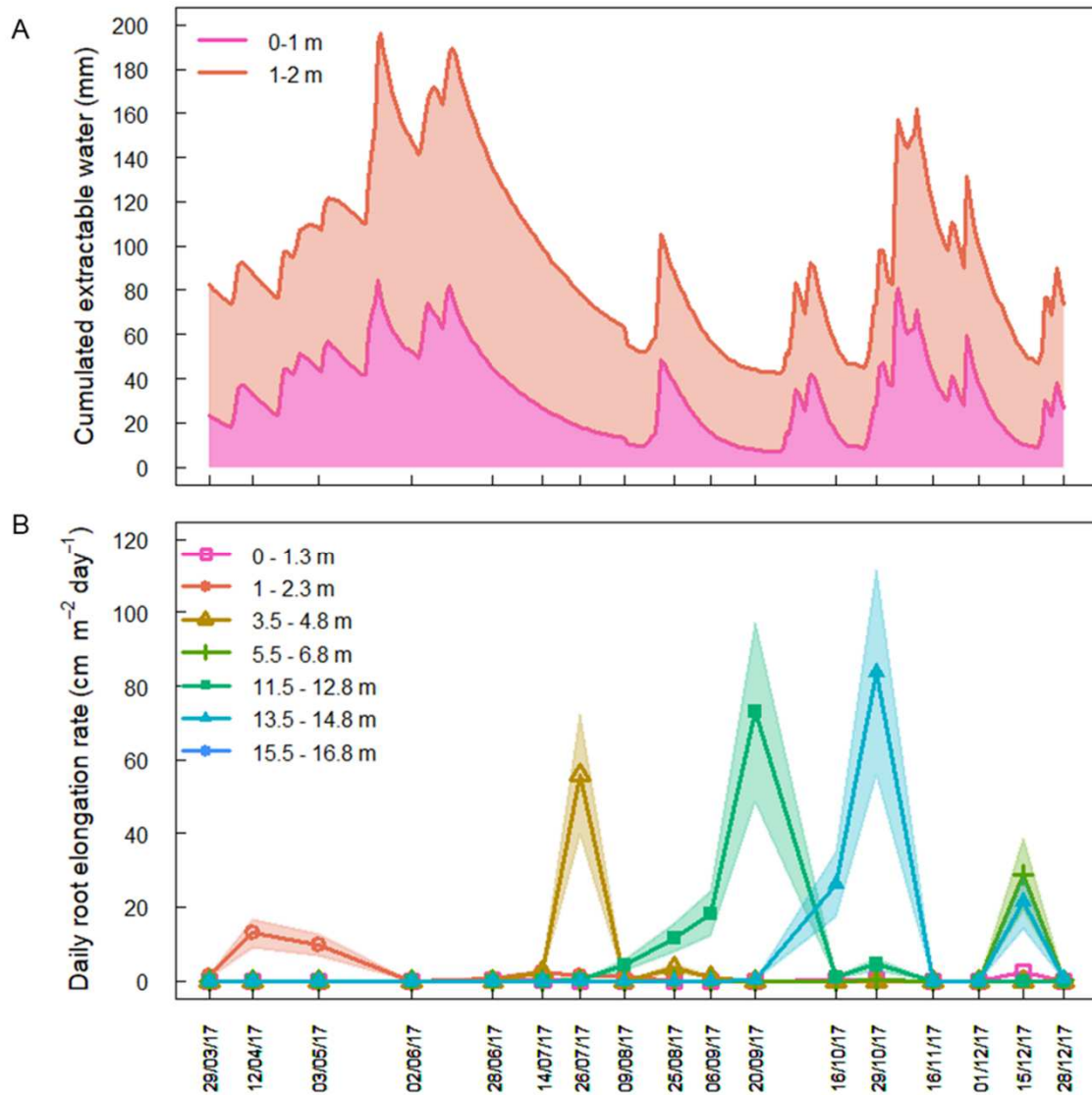
Figure 6: A) Time course of soil extractable water (mm) in soil layers 0-1 m and 1-2 m, in the
-W (37% of throughfall excluded by plastic sheets) coppice of block 1, from March 2017 (10
months after the clear-cut) to December 2017. The mean daily values of soil extractable water
were estimated from semi-hourly SWC measurements. B) Daily living root length production
on the surface of minirhizotron tubes (cm m^{-2} of minirhizotron area day^{-1}) estimated over the
same period and same plot as a), at two-week intervals, in soil layers 0–1.3 m, 1–2.3 m, 3.5-4.8
m, 5.5–6.8 m, 11.5-12.8 m, 13.5–14.8 m and 15.5-16.8 m. Standard errors are shown (shaded
area).

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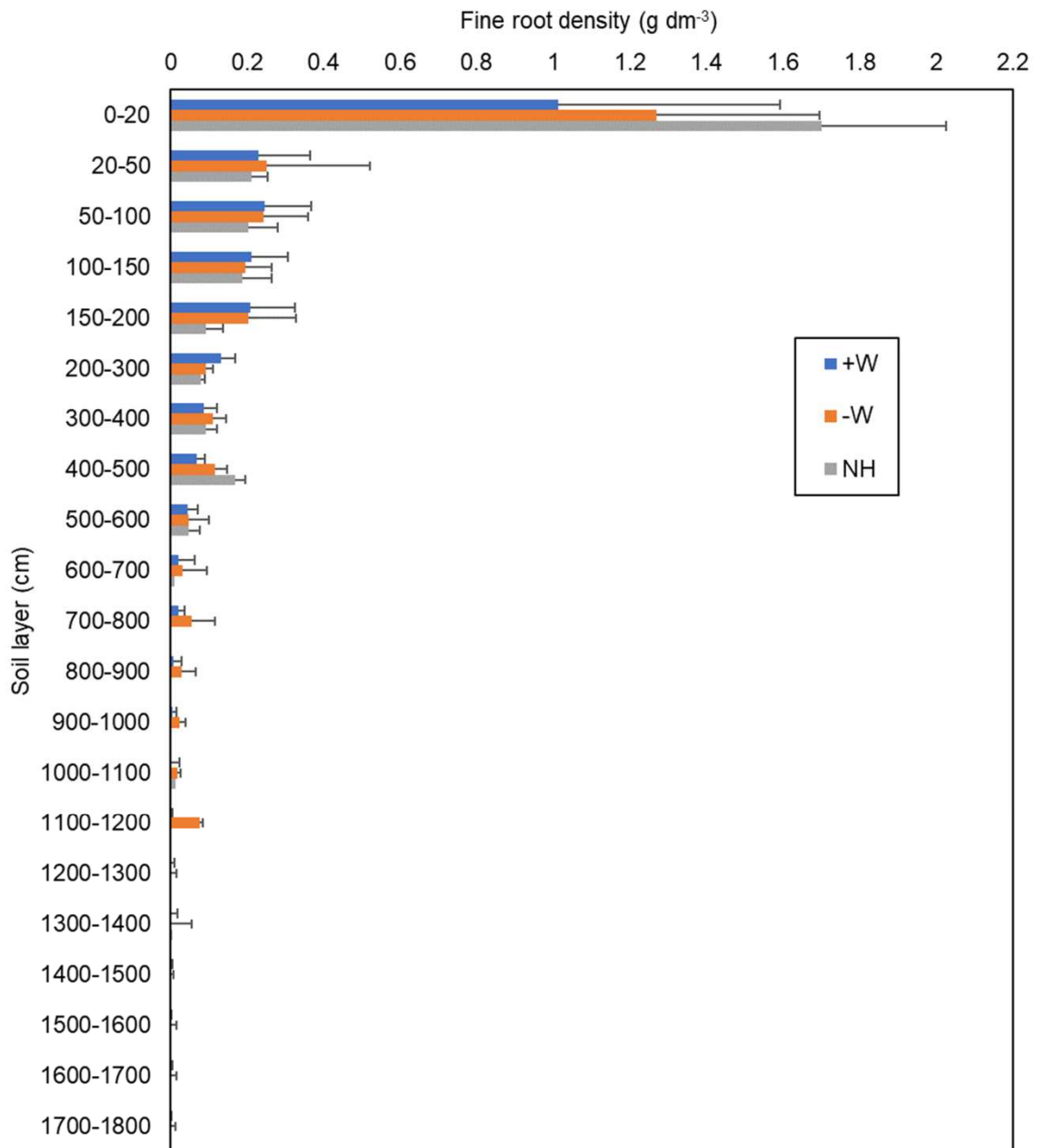
Figure 7: Mean fine root densities down to the root front in the undisturbed rainfall plots (+W, blue), in the plots with 37% of throughfall excluded by plastic sheets (-W, orange) and in the non-harvested plot (NH, gray). Standard deviations between blocks ($n = 3$) for -W and +W and between pseudo replicates in a single block for NH are shown.
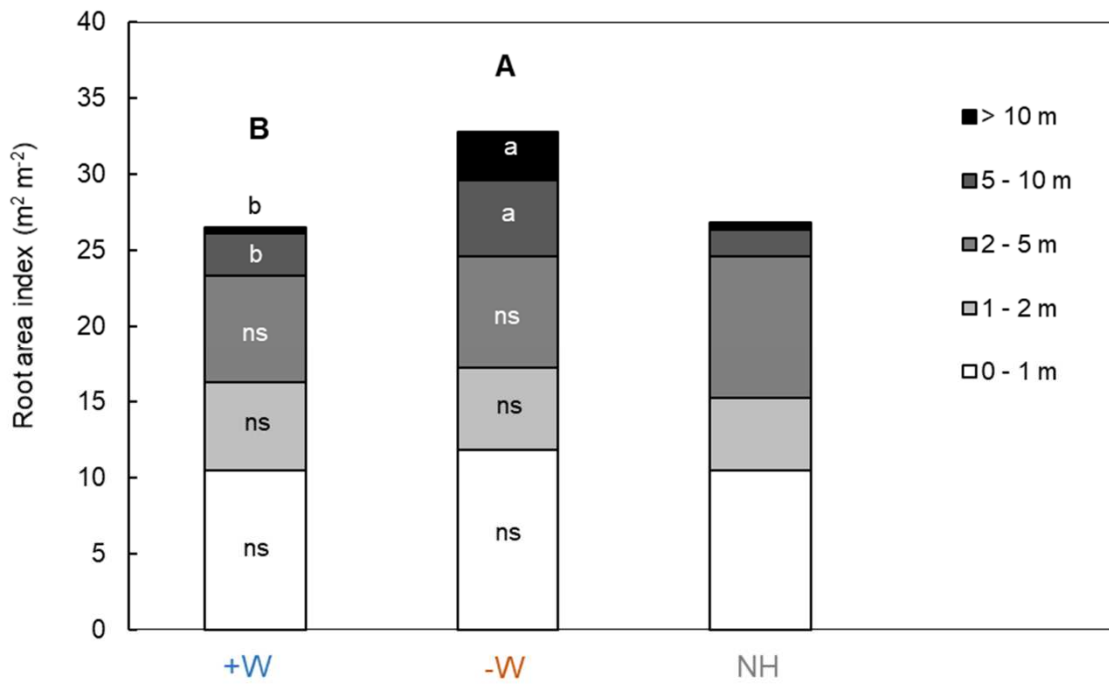
Figure 8: Root area index (m^2 m^{-2}) in the 0-1 m, 1-2 m, 2-5 m, 5-10 m and 10-17 m deep soil layers in the undisturbed rainfall plots (+W), in the plots with 37% of throughfall excluded by plastic sheets (-W) and in the non-harvested plot (NH). Different upper-case letters indicate significant differences between treatments for the cumulative indices and different lower-case letters indicate significant differences between treatments within each individual soil layer ($p <$ 0.05). NH was not included in the ANOVA because the three soil coring replicates were located in the same plot.