

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

Amandine Germon, Christophe Jourdan, Bruno Bordron, Agnès Robin, Yann Nouvellon, Lydie Chapuis-Lardy, Jose Leonardo de Moraes Goncalves, Céline Pradier, Irae Amaral Guerrini, Jean-Paul Laclau

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1	Consequences of clear-cutting and drought on fine root dynamics			
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5	Amandine Germon ^{1,2} *, Christophe Jourdan ^{2,3} , Bruno Bordron ⁴ , Agnès Robin ^{2,3,5} , Yann			
6	Nouvellon ^{2,3,4} , Lydie Chapuis-Lardy ^{2,6} , José Leonardo de Moraes Gonçalves ⁴ , Céline			
7	Pradier ^{2,3} , Iraê Amaral Guerrini ¹ , Jean-Paul Laclau ^{1,2,3,4}			
8				
9	¹ UNESP-São Paulo State University, School of Agricultural Sciences, Botucatu, São Paulo 18610-307, Brazil			
10	² Eco&Sols, Univ Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, Montpellier, France			
11	³ CIRAD, UMR Eco&Sols, F-34060 Montpellier, France			
12	⁴ ESALQ, Forest Science Department, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de São			
13	Paulo, CEP 13418-900 Piracicaba, SP, Brazil			
14	5 ESALQ, Soil Science Department, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de São			
15	Paulo, CEP 13418-900 Piracicaba, SP, Brazil			
16	⁶ IRD, UMR Eco&Sols, LMI IESOL, BP 1386, CP 18524 Dakar, Senegal			
17				
18	* Corresponding author, E-mail address: amandine.germon@gmail.com			
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20 Abstract

21 Improving our understanding of the spatiotemporal dynamics of fine roots in deep soil layers 22 is of utter importance to manage tropical planted forests in a context of climate change. Our 23 study aimed to assess the effect of clear-cutting and drought on fine-root dynamics down to 24 the water table in Brazilian ferralsol under eucalypt plantations conducted in coppice. Fine 25 roots (i.e. diameter < 2 mm) were sampled down to 17 m deep in a throughfall exclusion 26 experiment comparing stands with 37% of throughfall excluded by plastic sheets (-W) and 27 stands without rain exclusion (+W). Root dynamics were studied using minirhizotron in two 28 permanent pits down to 17 m deep, over 1 year before clear-cutting, then over 2 years in 29 coppice, as well as down to 4 m deep in a non-harvested plot (NH) serving as a control. After 30 harvesting, a spectacular fine root growth of trees conducted in coppice occurred in very deep 31 soil layers (> 13 m) and, surprisingly, root mortality remained extremely low whatever the 32 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 33 34 NH 7.5 years after planting. Specific root length and specific root area were about 15% higher 35 in -W than in +W. Proliferation of fine roots at great depths could be an adaptive mechanism 36 for tree survival, enhancing the access to water stored in the subsoil. The root system 37 established before clear-cutting provides access to water stored in very deep layers that 38 probably contribute to mitigate the risk of tree mortality during prolonged drought periods 39 when the eucalypt plantations is conducted in coppice after the clear-cut.

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

43

1. Introduction

44 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 45 46 mortality triggered by drought and changes in rainfall patterns has been reported worldwide 47 (Allen, 2009; Williams et al., 2013; McDowell et al., 2018). Tree survival greatly depends on 48 rooting system behavior and functioning (Nepstad *et al.*, 1994; Markewitz *et al.*, 2010; Pierik 49 and Testerink, 2014; Christina et al., 2017), as plant growth is highly dependent on the 50 absorptive function of fine roots for water and nutrients (Hinsinger, 2001). Fine roots also play 51 a major role in the global carbon (C) cycle, representing significant C input into the soil by the 52 incorporation of exudates and root necromass, and also generating a return of C to the 53 atmosphere through respiration and decomposition processes (Balesdent and Balabane, 1996; 54 Strand *et al.*, 2008). Improving our understanding of how root systems respond to drought is 55 therefore crucial for terrestrial biosphere models to predict the effect of climate change on tree 56 survival and carbon sequestration in forest and tree-based ecosystems.

57 Plant species use a large range of rooting patterns to cope with periodic drought, from "drought 58 tolerant strategies" with fine roots surviving in periodically dry soil, to "drought avoiding 59 strategies" shedding fine roots from dry soil horizons while rapidly developing roots in moister 60 areas (Brunner et al., 2015; Vries et al., 2016; Bristiel et al., 2018). Drought can increase the 61 root-to-shoot ratio, the root area or root length-to-leaf area ratio, as well as the proportion of 62 fine roots in deep soil layers and/or the specific root area (Markesteijn and Poorter, 2009; Ma 63 et al., 2018; Zhou et al., 2018). Root growth peaks have been shown in deep soil layers during 64 dry periods for eucalypt and rubber trees in tropical soils (Maeght et al., 2015; Lambais et al., 65 2017). Drought tolerance strategies are common for herbaceous plants, while drought avoiding 66 strategies are often adopted by trees in evergreen tropical forests (Brunner et al., 2015). Despite

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

a. Study site

116 The experiments were conducted at the research station owned by the Luiz de Queiroz College of Agriculture (ESALQ) near Itatinga (São Paulo, Brazil, 23°02'S 48°38'W). The study area, 117 118 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 was 1,557 mm and 2,303 mm in 2016 and 2017, respectively. The soils are very deep Ferralsols 125 126 (IUSS Working Group WRB, 2015) developed on Cretaceous sandstone. Clay content ranges 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 127 128 are mainly kaolinite (Christina et al., 2015).

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 layout with 6 treatments and 3 blocks was described in detail by Battie-Laclau et al. (2014). We 132 133 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 (at planting: 3.3 g P m⁻², 200 g m⁻² of dolomitic lime and trace elements; at 3 months of age: 12 139 g N m⁻², 0.45 mol K m⁻² applied as KCl) and herbicides were applied to avoid the presence of 140

other understory species. In +W and -W, the eucalypt stands were harvested six years after 141 142 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

The volumetric soil water content (SWC) was monitored in the +W and -W treatments throughout the study period at half-hourly intervals using CS616 probes (Campbell Scientific Inc., Logan, UT, USA) installed at the following depths: 0.15, 0.5, 1, 2, 3, 4, 6, 8, 10, 12, 14 and 16 m, with 3 probes at each depth in block 1. Extractable water (mm) was calculated as the difference between the current soil water stock (mm) and the minimum soil water stock (i.e. 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

(Figure 1). The high cost of opening up and securing these pits prevented further replications in the other two blocks. However, other measurements, including deep fine root sampling and tree growth were carried out in all three blocks, making it possible to extrapolate some of the observations made in the two deep pits. In October 2015, a third pit was excavated in the nonharvested 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).

Root dynamics were recorded using a circular scanner system (CI-600 Root Growth Monitoring System, CID, USA). This scanner was selected for the quality of the images it produces, an essential element for the analysis (Graefe *et al.*, 2008). In order to have a significant stabilization period after soil disturbance from the installation, fine root monitoring began eight months after minirhizotron installation (Graefe *et al.*, 2008; Germon *et al.*, 2016). Eight images (21.59 x 19.56 cm, 100 dpi) per tube (43 tubes in total) were taken every two weeks for more than three consecutive years from May 2015 to July 2018: over one year before the clear-cut and two years after harvesting, in a coppice. Images were taken at a resolution of 100 dpi, as we obtained the same root lengths and diameter compared to images of 300 dpi and 600 dpi, 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

As described in Germon et al. (2016) and Lambais et al. (2017) the following metrics were used to estimate root production and the root elongation rate: living and dead root length production (LP, cm m⁻²) was calculated for each root as the individual root length (living or dead) at time t divided by the observed soil area of each image. The cumulative living or dead root length production (CLP, cm m⁻²) was calculated summing, at each time t, the individual length of all the roots observed, divided by the observed soil area of each image. The individual root

elongation rate (RER, cm day⁻¹) was calculated as the difference in individual root length 213 214 observed between two consecutive sessions (t and t₋₁) divided by the time in days between t and t₋₁. The daily root elongation rate (DRER, cm $m^{-2} day^{-1}$) was calculated by summing, at each 215 216 time t, each individual root elongation rate of all the roots observed, divided by the observed soil area of each image. The mean root elongation rate (MeanRER, cm day⁻¹) and the maximum 217 218 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.

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 (SRL, m g⁻¹, i.e. total length of scanned roots divided by their dry mass) and specific root area 259 (SRA, cm² g⁻¹, i.e. total area of scanned roots divided by their dry mass) were calculated for 260 261 each soil sample. Fine root mass density (g kg⁻¹ soil) was calculated as the total root dry mass divided by the dry weight of the soil used for root separation. Fine root density (FRD, g dm⁻³ 262

soil) was obtained by multiplying fine root mass density by the soil bulk densities (measured by the standard core method down to a depth of 17 m in each treatment). Fine root biomasses (FRB, g m⁻²) were calculated in each soil layer multiplying the mean fine root density by the soil layer volume (dm³). The root area index (RAI, m² m⁻²) was calculated as the surface area and length of fine roots divided by the sampled soil area respectively. FRD, FRB, SRL, SRA, and RAI were obtained for each soil layer from the soil surface down to a depth of 17 m, for the sampling position, +W, -W and NH treatments, and blocks.

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).

3. Results

a. Tree growth

Initial vertical growth was faster in the coppices than in the replanting: nine months after harvesting (in February 2011 for the replanting, and February 2017 for the coppices), mean tree 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 +W and -W coppice plots, respectively (Figure 2). There were no significant differences in vertical growth between the +W and -W treatments for either replanting or coppice in the first 3 years after harvesting.

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 $12.9 \pm$ 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 reached a depth of 16 m only 10 months after clear-cutting, while in -W they reached a 306 307 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

The highest cumulative root length production (CLP) over the study period was at depths > 4 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 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 in an intermediate soil layer (5.5-6.8 m deep) with a CLP of 18.9 m m⁻². CLP reached about 12 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 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 about 6 months after clear-cutting in the topsoil, 12 months after clear-cutting in the 3.5-4.8 m 325 326 soil layer and 16 months after clear-cutting in the 13.5-14.8 m soil layer, in both +W and -W. Moreover, DRER sharply increased in the 15.5-16.8 m layer of +W 18 months after clear-327 328 cutting.

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 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 about 14 m in -W. The maximum elongation rate of individual roots (MaxRER) reached 4.3 cm day⁻¹ in -W and 3.0 cm day⁻¹ in +W (Table 1) and was much higher at great depths than in the topsoil (data not shown). DRER values peaked at the end of the dry season in all the soil layers at depths > 6 m when SWC decreased in the upper soil layers (Figure 3, Figure 5). Thus, DRER values were not necessarily correlated with soil water contents for a given soil layer. A synchrony between the decrease in cumulated extractable water in the topsoil and DRER peaks was observed in -W (Figure 6) after the clear-cut. Successive DRER peaks appeared more and more deeply at the end of the dry season when the extractable water stocks in the 0-2 m layer 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 1.5 years after clear-cutting showed a similar pattern of deep rooting, whatever the treatment 342 343 (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. Total fine root biomass down to a depth of 17 m was 1,078 g m⁻² in NH, 1,017 \pm 301 g m⁻² in 345 +W and $1,266 \pm 363$ g m⁻² in -W (Table 2). Fine root densities were about 25% higher in -W 346 347 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

The total root area index (RAI) was significantly (F = 32.78, P < 0.001) higher in -W (32.8 m²) 350 m^{-2}) than in +W (26.5 $m^2 m^{-2}$) (Figure 8). Similar RAI values in the NH stand (26.8 $m^2 m^{-2}$) 351 352 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 to the water table in NH, +W and -W (about 11 m² m⁻² on average). Significant differences 355 356 between +W and -W were found at depths > 5 m (P < 0.001, Figure 8). In the 5-10 m soil layers, RAI was 5.0 m² m⁻² in -W and 2.8 m² m⁻² in +W. At depths > 10 m, RAI was 3.2 m² m⁻² in -W 357 and only $0.4 \text{ m}^2 \text{ m}^{-2} \text{ in +W}$. 358

In the NH, +W and -W treatments, depth had little effect on specific root length (SRL), specific root area (SRA) and fine root diameter (data not shown). SRL and SRA were significantly higher in -W than in +W (P < 0.001), and similar values were observed in +W and NH, although the sampling in NH (pseudo-replication on one block) did not allow a confirmation with statistics (Table 2). Down to a depth of 17 m, mean SRL values were 28.8, 30.6 and 34.4 m g⁻¹, mean SRA values were 258.8, 267.5 and 305.3 cm² g⁻¹, and mean fine root diameters were 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

limitations, direct observations from minirhizotron tubes or field rhizotrons is for now the most
accurate way of studying fine root phenology in situ (Dipesh and Schuler, 2013; Radville *et 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 the dry season and the first months after the onset of the rainy season in +W and -W might have resulted from a rapid exhaustion of water resources in the topsoil, inducing tree roots to grow deeper in the soil (Schenk and Jackson, 2002; Billings, 2015). Furthermore, a strong increase in sugar sap concentration and sugar allocation belowground has been shown in forests during dry periods (Pate and Arthur, 1998; Scartazza *et al.*, 2015), which could be a physiological response to a rapid exhaustion of water in the top soil and could help to explain the root growth 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 soil profiles. 468

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 CH₄ 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 clear483 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

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

	+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

Table 2: Total living fine root biomass (g m⁻²), total fine root necromass (g m⁻²), mean specific root length (m g⁻¹), mean specific root area (cm² g⁻¹) and mean root diameter down to a depth of 17 m in the undisturbed rainfall plots +W, in the plot with 37% of throughfall excluded by plastic sheets (-W), both in coppices and 1.5 years after the clear-cut, and in the non-harvested plot (NH), i.e. a 7.5-year-old tree plantation. Standard deviations are indicated. Different lowercase letters indicate significant differences between treatments +W and -W (p < 0.05). NH was not included in statistical analyses because the three soil coring replicates were located in the same plot.

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	+W	-W	NH
Fine root biomass (g m ⁻²)	$1,016.5 \pm 362.8$	$1,265.8 \pm 301.4$	$1,078.3 \pm 83.9$
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 (-

792 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.



Figure 4: Cumulated root length production (CLP) on minirhizotron tubes (m m⁻² of minirhizotron area) measured every 14 days from May 2015

800 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-
- CLP started in May 2015 in the +w and -w piots, and in March 2016 in the NH stand, where only the first three layers (0-1.5 m, 1-
 - 4.5 m) were sampled.



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

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

- 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
- 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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813 Figure 6: A) Time course of soil extractable water (mm) in soil layers 0-1 m and 1-2 m, in the 814 -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 815 were estimated from semi-hourly SWC measurements. B) Daily living root length production 816 on the surface of minirhizotron tubes (cm m⁻² of minirhizotron area day⁻¹) estimated over the 817 818 same period and same plot as a), at two-week intervals, in soil layers 0-1.3 m, 1-2.3 m, 3.5-4.8 819 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 820 area).



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

- 824 non-harvested plot (NH, gray). Standard deviations between blocks (n = 3) for -W and +W and
- 825 between pseudo replicates in a single block for NH are shown.



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Figure 8: Root area index (m² 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.