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Amandine Germon [1,2]*, Christophe Jourdan [2,3], Bruno Bordron [4], Agnès Robin [2,3,5], Yann Nouvellon [2,3,4], Lydie Chapuis-Lardy [2,6], José Leonardo de Moraes Gonçalves [4], Céline Pradier [2,3], Iraê Amaral Guerrini [1], Jean-Paul Laclau [1,2,3,4]

[1] UNESP-São Paulo State University, School of Agricultural Sciences, Botucatu, São Paulo 18610-307, Brazil

[2] Eco&Sols, Univ Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, Montpellier, France

[3] CIRAD, UMR Eco&Sols, F-34060 Montpellier, France

[4] ESALQ, Forest Science Department, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de São Paulo, CEP 13418-900 Piracicaba, SP, Brazil

5 ESALQ, Soil Science Department, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de São Paulo, CEP 13418-900 Piracicaba, SP, Brazil

[6] IRD, UMR Eco&Sols, LMI IESOL, BP 1386, CP 18524 Dakar, Senegal

* Corresponding author, E-mail address: amandine.germon@gmail.com

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

other understory species. In +W and -W, the eucalypt stands were harvested six years after planting, in June 2016, and the plantation was coppice-managed thereafter. Several new shoots were regenerated from the stumps after the clear-cut and 1 or 2 shoots per stump were selected to maintain the same stocking density and prevent the growth of additional new shoots. A third treatment served as a control, with undisturbed rainfall and no harvest (NH), to assess the clear-cutting effect. Tree height and circumference at breast height were recorded each year after the clear-cut on 36 central trees per plot during the first rotation (May 2010 - June 2016) and during the second rotation in coppice (starting in June 2016).

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).

d. Deep permanent pits for root phenology observations

Between February and March 2014, two deep permanent pits were excavated in +W and -W in block 1 to gain access to the complete soil profile from the top soil down to the water table. The pits were 1.5 m in diameter and reached a depth of 17 m and were located between four *Eucalyptus* trees (Figure 1) at a distance of 90 cm, 90 cm, 130 cm and 130 cm from each four trees respectively. The pit walls were made of concrete rings in direct contact with the soil. Clear-colored roofs of the same diameter as the pits were used to prevent light and rain entering the pits. Platforms were set up at two-meter intervals in the pits, equipped with artificial lighting 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 non-harvested treatment (NH) down to 3.5 m to determine the clear-cut effect.

e. Minirhizotrons

Fine root dynamics were studied through transparent polyvinyl chloride tubes (length:180 cm; inner diameter: 6.5 cm), commonly called minirhizotrons (Maeght *et al.*, 2013). In October 2014, twenty-four transparent minirhizotrons were installed using a powerhead drill in the +W and -W treatments of block 1. Outside the pits, three minirhizotrons were inserted into the soil surface in the same plots a minimum of 10 m apart and at a distance of 90 cm from the trunk (Figure 1). Nine tubes were inserted into the pit walls down to a depth of 17 m: two tubes at a 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 were inserted at a 45-degree angle and allowed an observation depth of 1.3 m below the depth at which they were inserted into the soil profile. In October 2015, 3 additional tubes were installed at the soil surface in the +W and -W treatments of blocks 2 and 3 (12 tubes in total) to increase the number of replications in the top meter. In October 2015, seven tubes were installed in the NH treatments (3 into the soil surface, 2 tubes inserted at depths of 1 m and 3.5 m into 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

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

elongation rate (RER, cm day^{-1}) was calculated as the difference in individual root length 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 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 root elongation rate (MaxRER, cm day^{-1}) were calculated as the mean and the maximum of individual root elongation rates considering all the roots growing during the study period. LLP, CLP, RER, DRER, MeanRER and MaxRER were estimated for each treatment (+W, -W and NH), each soil layer and between consecutive image sessions over the entire study period.

h. Root sampling

In order to check the consistency of fine root dynamics in deep soil layers observed by the minirhizotron method, total fine root biomass, fine root length and fine root area down to the water table were measured in October 2017, i.e. 1.5 years after the clear-cut in the coppices (+W and -W) and 7.5 years after planting in NH. Fine roots (diameter < 2 mm) were sampled down to 17 m in the two treatments (+W and -W) inside the three blocks and in the non-harvested (NH) treatment inside one block. Four trees were randomly selected in each plot and soil samples were collected around each tree between the topsoil and a depth of 2 m and around 2 other trees between depths of 2 and 17 m (i.e. 12 sampling points down to a depth of 2 m and 6 further down to a depth of 17 m in the +W and -W treatments and 4 sampling points down to a depth of 2 m and 2 down to a depth of 17 m in the NH treatment). At each sampling position, 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 an inner diameter of 4.5 cm. The Brazilian “cavadeira” tool, a cylindrical auger with an inner diameter of 9 cm and a length of 30 cm, was used to collect soil cores every 50 cm from 2 m down to a depth of 17 m. From each soil core, about 1.5 and 2 kg of soil was collected using the same methodology as described in Germon et al. (2018) and Christina et al. (2011). To

avoid contamination of the collected soil samples, only soil blocks from the inner part of the auger were considered. Total fresh soil mass was measured, and a sub-sample of 5 g was weighed in the laboratory to estimate the soil water content by drying the sample at 105°C for 72 h. Each soil sample was identified and stored at 4°C before being processed a maximum of 1 week after sampling. Living roots (i.e. living stele, bright color and elasticity) and dead roots (i.e. by sight, touch and flotation) > 1 cm long were carefully separated by hand after gentle washing away of the soil with tap water on a sieve with a mesh size of 0.5 mm. For the 0-0.2, 0.2-0.5 and 0.5-1 m soil layers, 10 % of the weight of each soil sample was used to estimate the mass of extremely fine roots (i.e. length < 1 cm). For the other soil layers 100% of the weight was considered. Living and dead roots more than 1 cm in length were scanned using a double-sided scanning procedure at a resolution of 800 dpi. Then, living roots and dead roots over > 1 cm in length and fragments of living and dead roots less than 1 cm in length were dried for 72h at 65° C and weighed (±0.1 mg). For the upper layers where only 10% of the weight of the soil was screened for living and dead roots < 1 cm in length, the mass of fragments was multiplied by 10 to estimate the mass of fragments of the whole soil sample. Root weight was then obtained for each soil layer, sampling position, treatment and block.

i. Root trait calculations

The fine root scans obtained where analyzed using WinRhizo Version Pro V. 2009c software (Régent Instruments Inc., Quebec, Canada) to estimate root lengths and areas per soil layer, sampling position, treatments (+W, -W and NH) and blocks. As described in Germon et al. (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 (SRA, cm^2 g^{-1}, i.e. total area of scanned roots divided by their dry mass) were calculated for 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}

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 (dm^3). The root area index (RAI, m^2 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

Linear mixed-effect models were used to test the effect of soil depth, treatment and the interaction between depth and treatment on cumulative length production (CLP), root elongation rate (RER), daily root elongation rate (DRER), mean root elongation rate (MeanRER), maximum root elongation rate (MaxRER), fine root density (FRD), fine root biomass (FRB), specific root length (SRL), specific root area (SRA), root area index (RAI) and root diameter for the whole soil profile. Blocks were considered as fixed effects and residues were modeled by a first-order autoregressive correlation model to account for the correlations between soil depths. Two-way analyses of variance (ANOVAs) were used to assess the effect of treatments and blocks for individual soil layers on CLP, RER, DRER, MeanRER, MaxRER, FRD, FRB, SRL, SRA, RAI and root diameter. Measurements within a given soil layer were considered independent, since the sampling positions were located near different trees in each treatment and plot. The homogeneity of variances was verified, and log-transformations were used when the residuals did not follow a normal distribution. Tukey's post-hoc Honest Significant Difference (HSD) was used to determine the significant differences between treatments. R software version 3.4.4 (Team R 2013) was used for all the calculations and statistical analyses with a 5% significance level. The "lmerTest" package was used to perform 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)

In both the +W and -W treatments, rainfall events led to large variations in SWC (Figure 3). At 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 depth of 14 m, SWC ranged from 9.9% to 10.9% in -W and from 11.3% to 18.1% in +W. Over the study period, throughfall reduction led to a sharp decrease in SWC, on average, by 12.9 ± 4.9% from the topsoil to a depth of 16 m. At the end of the rainy season, the mean SWC values of the soil profile in April 2016, i.e. 2 months before the clear-cut, were 12.5% and 14.0% in -W and +W, respectively and in April 2017, i.e. 10 months after the clear-cut, there were 14.4% and 16.2% in -W and +W, respectively. After clear-cutting, the soil profiles were recharged 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 maximum depth of only 12 m 13 months after clear-cutting. Gravitational soil solutions did not reach the water table in -W over the study period (one year before the clear-cut and the first 2 years of coppice management).

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.

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 cm^2 g^{-1}, and mean fine root diameters were 0.31, 0.32 and 0.36 mm in NH, +W and -W, respectively (Table 2).

g. Fine root mortality

Cumulative dead root length in the minirhizotron images over the study period of 3 years across all soil layers accounted for only 6-7% of cumulative root length production, in both +W and -W (Table 1). Surprisingly, dead fine root length did not increase after clear-cutting and did not differ between depths and between the +W and -W treatments. Dead fine root mass estimated 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).

4. Discussion

The main novelty of our results lies in the first direct observation of fine root phenology at depths of more than 10 m and derived knowledge raised from a comparison between the treatments. The consequences of tree harvesting on fine root dynamics in coppice-managed plantations raise specific questions never studied before along a deep tropical soil profile. Since the 1980s, the minirhizotron technique has been widely used to study fine root dynamics and turnover (Graefe *et al.*, 2008; Maeght *et al.*, 2013). Many studies have shown that the soil environment close to minirhizotrons can be modified relative to undisturbed soil (Majdi and Nylund, 1996), which is likely to influence fine root dynamics. However, in our study the very low root mortality rates after clear-cutting revealed by minirhizotron monitoring was consistent 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).

Key role of deep roots in coppice management

Contrary to our third hypothesis, relatively few roots were lost by mortality (< 10% out of all the roots observed over 3 years), which suggested that most of the root system remained functional after clear-cutting. The effect of clear-cutting on fine root mortality remains unclear in coppice-managed forest plantations. Unlike our observations, sequential coring in the 0-1 m soil layer showed a decrease in fine root density after harvesting coppice-managed *E. grandis* stands in Brazil (Mello *et al.*, 2007). Wildy and Pate (2002) also showed high fine root mortality rates after cutting the trees in plantations of *Eucalyptus kochii* Maiden & Blakely subsp. plenissima Gardner (Brooker), but the root system superstructure was sustained down to a depth of at least 4 m. Teixeira et al. (2002) showed from sequential coring in the 0-0.6 m soil layer that fine-, medium- and coarse-root biomasses increased over time after harvesting coppice-managed *Eucalyptus urophylla* S. T. Blake trees. Using the minirhizotron technique, Dickmann *et al.* (1996) showed an absence of root mortality for coppice-managed poplar clones. Our study suggested that 6-year-old *Eucalyptus grandis* trees have enough reserves within the root system and the appropriate edaphic surrounding conditions to maintain the fine root biomass established down to the water table after clear-cutting, which probably contributed to promoting early shoot growth (Drake *et al.*, 2013; Brunner *et al.*, 2015).

Fine root growth after clear-cutting started in the topsoil, then continued successively in deeper and deeper soil layers, which confirmed our third hypothesis, even though the lapse of several months after clear-cutting was not expected. This pattern might have resulted from high nutrient and water availabilities in the upper layers after harvesting *Eucalyptus* stands due to an interruption of tree water uptake and fertilizer application (Laclau *et al.*, 2010). The asynchrony within the root system, delaying root growth in deep soil layers, might be a strategy for maximizing the water and nutrient uptake needed to meet the high demand of these fast-growing 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-

cutting in our experiment were therefore consistent with the low rates of root mortality observed. On the other hand, deep roots might also contribute to sequestrating large amounts of C in soil. Total below-ground carbon allocations account for about 20-30% of gross primary production in *Eucalyptus* plantations (Ryan *et al.*, 2010; Epron *et al.*, 2012; Nouvellon *et al.*, 2012). Fine root elongation rates were higher at great depth compared to the topsoil, with an increase in fine root density after the clear-cut in very deep horizons. Moreover, microbial biomass is lower in deep soil layers than in the topsoil, which in combination with oxygen limitations could enhance C sequestration as a result of low mineralization rates (Taylor *et al.*, 2002; Rumpel and Kögel-Knabner, 2011). C from roots is generally retained more in the soil than C from aboveground litter, which is more affected by physicochemical processes and also due to structural composition differences between leaves and roots (Rasse *et al.*, 2005; Schmidt *et al.*, 2011; Menichetti *et al.*, 2015). Further studies are needed to assess whether the management of *Eucalyptus* plantations in very deep soils could be an effective option to help mitigate the increase in CO_2 in the atmosphere.

Conclusions

The fine root phenology of coppice-managed *Eucalyptus* trees under contrasting water supply regimes revealed unexpected low rates of root mortality. The early growth of the sprouts after cutting the trees benefited from the root system established over the previous rotation cycle, and the asynchrony of fine root growth depending on depth highlighted tree plasticity in response to soil conditions. Establishing deep root systems in tropical planted forests could help trees withstand the long drought periods expected under climate change in many tropical regions. Our study suggested that coppice management might be an interesting option in tropical *Eucalyptus* plantations, both to improve tree tolerance to drought and store carbon at great depth in the soil.

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Zhou, G., Zhou, X., Nie, Y., Bai, S.H., Zhou, L., Shao, J., Cheng, W., Wang, J., Hu, F., Fu, Y., 2018. Drought-induced changes in root biomass largely result from altered root morphological traits: evidence from a synthesis of global field trials. Plant, cell & environment 41, 2589-2599.

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
770 Maximum root elongation rate (cm day^{-1})	3.0	4.3
Number of roots observed	12,247	14,118
771 Mortality (%)	7.4	5.7

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.

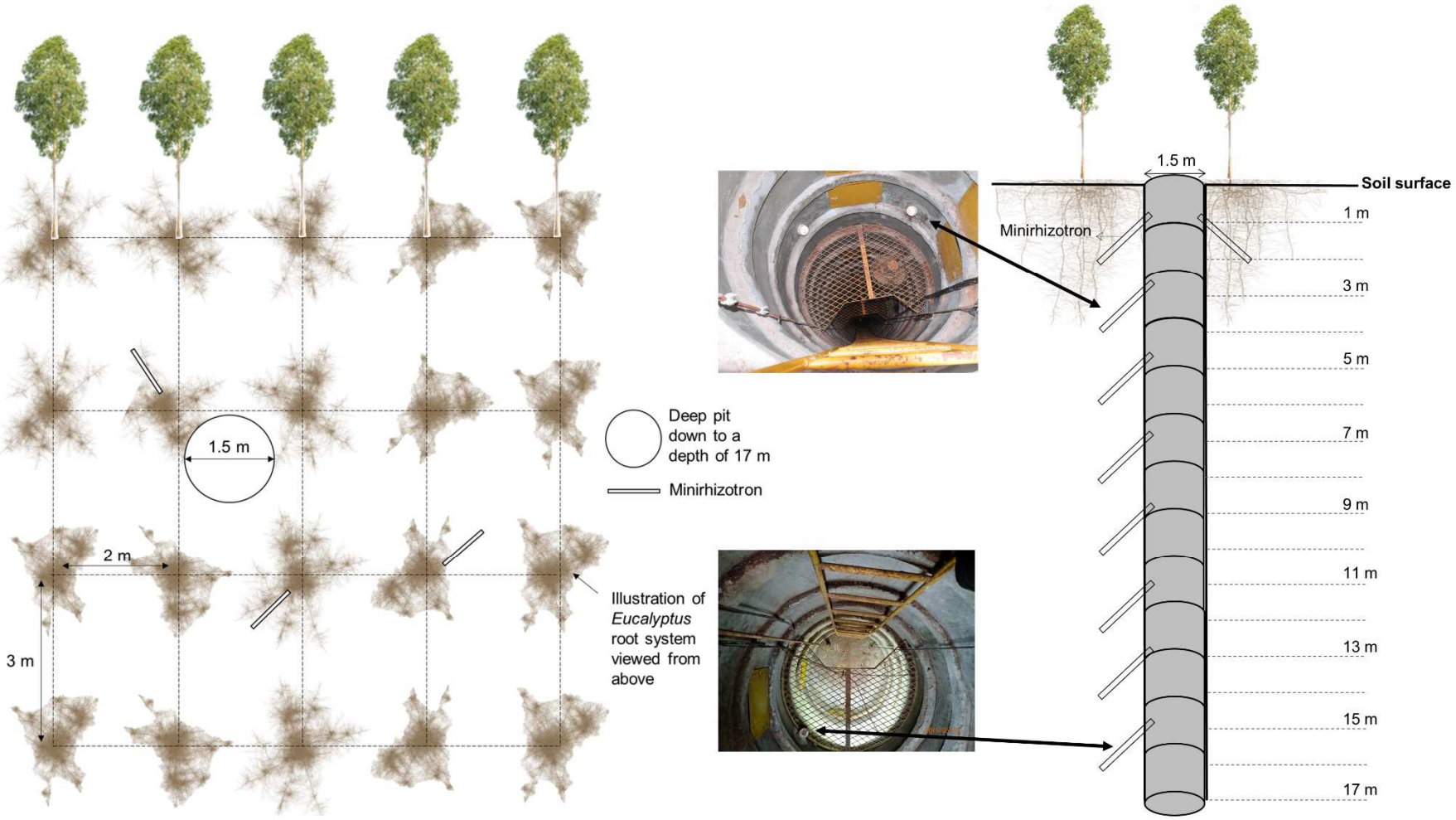
781

	+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

782

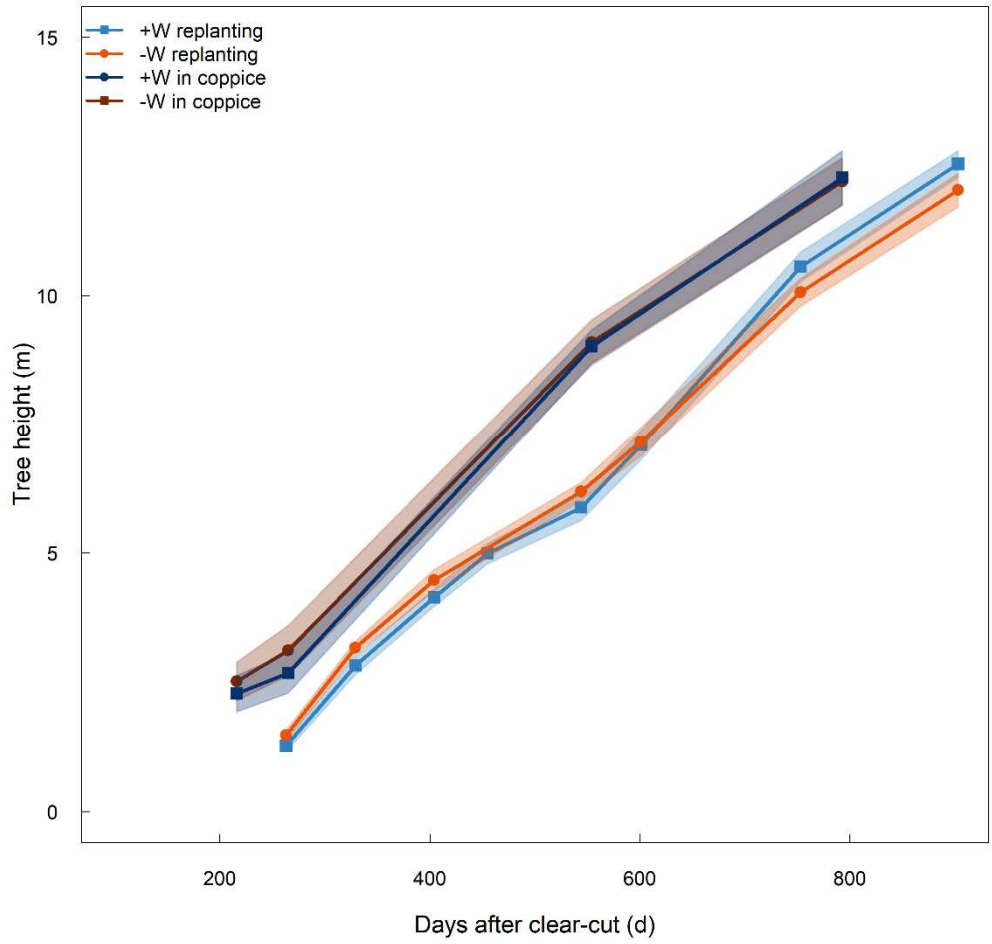
783

784



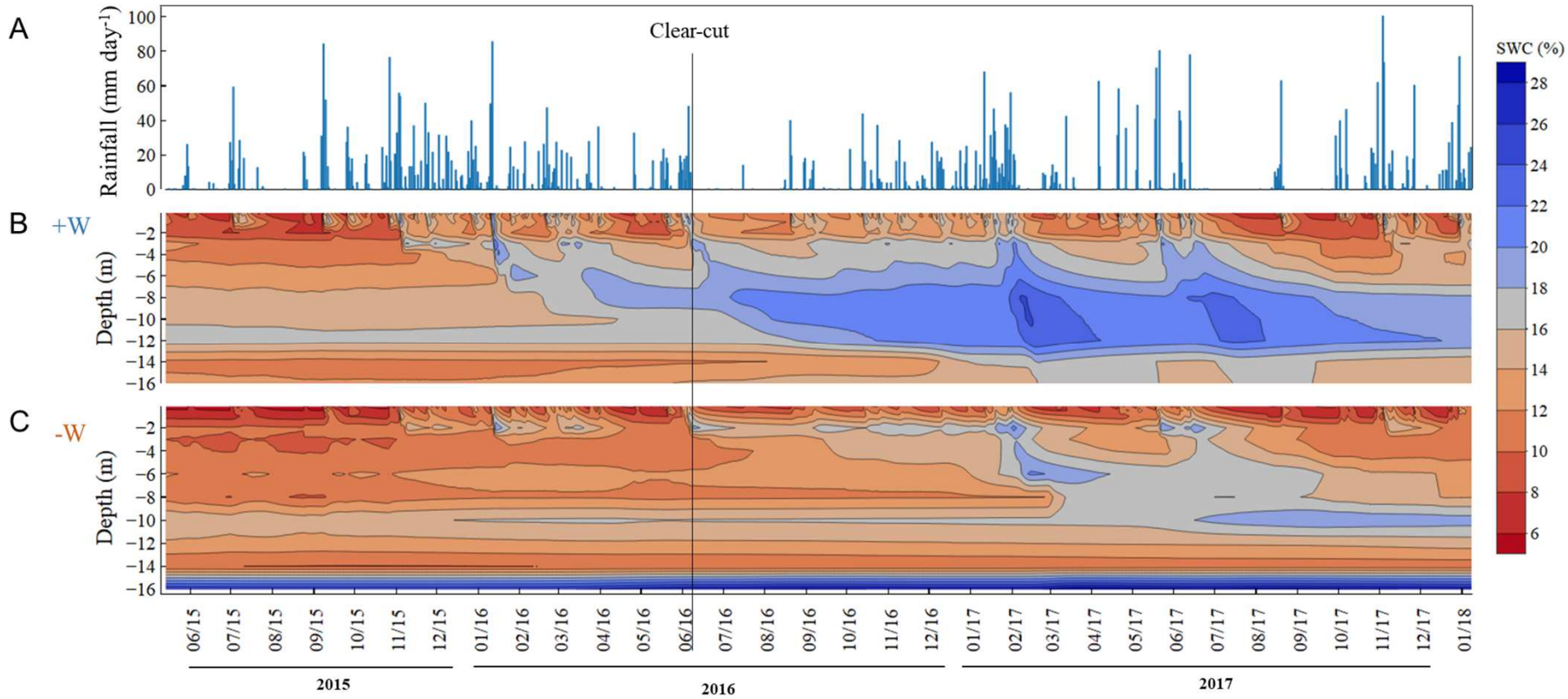
785

786 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
787 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.



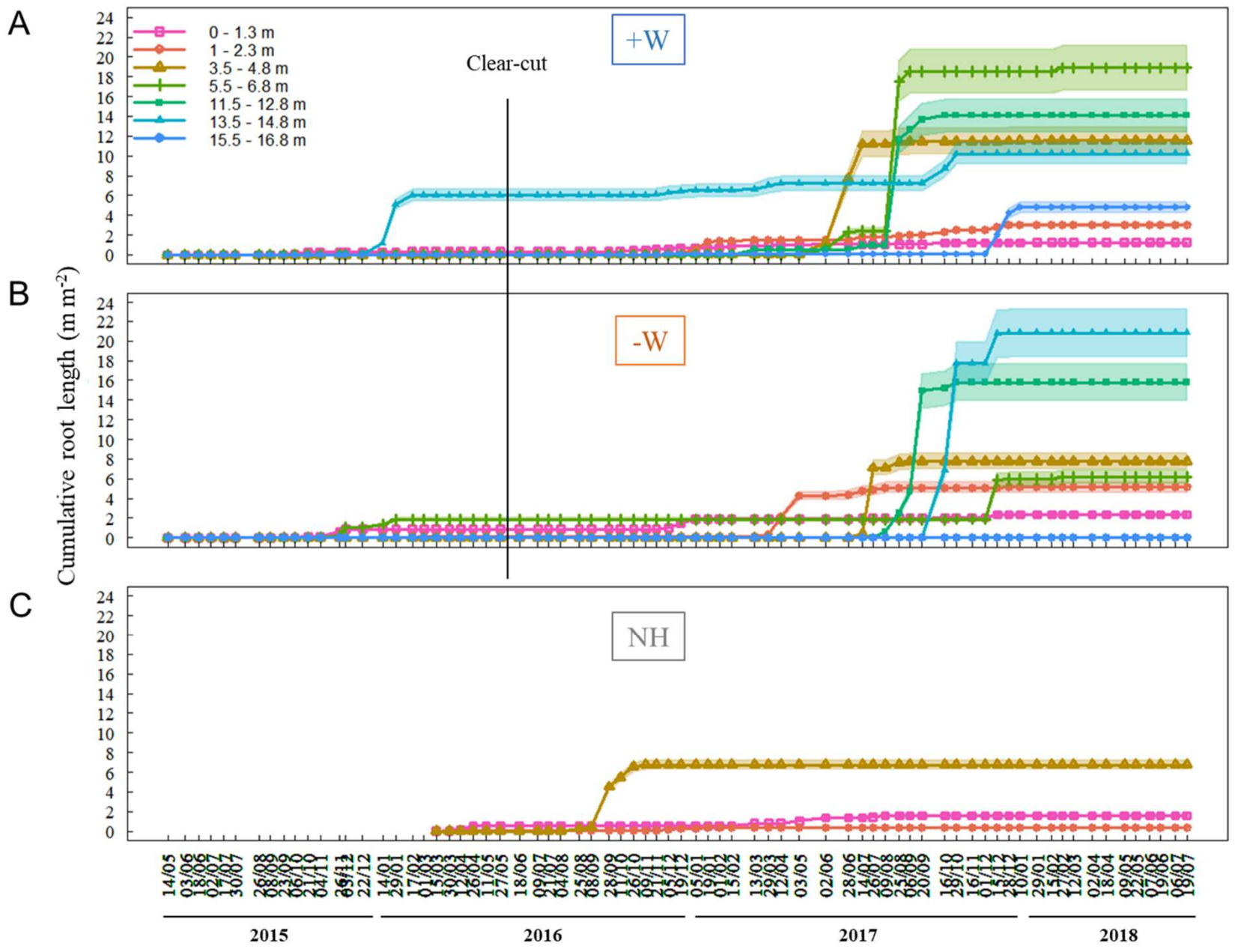
788

789 Figure 2: Vertical growth (m) over the first 2.5 years after harvesting of the previous stands for
790 the replanting (June 2010-June 2016) and the coppice (from June 2016) in the undisturbed
791 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).



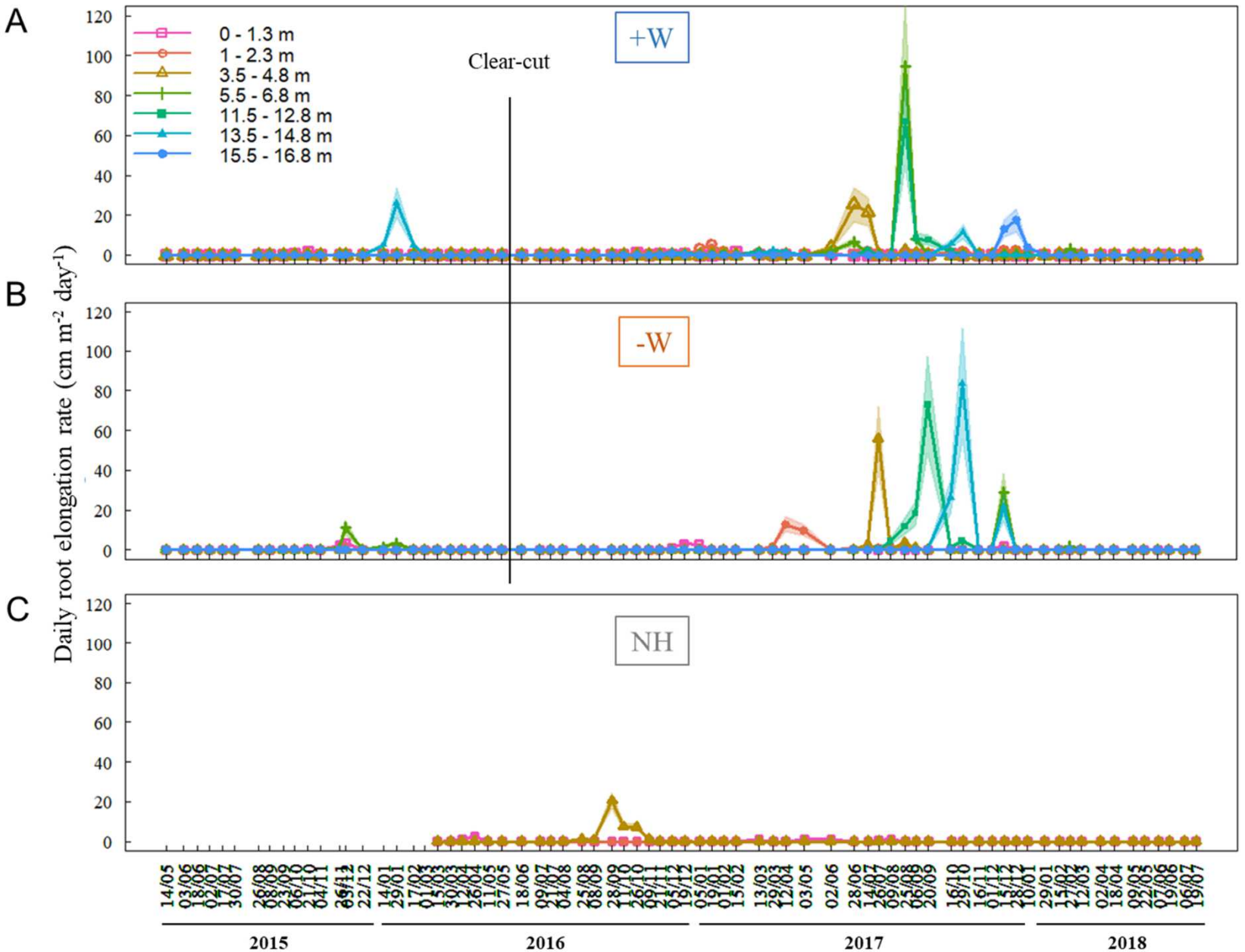
793

794 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,
795 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
796 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.
797 The clear-cut date is indicated by a vertical line. The stand was coppice-managed after the clear-cut.


A
B
C
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
Clear-cut
+W
-W
NH
Cumulative root length (m m-2)
2015
2016
2017
2018

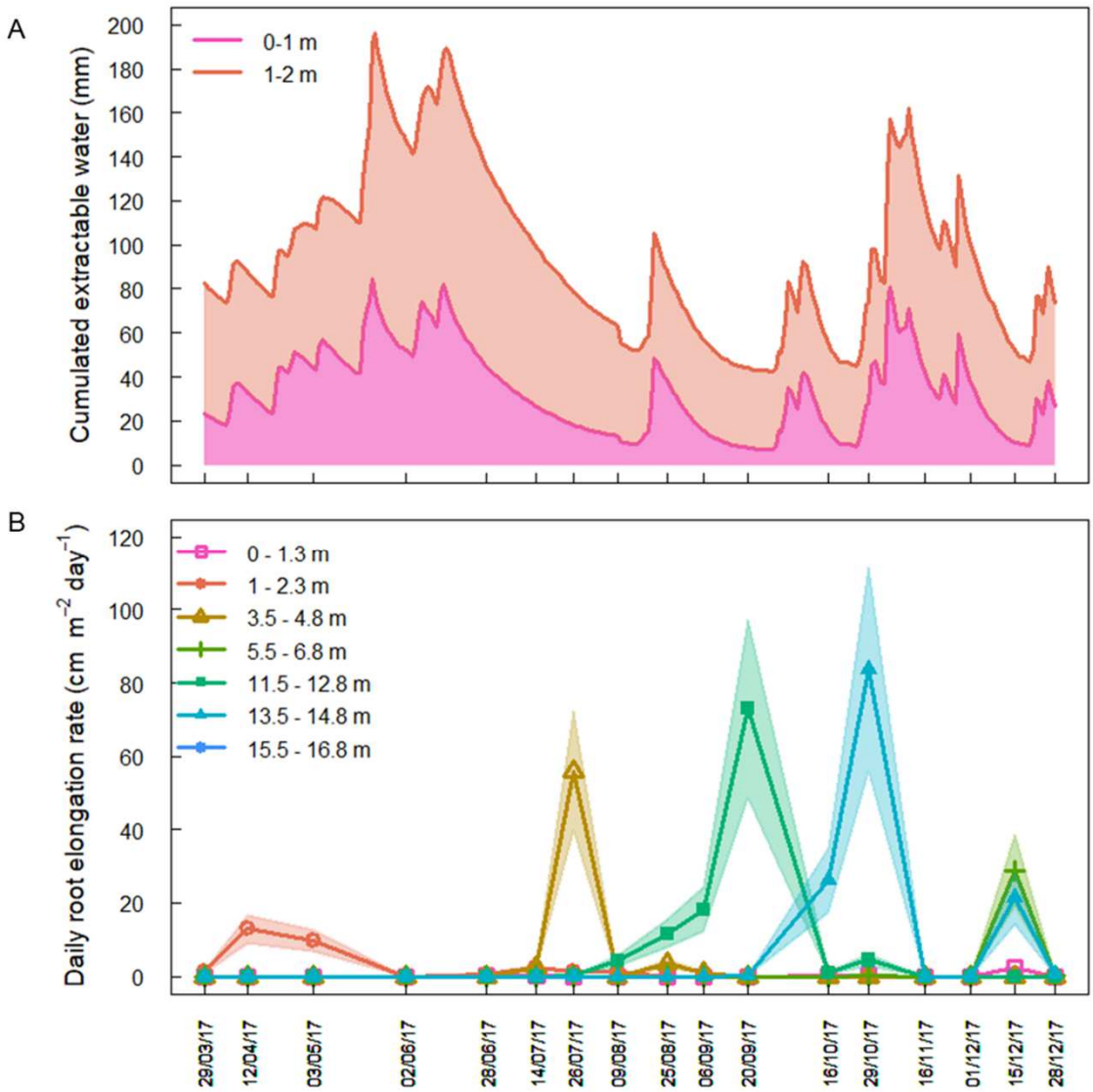
798

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.


A
B
C
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
Clear-cut
+W
-W
NH
Daily root elongation rate (cm m-2 day-1)
2015
2016
2017
2018

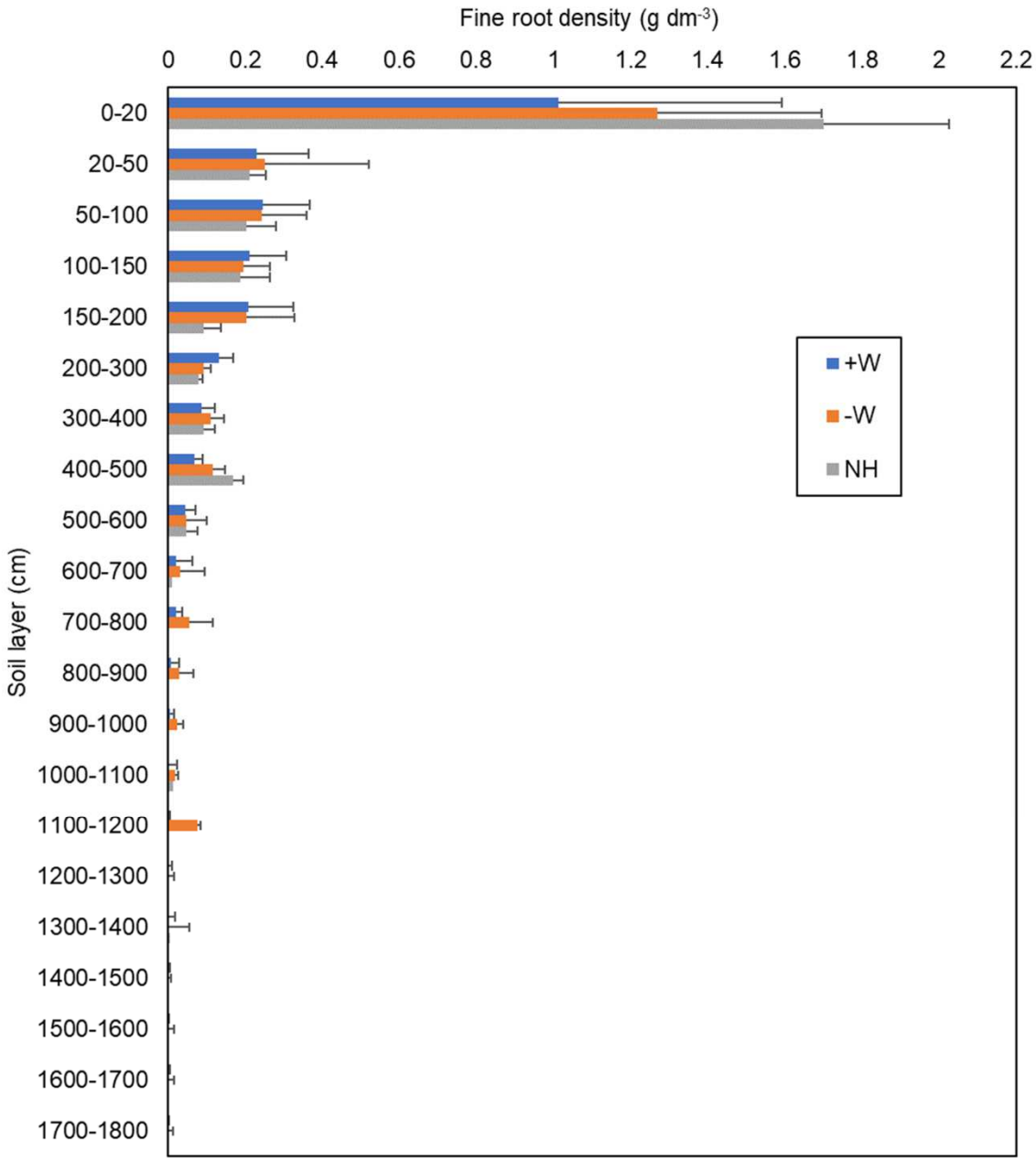
805

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 (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 3.5-4.5 m) were sampled.



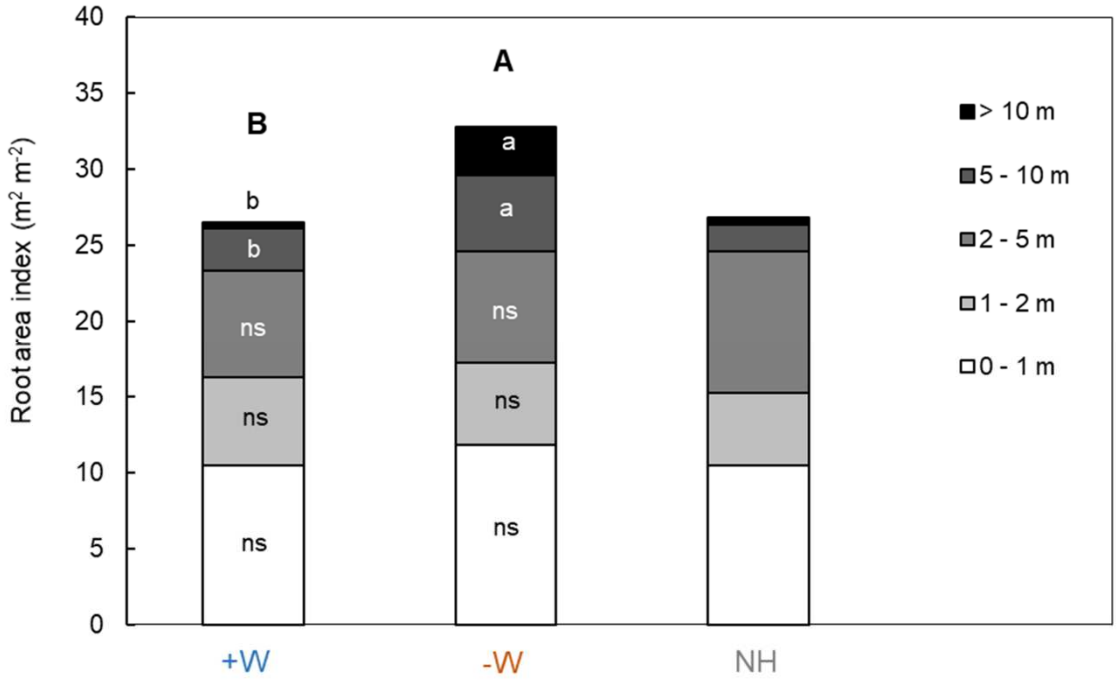
812

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
815 months after the clear-cut) to December 2017. The mean daily values of soil extractable water
816 were estimated from semi-hourly SWC measurements. B) Daily living root length production
817 on the surface of minirhizotron tubes (cm m^{-2} of minirhizotron area day^{-1}) estimated over the
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).



821

822 Figure 7: Mean fine root densities down to the root front in the undisturbed rainfall plots (+W,
823 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.



826

827 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
828 layers in the undisturbed rainfall plots (+W), in the plots with 37% of throughfall excluded by
829 plastic sheets (-W) and in the non-harvested plot (NH). Different upper-case letters indicate
830 significant differences between treatments for the cumulative indices and different lower-case
831 letters indicate significant differences between treatments within each individual soil layer ($p <$
832 0.05). NH was not included in the ANOVA because the three soil coring replicates were located
833 in the same plot.

834