Forest Ecology and Management 445 (2019) 48–59

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Amandine Germon[a,b,*], Christophe Jourdan[b,c], Bruno Bordron[d], Agnès Robin[b,c,e], Yann Nouvellon[b,c,d], Lydie Chapuis-Lardy[b,f], José Leonardo de Moraes Gonçalves[d], Céline Pradier[b,c], Iraê Amaral Guerrini[a], Jean-Paul Laclau[a,b,c,d]

[a] UNESP-São Paulo State University, School of Agricultural Sciences, Botucatu, São Paulo 18610-307, Brazil
[b] Eco&Sols, Univ Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, Montpellier, France
[c] CIRAD, UMR Eco&Sols, F-34060 Montpellier, France
[d] ESALQ, Forest Science Department, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de São Paulo, CEP 13418-900 Piracicaba, SP, Brazil
[e] ESALQ, Soil Science Department, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de São Paulo, CEP 13418-900 Piracicaba, SP, Brazil
[f] IRD, UMR Eco&Sols, LMI IESOL, BP 1386, CP 18524 Dakar, Senegal

ARTICLE INFO

Keywords:
Brazil
Coppice
Deep ferralsol profile
Deep root growth
Eucalyptus grandis
Minirhizotron
Throughfall exclusion

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 1266 and 1017 $g\,m^{-2}$ in +W and −W, respectively, at 1.5 year after the clear-cut and was 1078 $g\,m^{-2}$ 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.

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

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[*] Corresponding author at: UNESP-São Paulo State University, School of Agricultural Sciences, Botucatu, São Paulo 18610-307, Brazil.
E-mail address: amandine.germon@gmail.com (A. Germon).

https://doi.org/10.1016/j.foreco.2019.05.010
Received 11 February 2019; Received in revised form 2 May 2019; Accepted 6 May 2019

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 the crucial role of fine roots in coping with drought, root phenology remains poorly understood in comparison to leaf ecophysiology (Radville et al., 2016).

Deep roots commonly reported as roots growing beyond 1 m in depth can play an important role in supplying water to trees (Kell, 2012; Pierret et al., 2016). Trees can be deeply rooted (Canadell et al., 1996; Schenk and Jackson, 2002), and some studies suggest that very deep roots (at depths > 10 m) are common in highly weathered tropical soils (Nepstad et al., 1994; Saleska et al., 2007; Broedel et al., 2017). Even though low fine root densities are generally found at great depth (Pierret et al., 2016), they can take up substantial amounts of water needed for tree survival during drought periods (McDowell et al., 2008; Nardini et al., 2016). Deep roots can also contribute to closing the biogeochemical cycles in tropical forests through nutrient uptake in deep soil layers (Lehmann, 2003; Jobbágy and Jackson, 2004; Da Silva et al., 2011; Bordron et al., 2018), which reduces nutrient losses by deep leaching (Lehmann and Schroth, 2003; Laclau et al., 2010). While many studies show that the role of very deep roots in tropical forest functioning and productivity has been greatly underestimated (Jackson et al., 2000; Markewitz et al., 2010; Freycon et al., 2015), as far as we are aware, fine root dynamics and mortality have never been studied at depths > 10 m.

Eucalyptus plantations cover $>$ 20 million hectares and account for around 8% of forest plantations in the world (Booth, 2013). The diversity of *Eucalyptus* species planted in tropical regions has led to a wide range of products and management practices (Gonçalves et al., 2013). Although many *Eucalyptus* plantations are intensively managed to produce raw materials for industry (mainly pulp and paper, but also solid-wood products, fiberboards and charcoal for steel production), used as a domestic source of energy and also contributes to alleviating poverty in developing countries (Cossalter and Pye-Smith, 2003). Most eucalypt plantations are located in areas with low soil fertility and prolonged drought periods (Keenan et al., 2015). Coppice management could be an adaptive solution to cope with water deficit in these plantations, because the sprouts growing on stumps are likely to benefit from the pre-existing root system that explores deep soil layers where water availability is generally higher than in the topsoil. The effects of clear-cutting on fine root dynamics in coppiced-managed forest plantations are poorly documented and tendencies are not clear. Sequential coring in Brazilian coppiced-managed eucalypt plantations showed that fine root density decreased in the 0–1 m soil layer in the first 60 days after harvesting, while fine root decomposition was accelerated (Mello et al., 2007). Fine root mortality exceeded fine root production after clear-cutting in *Populus* stands (Berhongaray et al., 2015). In contrast, Dickmann et al. (1996) observed little change in fine root production and mortality in the 0–1 m soil layer after clear-cutting in other *Populus* stands. While 50% of fine root biomass can be found below a depth of 1 m in tropical eucalypt plantations (Christina et al., 2011; Laclau et al., 2013), fine root dynamics in coppice-managed forests have only been studied in the upper meter of the soil profile.

Our study was carried out in *Eucalyptus grandis* (Hill ex. Maid) stands planted in a throughfall exclusion experiment in Brazil (Battie-Laclau et al., 2014). We aimed to gain insight into the effects of contrasting rainfall regimes on fine root dynamics in coppice-managed eucalypt plantations after tree clear-cutting in very deep tropical soils. We put forward the hypothesis that trees invest in belowground biomass in response to throughfall exclusion, in order to increase the exploration of fine roots in deep soil layers (H1), and that they adjust fine root traits to increase the specific root area, in order to capture more resources per gram of C invested in fine roots (H2). In addition, we put forward the hypothesis that *Eucalyptus grandis* stands with clear-cutting and tree regrowth in coppices would increase fine root turnover throughout the soil profile (H3).

2. Materials and methods

2.1. Study site

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, located 300 km from the sea, has a relief typical of the São Paulo Western Plateau, with a topography varying from flat to hilly (slopes $<$ 3%). The altitude is 850 m, and the climate is humid subtropical with a dry winter (Cwa) according to the Köppen classification. Over the 15 years prior to this study, the mean annual rainfall was 1390 mm (with 74% between October and May), and the mean air temperature and relative humidity were 20 °C and 77%, respectively. A dry and cool (15 °C) season occurs between June and September. The total rainfall over the study period (from May 2015 to July 2018) was 5629 mm. The annual rainfall was 1557 mm and 2303 mm in 2016 and 2017, respectively. The soils are very deep Ferralsols (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 are mainly kaolinite (Christina et al., 2015).

2.2. Experimental layout

A split-plot experimental design was set up in June 2010 with a *Eucalyptus grandis* clone used 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 studied two treatments out of all those available in the experimental design: one treatment with undisturbed rainfall (+W) and one treatment with throughfall exclusion (−W), which was equipped with plastic sheets installed since September 2010, allowing the exclusion of 37% of throughfall (Battie-Laclau et al., 2014). Treatments −W and +W were used to determine the water deficit effect. The trees were planted in June 2010 at a spacing of 3 m × 2 m with a 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 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).

2.3. 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

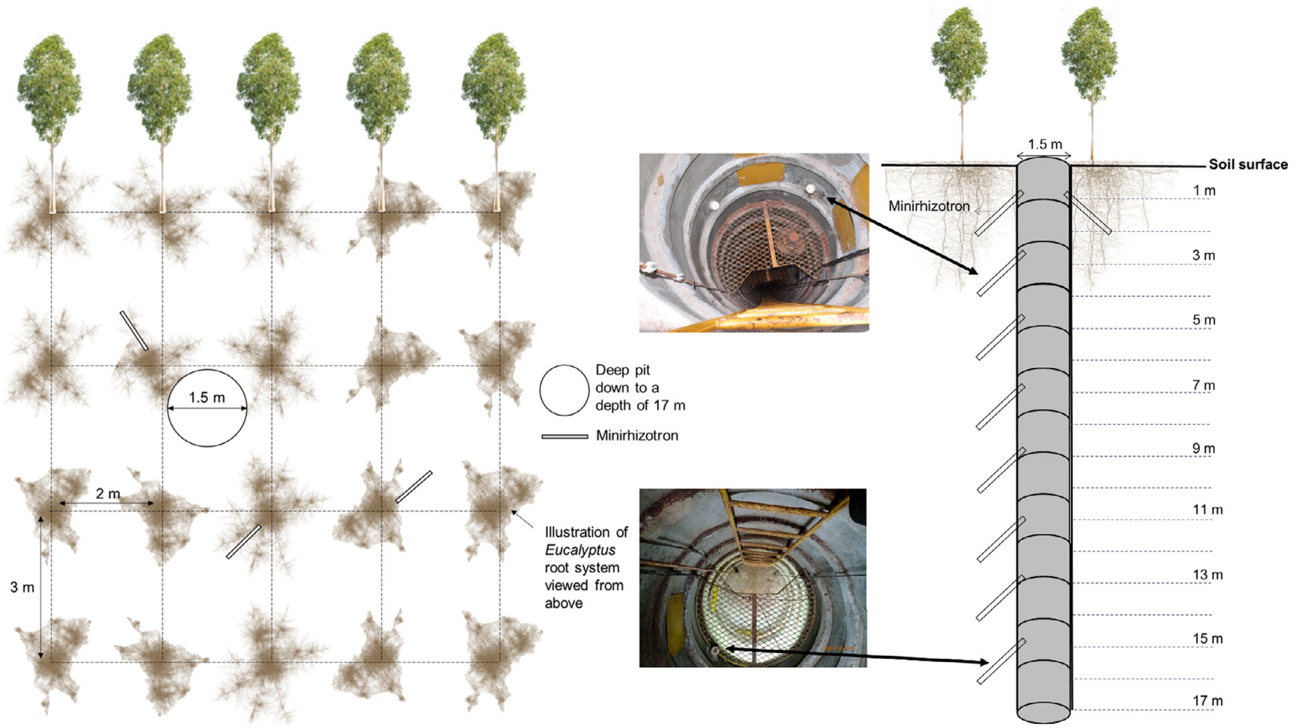

Fig. 1. Layout of the position of the pit in the +W treatment of block 1 and distribution of minirhizotron tubes at the soil surface (n = 3) and in the permanent pit from 1 m (n = 2) down 17 m (n = 1 per m in depth). The same set-up was used for the −W treatment.

stock (mm) and the minimum soil water stock (i.e. lower limit of soil water content in mm) (Granier et al., 1999).

2.4. 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 (Fig. 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 (Fig. 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.

2.5. 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 (Fig. 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 (Fig. 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 (21.59 × 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.

2.6. Root image processing

WinRhizoTron™ software (Régent Instrument Inc., Quebec, Canada) was used to analyze > 24,000 root images taken in the minirhizotrons. This software was chosen as it allowed the analysis of large number of images and overlayed the images to visualize the time evolution of the roots throughout the tubes. This manual root measurement program estimated the length and diameter of each root observed and stored each data item in a text file. By comparing two consecutive images chronologically, it was possible to estimate changes in root length and phenology features. Root mortality was evaluated based on the absence of growth over the entire study period up to the last images, when roots turned black and presented clear signs of decomposition (Germon et al., 2016; Lambais et al., 2017). For each fine root (diameter < 2 mm) we recorded the time of the first appearance, the diameter, the length over time, and the time of disappearance. In this study, we considered only root appearing during the study period.

2.7. 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 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.

2.8. 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 > 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 < 1 cm in length were dried for 72 h 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.

2.9. 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.

2.10. 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

3.1. 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 (Fig. 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.

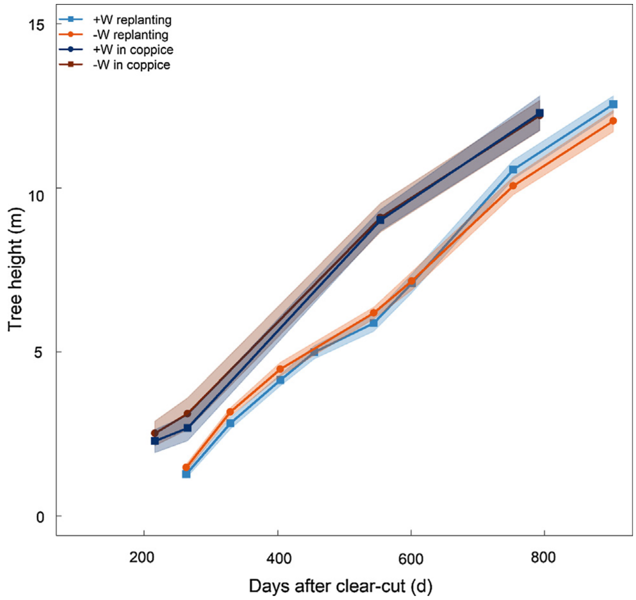

Fig. 2. Vertical growth (m) over the first 2.5 years after harvesting of the previous stands for the replanting (June 2010–June 2016) and the coppice (from June 2016) in the undisturbed rainfall plots (+W, blue) and in the plots with 37% of throughfall excluded by plastic sheets (−W, orange). Standard errors are shown (shaded area). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Volumetric soil water contents (SWCs)

In both the +W and −W treatments, rainfall events led to large variations in SWC (Fig. 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).

3.3. 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 (Fig. 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.

3.4. Fine root elongation rates

Daily root elongation rates (DRERs) were highly variable between the soil layer and the season, in both +W and −W (Fig. 5). Fine root growth started in the top soil after the clear-cut and occurred more and more deeply over time in +W and −W. The intensity (measured as the maximum DRER) and the period of fine root growth differed depending on soil depth. DRER measured during flushes of root growth was much lower in the topsoil than at great depth in +W, −W and NH (no observation below 4.8 m in NH). At a depth of 3.5–4.8 m, flushes of DRER 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 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-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

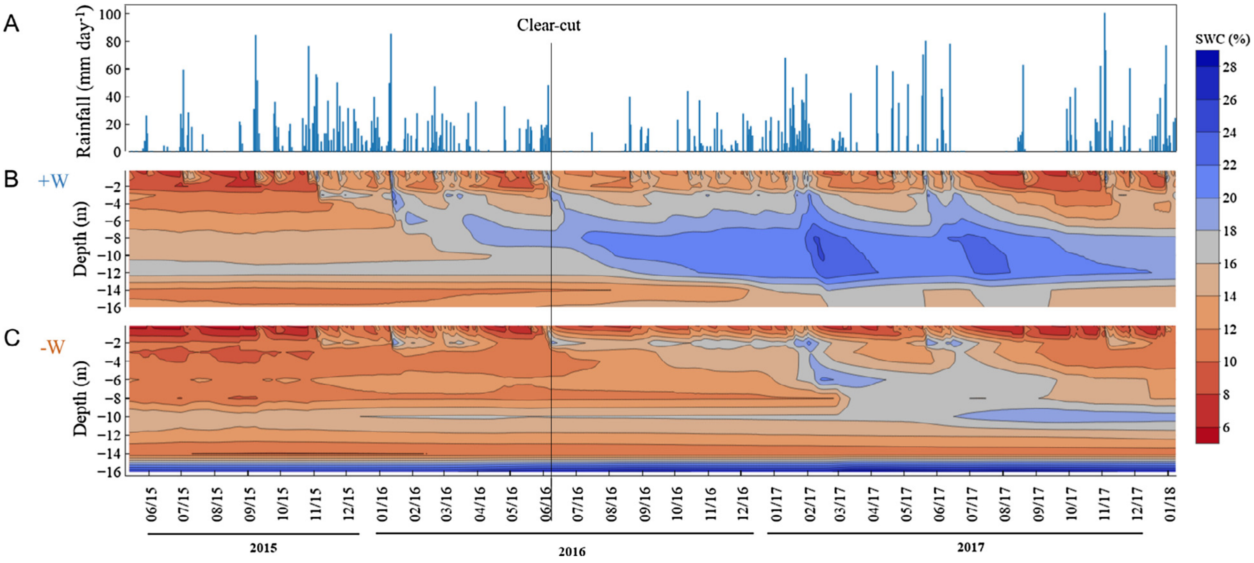

Fig. 3. Daily rainfall (A) and soil water content (SWC, %) within the soil profiles down to a depth of 16 m in the undisturbed rainfall plots (+W, B) and in the plots with 37% of throughfall excluded by plastic sheets (−W, C) from May 2015 to January 2018. SWC graphical representation is a contour line 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.

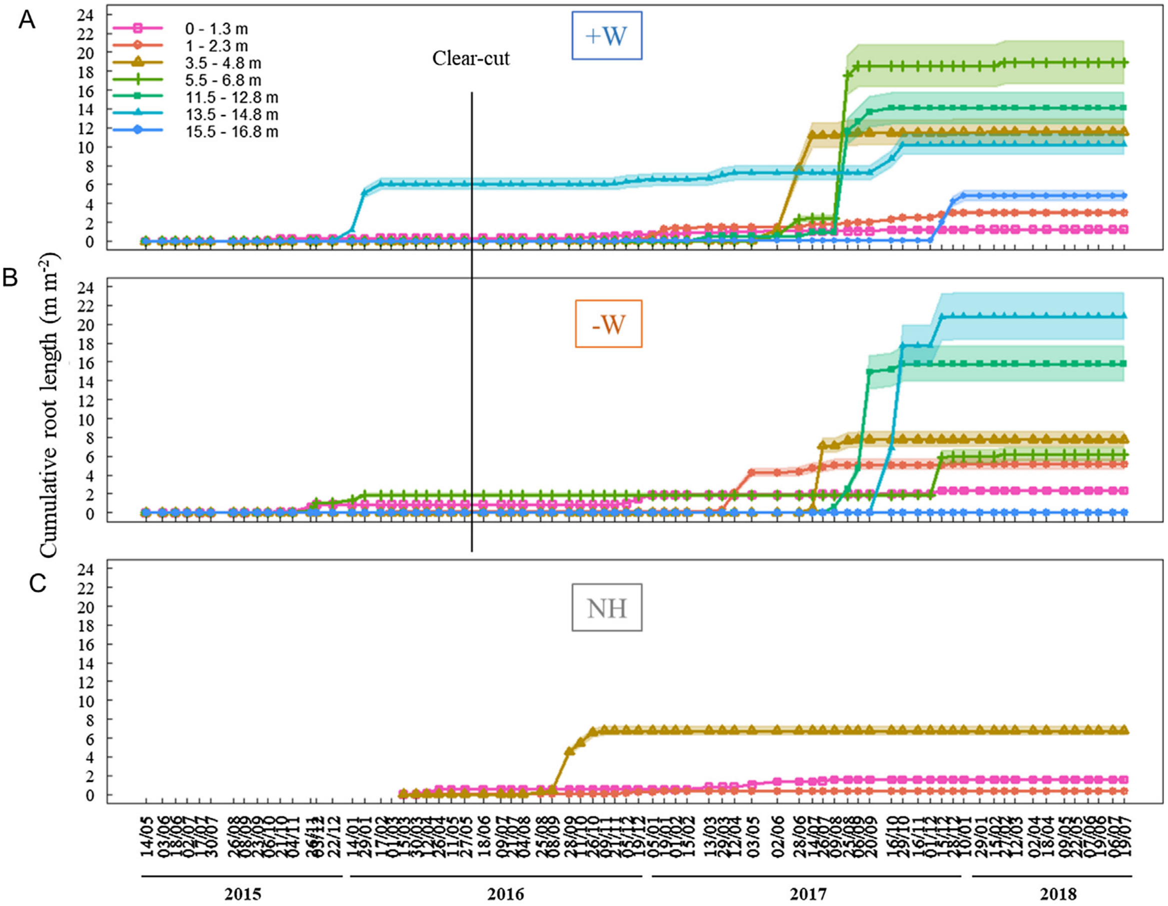

Fig. 4. Cumulated root length production (CLP) on minirhizotron tubes (m m^{-2} of minirhizotron area) measured every 14 days from May 2015 to July 2018 in soil layers 0–1.3 m, 1–2.3 m, 3.5–4.8 m, 5.5–6.8 m, 11.5–12.8 m, 13.5–14.8 m and 15.5–16.8 m in the undisturbed rainfall plot (+W, A), in the plot 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.

(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 (Fig. 3, Fig. 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 (Fig. 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.

3.5. Fine root distributions

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 (Fig. 7). Fine root densities dropped below a depth of 20 cm, then decreased gradually down 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 1078 g m^{-2} in NH, 1017 ± 301 g m^{-2} in +W and 1266 ± 363 g m^{-2} in −W (Table 2). Fine root densities were about 25% higher in −W than in +W and NH in most of the soil layers. At depths > 7 m, fine root densities were at least twice as high in −W as in +W and NH.

3.6. Fine root traits

The total root area index (RAI) was significantly ($F = 32.78$, $P < 0.001$) higher in –W (32.8 m^2 m^{-2}) than in +W (26.5 m^2 m^{-2}) (Fig. 8). Similar RAI values in the NH stand (26.8 m^2 m^{-2}) and in the +W coppice suggested that the effect of clear-cutting on fine root dynamics was low, in agreement with elongation and mortality rates observed in the upper 4 m on minirhizotron 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 m^2 m^{-2} on average). Significant differences between +W and −W were found at depths > 5 m ($P < 0.001$, Fig. 8). In the 5–10 m soil layers, 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 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).

3.7. 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).

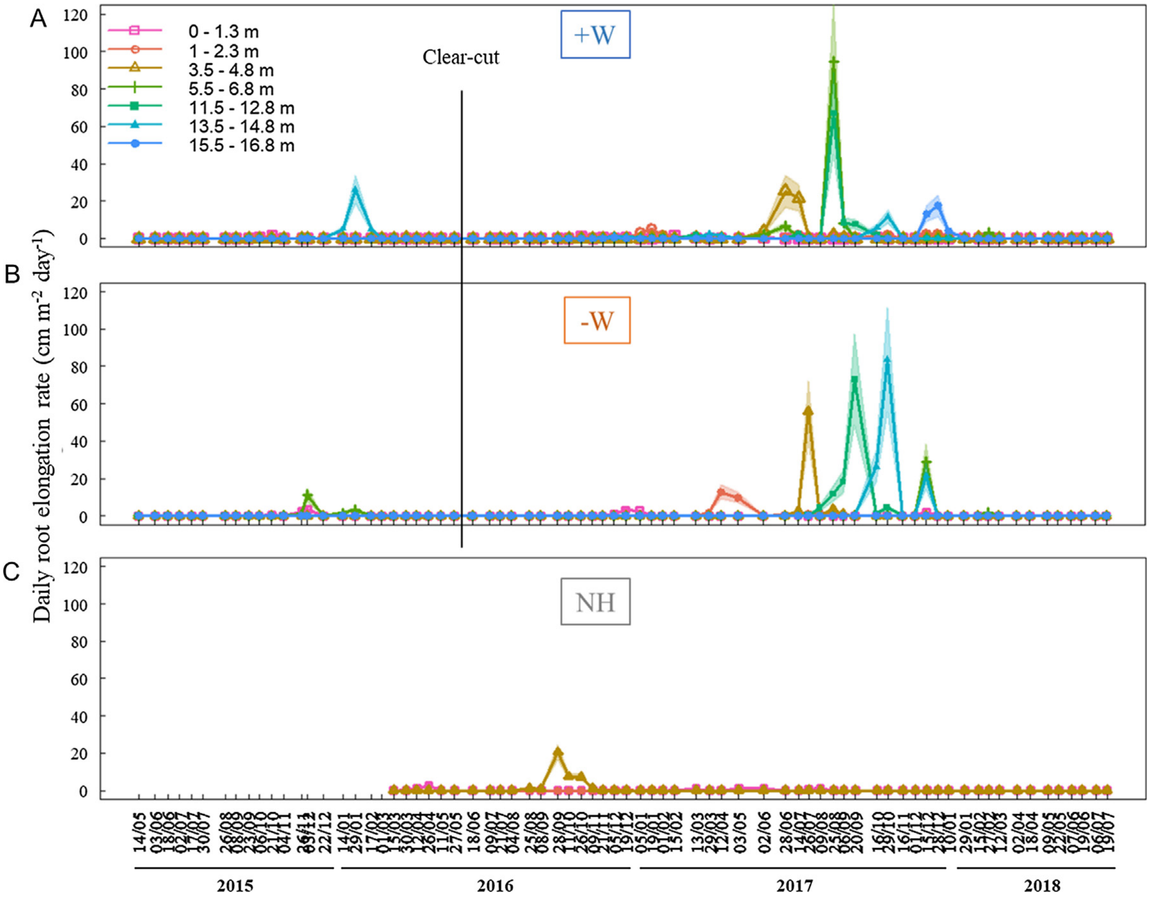

Fig. 5. Daily living root elongation rate (DRER) on minirhizotron tubes (cm m^{-2} of minirhizotron area day^{-1}) estimated every 14 days from May 2015 to July 2018 in soil layers 0–1.3 m, 1–2.3 m, 3.5–4.8 m, 5.5–6.8 m, 11.5–12.8 m, 13.5–14.8 m and 15.5–16.8 m in the undisturbed rainfall plot (+W, A), 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.

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

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 > 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 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).

4.1. Root behavior in response to drought

The main purpose of our study was to investigate whether fine roots explore very deep soil layers and do so more intensively when trees are subjected to prolonged drought periods. This study, carried out in a throughfall exclusion experiment and including a non-harvested plot, made it possible to assess the effect of clear-cutting under two contrasting rainfall regimes. In agreement with our first hypothesis, *Eucalyptus* trees responded to drought by increasing fine root densities at great depth. Previous studies in Brazil showed that *Eucalyptus* trees have the ability to explore very deep layers in soils without hindrance to root growth (Christina et al., 2011; Pinheiro et al., 2016). In a survey of 62 tropical tree species, Markesteijn and Poorter (2009) showed that trees increase belowground biomass and the proportion of deep roots in response to dry conditions. Root growth in deep soil layers can increase the amount of water available to sustain tree growth, which could be a key advantage for eucalypt trees in coping with severe drought events

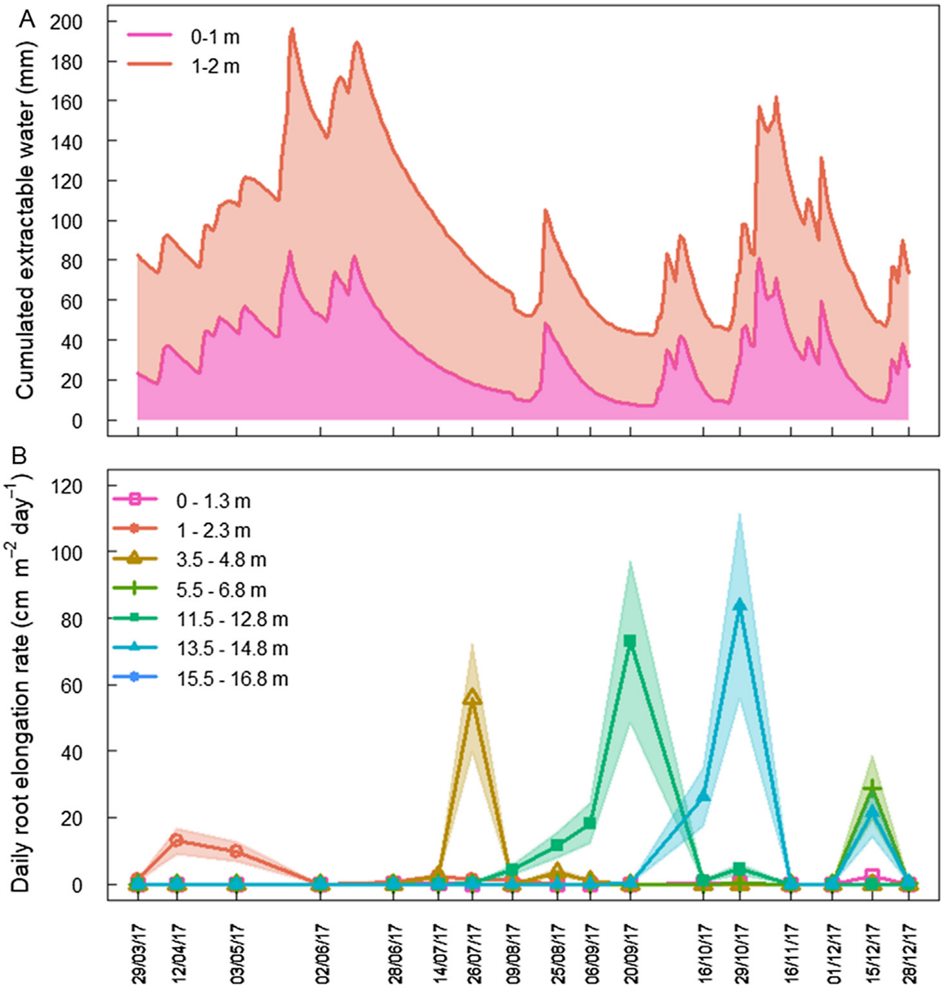

Fig. 6. (A) Time course of soil extractable water (mm) in soil layers 0–1 m and 1–2 m, in the −W (37% of throughfall excluded by plastic sheets) coppice of block 1, from March 2017 (10 months after the clear-cut) to December 2017. The mean daily values of soil extractable water were estimated from semi-hourly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

(Christina et al., 2017).

After clear-cutting, fine root growth at > 4 m deep was spectacular at the end of the dry season, whatever the water supply regime. Lambais et al. (2017) also showed flushes of fine root growth down to a depth of 6 m at the end of dry periods in a Brazilian eucalypt plantation. Fine root growth in deep soil layers was initiated when the extractable water content in the 0–2 m soil layer fell below a threshold of about 80 mm, which suggests that soil water content in a particular soil layer was not the main driver of fine root growth. Endogenous and exogenous factors are major drivers of fine root phenology (Moroni et al., 2003; Tierney et al., 2003; Abramoff and Finzi, 2015), but are difficult to disentangle in deep soil layers. The 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.

In agreement with our second hypothesis, *Eucalyptus* trees facing drought adapted their root morphology to maximize the root surface area to take up limited resources. SRL and SRA were higher in −W than in +W, which in combination with higher fine root densities led to a much higher root area index. Despite many uncertainties due to soil disturbance by the auger, the results obtained are consistent with those of other studies in plantations of the same type (Germon et al., 2018) as well as with other methods based on excavations (Maurice et al., 2010; Laclau et al., 2013). In a meta-analysis, Ostonen et al. (2007) showed that SRL response to drought varies greatly between species. While Arend et al. (2011) did not observe any significant change in SRL, root area index and root tissue density for oak trees (*Quercus* sp.) exposed to drought, Olmo et al. (2014) showed an increase in SRL and root tissue density under drought conditions for 10 tree species. *Eucalyptus grandis* trees coped with drought in our experiment by increasing their capacity to take up soil resources for a relatively low investment in belowground biomass. A large increase in SRL and SRA was recently shown throughout deep soil profiles down to 17 m deep for *Acacia mangium* Wild and *E. grandis* roots in response to the mixture relative to monospecific stands (Germon et al., 2018). Our study showed that *Eucalyptus* trees can modify fine root traits to enhance resource capture and the exploration of very deep soil layers to survive in a context of climate change, which contributes to maintaining water uptake during dry periods (Brunner et al., 2015; Christina et al., 2017).

4.2. 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

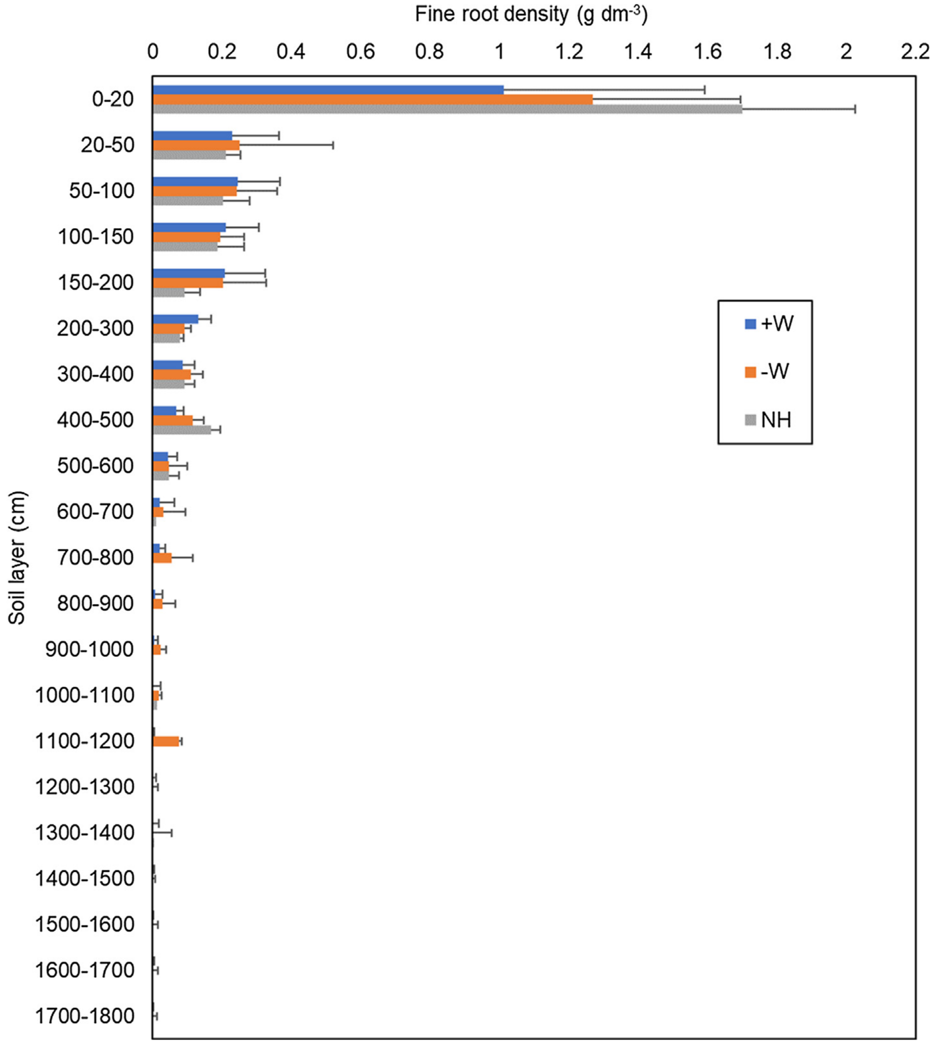

Fig. 7. Mean fine root densities down to the root front in the undisturbed rainfall plots (+W, blue), in the plots with 37% of throughfall excluded by plastic sheets (−W, orange) and in the non-harvested plot (NH, gray). Standard deviations between blocks (n = 3) for −W and +W and between pseudo replicates in a single block for NH are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(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

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 (cm^2 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 lower-case 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.

	+W	−W	NH
Fine root biomass (g m^{-2})	1016.5 ± 362.8	1265.8 ± 301.4	1078.3 ± 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 ± 6.9b	34.4 ± 14.1 a	28.8 ± 7.6
Specific root area (cm^2 g^{-1})	267.5 ± 55.7b	305.3 ± 150.1 a	258.9 ± 92.6
Root diameter (mm)	0.32 ± 0.08b	0.36 ± 0.13 a	0.31 ± 0.08

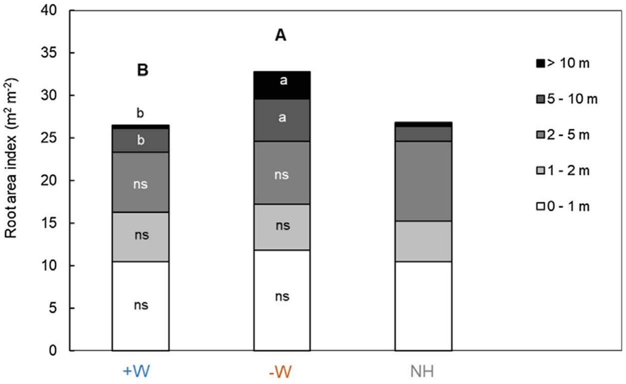

Fig. 8. Root area index ($m^2\ m^{-2}$) in the 0–1 m, 1–2 m, 2–5 m, 5–10 m and 10–17 m deep soil layers in the undisturbed rainfall plots (+W), in the plots with 37% of throughfall excluded by plastic sheets (−W) and in the non-harvested plot (NH). Different upper-case letters indicate significant differences between treatments for the cumulative indices and different lower-case letters indicate significant differences between treatments within each individual soil layer ($p < 0.05$). NH was not included in the ANOVA because the three soil coring replicates were located in the same plot.

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 other types of coppice stands where repeated clear-cutting increased root growth in the top soil and increased tree sensitivity to drought (Corcuera et al., 2006; Zadworny et al., 2014). In this study, root growth occurred at a depth of 14 m less than one year after clear-cutting of coppice-managed *E. grandis* trees, while the maximum depth reached by *E. grandis* roots one year after planting is about 7 m in very deep soils (Christina et al., 2011; Laclau et al., 2013). Deep roots can provide access to large amounts of water stored in the subsoil after clear-cutting and small fine root densities in deep soil layers can be sufficient to take up substantial amounts of water (Christina et al., 2017). Low fine root mortality rates after clear-cutting suggest that coppice-management of *Eucalyptus* plantations might be a promising option for coping with water scarcity, since the pre-existing root system can provide access to water stored throughout deep soil profiles.

4.3. Carbon sequestration and implication for the management of eucalypt plantations

Surprisingly, cutting the trees did not lead to an increase in root mortality throughout the soil profile, whatever the water supply regime. Fine roots play an active role in carbon (C) cycling in forest ecosystems, through respiratory processes, exudation and root mortality (Balesdent and Balabane, 1996; Marsden et al., 2008; Strand et al., 2008). The consequences of deep rooting on subsoil C stocks in tropical planted forests and other forest ecosystems remain poorly known (Nepstad et al., 1994; Harper and Tibbett, 2013; Gao et al., 2018; Meyer et al., 2018). On the one hand, the supply of fresh carbon might promote the activity of microbes and affect the stability of pre-existing organic matter through a “priming effect” (Kuzyakov et al., 2000; Fontaine et al., 2007; Derrien et al., 2014). Promoting the mineralization of ancient C would result in high emissions of carbon dioxide (CO_2) under aerobic conditions and of methane (CH_4) under anaerobic conditions. However, a complementary study in our plots showed that CO_2 and CH_4 emissions did not increase significantly after clear-cutting in the coppice-managed stands 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 belowground 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.

5. 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.

Acknowledgments

The study was funded by São Paulo Research Foundation (FAPESP, Project 2015/24911-8), Centre de cooperation Internationale en Recherche Agronomique pour le Développement (CIRAD) and São Paulo University. This study belongs to SOERE F-ORE-T, which is supported annually by Ecofor, Allenvi and the French National Research Infrastructure ANAEE-F (http://www.anaee-france.fr/fr/). We are grateful to the staff at the Itatinga Research Station (ESALQ/USP), Floragro Apoio for their technical support, in particular Eder Araujo da Silva (http://www.floragroapoio.com.br) and our CIRAD colleague Maxime Duthoit. We are grateful to Peter Biggins for correcting the English language.

References

Abramoff, R.Z., Finzi, A.C., 2015. Are above-and below-ground phenology in sync? New Phytol. 205, 1054–1061.

Allen, C.D., 2009. Climate-induced forest dieback: an escalating global phenomenon. Unasylva 231, 60.

Arend, M., Kuster, T., Günthardt-Goerg, M.S., Dobbertin, M., 2011. Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). Tree Physiol. 31, 287–297.

Balesdent, J., Balabane, M., 1996. Major contribution of roots to soil carbon storage inferred from maize cultivated soils. Soil Biol. Biochem. 28, 1261–1263.

Battie-Laclau, P., Laclau, J.P., Domec, J.C., Christina, M., Bouillet, J.P., Cassia Piccolo, M., Moraes Gonçalves, J.L., Krusche, A.V., Bouvet, J.M., Nouvellon, Y., 2014. Effects of potassium and sodium supply on drought-adaptive mechanisms in *Eucalyptus grandis* plantations. New Phytol. 203, 401–413.

Berhongaray, G., Verlinden, M., Broeckx, L., Ceulemans, R., 2015. Changes in belowground biomass after coppice in two Populus genotypes. For. Ecol. Manage. 337, 1–10.

Billings, S.A., 2015. ‘One physical system’: Tansley's ecosystem as Earth's critical zone. New Phytol. 206, 900–912.

Booth, T.H., 2013. Eucalypt plantations and climate change. For. Ecol. Manage. 301, 28–34.

Bordron, B., Robin, A., Oliveira, I., Guillemot, J., Laclau, J.-P., Jourdan, C., Nouvellon, Y., Abreu-Junior, C., Trivelin, P., Gonçalves, J., 2018. Fertilization increases the functional specialization of fine roots in deep soil layers for young *Eucalyptus grandis* trees. For. Ecol. Manage. 431, 6–16.

Bristiel, P., Roumet, C., Violle, C., Volaire, F., 2018. Coping with drought: root trait variability within the perennial grass *Dactylis glomerata* captures a trade-off between dehydration avoidance and dehydration tolerance. Plant Soil. https://doi.org/10.1007/s11104-11018-13854-11108.

Broedel, E., Tomasella, J., Cândido, L.A., von Randow, C., 2017. Deep soil water dynamics in an undisturbed primary forest in central Amazonia: differences between normal years and the 2005 drought. Hydrol. Process. 31, 1749–1759.

Brunner, I., Herzog, C., Dawes, M.A., Arend, M., Sperisen, C., 2015. How tree roots respond to drought. Front. Plant Sci. 6, 547.

Canadell, J., Jackson, R., Ehleringer, J., Mooney, H., Sala, O., Schulze, E.-D., 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108, 583–595.

Christina, M., Laclau, J.-P., Gonçalves, J.L.M., Jourdan, C., Nouvellon, Y., Bouillet, J.-P., 2011. Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. Ecosphere 2, 1–10.

Christina, M., Le Maire, G., Battie-Laclau, P., Nouvellon, Y., Bouillet, J.P., Jourdan, C., de Moraes Gonçalves, J.L., Laclau, J.P., 2015. Measured and modeled interactive effects of potassium deficiency and water deficit on gross primary productivity and light-use efficiency in *Eucalyptus grandis* plantations. Glob. Change Biol. 21, 2022–2039.

Christina, M., Nouvellon, Y., Laclau, J.P., Stape, J.L., Bouillet, J.P., Lambais, G.R., Maire, G., 2017. Importance of deep water uptake in tropical eucalypt forest. Funct. Ecol. 31, 509–519.

Corcuera, L., Camarero, J.J., Sisó, S., Gil-Pelegrín, E., 2006. Radial-growth and wood-anatomical changes in overaged Quercus pyrenaica coppice stands: functional responses in a new Mediterranean landscape. Trees 20, 91–98.

Cossalter, C., Pye-Smith, C., 2003. Fast-wood Forestry: Myths and Realities. CIFOR.

Da Silva, E.V., Bouillet, J.P., de Moraes Gonçalves, J.L., Junior, C.H.A., Trivelin, P.C.O., Hinsinger, P., Jourdan, C., Nouvellon, Y., Stape, J.L., Laclau, J.P., 2011. Functional specialization of Eucalyptus fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. Funct. Ecol. 25, 996–1006.

Dai, A., 2011. Drought under global warming: a review. Wiley Interdiscip. Rev. Clim. Change 2, 45–65.

Derrien, D., Plain, C., Courty, P.-E., Gelhaye, L., Moerdijk-Poortvliet, T.C., Thomas, F., Versini, A., Zeller, B., Koutika, L.-S., Boschker, H.T., 2014. Does the addition of labile substrate destabilise old soil organic matter? Soil Biol. Biochem. 76, 149–160.

Dickmann, D.I., Nguyen, P.V., Pregitzer, K.S., 1996. Effects of irrigation and coppicing on above-ground growth, physiology, and fine-root dynamics of two field-grown hybrid poplar clones. For. Ecol. Manage. 80, 163–174.

Dipesh, K., Schuler, J.L., 2013. Estimating fine-root production and mortality in the biomass plantations. Commun. Soil Sci. Plant Anal. 44, 2514–2523.

Drake, P.L., Mendham, D.S., Ogden, G.N., 2013. Plant carbon pools and fluxes in coppice regrowth of *Eucalyptus globulus*. For. Ecol. Manage. 306, 161–170.

Epron, D., Laclau, J.-P., Almeida, J.C., Gonçalves, J.L.M., Ponton, S., Sette Jr, C.R., Delgado-Rojas, J.S., Bouillet, J.-P., Nouvellon, Y., 2012. Do changes in carbon allocation account for the growth response to potassium and sodium applications in tropical Eucalyptus plantations? Tree Physiol. 32, 667–679.

Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450, 277.

Freycon, V., Wonkam, C., Fayolle, A., Laclau, J.-P., Lucot, E., Jourdan, C., Cornu, G., Gourlet-Fleury, S., 2015. Tree roots can penetrate deeply in African semi-deciduous rain forests: evidence from two common soil types. J. Trop. Ecol. 31, 13–23.

Gao, X., Li, H., Zhao, X., Ma, W., Wu, P., 2018. Identifying a suitable revegetation technique for soil restoration on water-limited and degraded land: considering both deep soil moisture deficit and soil organic carbon sequestration. Geoderma 319, 61–69.

Germon, A., Cardinael, R., Prieto, I., Mao, Z., Kim, J., Stokes, A., Dupraz, C., Laclau, J.-P., Jourdan, C., 2016. Unexpected phenology and lifespan of shallow and deep fine roots of walnut trees grown in a silvoarable Mediterranean agroforestry system. Plant Soil 401, 409–426.

Germon, A., Guerrini, I.A., Bordron, B., Bouillet, J.-P., Nouvellon, Y., de Moraes Gonçalves, J.L., Jourdan, C., Paula, R.R., Laclau, J.-P., 2018. Consequences of mixing *Acacia mangium* and *Eucalyptus grandis* trees on soil exploration by fine-roots down to a depth of 17 m. Plant Soil 424, 203–220.

Gonçalves, J.L.d.M., Alvares, C.A., Higa, A.R., Silva, L.D., Alfenas, A.C., Stahl, J., de Barros Ferraz, S.F., de Paula Lima, W., Brancalion, P.H.S., Hubner, A., 2013. Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. For. Ecol. Manage. 301, 6–27.

Graefe, S., Hertel, D., Leuschner, C., 2008. Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. Biotropica 40, 536–542.

Granier, A., Bréda, N., Biron, P., Villette, S., 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecol. Model. 116, 269–283.

Harper, R., Tibbett, M., 2013. The hidden organic carbon in deep mineral soils. Plant Soil 368, 641–648.

He, J., Soden, B.J., 2017. A re-examination of the projected subtropical precipitation decline. Nat. Clim. Change 7, 53.

Hinsinger, P., 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil 237, 173–195.

Jackson, R.B., Schenk, H., Jobbagy, E., Canadell, J., Colello, G., Dickinson, R., Field, C., Friedlingstein, P., Heimann, M., Hibbard, K., 2000. Belowground consequences of vegetation change and their treatment in models. Ecol. Appl. 10, 470–483.

Jobbágy, E.G., Jackson, R.B., 2004. Groundwater use and salinization with grassland afforestation. Glob. Change Biol. 10, 1299–1312.

Keenan, R.J., Reams, G.A., Achard, F., de Freitas, J.V., Grainger, A., Lindquist, E., 2015. Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. For. Ecol. Manage. 352, 9–20.

Kell, D.B., 2012. Large-scale sequestration of atmospheric carbon via plant roots in natural and agricultural ecosystems: why and how. Phil. Trans. R. Soc. B 367, 1589–1597.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82.

Kuzyakov, Y., Friedel, J., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biol. Biochem. 32, 1485–1498.

Laclau, J.-P., Ranger, J., de Moraes Gonçalves, J.L., Maquère, V., Krusche, A.V., M'Bou, A.T., Nouvellon, Y., Saint-André, L., Bouillet, J.-P., de Cassia Piccolo, M., 2010. Biogeochemical cycles of nutrients in tropical Eucalyptus plantations: main features shown by intensive monitoring in Congo and Brazil. For. Ecol. Manage. 259, 1771–1785.

Laclau, J.-P., Silva, E.A.d., Rodrigues Lambais, G., Bernoux, M., Le Maire, G., Stape, J.L., Bouillet, J.-P., Jourdan, C., Nouvellon, Y., 2013. Dynamics of soil exploration by fine roots down to a depth of 10 m throughout the entire rotation in *Eucalyptus grandis* plantations. Front. Plant Sci. 4, 243. https://doi.org/10.3389/fpls.2013.00243.

Lambais, G.R., Jourdan, C., de Cássia Piccolo, M., Germon, A., Pinheiro, R.C., Nouvellon, Y., Stape, J.L., Campoe, O.C., Robin, A., Bouillet, J.-P., 2017. Contrasting phenology of *Eucalyptus grandis* fine roots in upper and very deep soil layers in Brazil. Plant Soil 421, 301–318.

Lehmann, J., 2003. Subsoil root activity in tree-based cropping systems. In: Roots: The Dynamic Interface between Plants and the Earth, pp. 319–331.

Lehmann, J., Schroth, G., 2003. Nutrient leaching. Trees, Crops and Soil Fertility. CABI Publishing, Wallingford, pp. 151–166.

Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R.D., Eissenstat, D.M., McCormack, M.L., Hedin, L.O., 2018. Evolutionary history resolves global organization of root functional traits. Nature 555, 94.

Maeght, J.-L., Gonkhamdee, S., Clément, C., Isarangkool Na Ayutthaya, S., Stokes, A., Pierret, A., 2015. Seasonal patterns of fine root production and turnover in a mature rubber tree (Hevea brasiliensis Müll. Arg.) stand-differentiation with soil depth and implications for soil carbon stocks. Front. Plant Sci. 6, 1022 doi: 1010.3389/fpls.2015.01022.

Maeght, J.-L., Rewald, B., Pierret, A., 2013. How to study deep roots—and why it matters. Front. Plant Sci. 4, 299. https://doi.org/10.3389/fpls.2013.00299.

Majdi, H., Nylund, J.-E., 1996. Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots? Plant Soil 185, 305–309.

Markesteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought-and shade-tolerance. J. Ecol. 97, 311–325.

Markewitz, D., Devine, S., Davidson, E.A., Brando, P., Nepstad, D.C., 2010. Soil moisture depletion under simulated drought in the Amazon: impacts on deep root uptake. New Phytol. 187, 592–607.

Marsden, C., Nouvellon, Y., M'Bou, A.T., Saint-Andre, L., Jourdan, C., Kinana, A., Epron, D., 2008. Two independent estimations of stand-level root respiration on clonal Eucalyptus stands in Congo: up scaling of direct measurements on roots versus the trenched-plot technique. New Phytol. 177, 676–687.

Maurice, J., Laclau, J.-P., Re, D.S., de Moraes Gonçalves, J.L., Nouvellon, Y., Bouillet, J.-P., Stape, J.L., Ranger, J., Behling, M., Chopart, J.-L., 2010. Fine root isotropy in Eucalyptus grandis plantations. towards the prediction of root length densities from root counts on trench walls. Plant Soil 334, 261–275.

McDowell, N., Allen, C.D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., 2018. Drivers and mechanisms of tree mortality in moist tropical forests. New Phytol. https://doi.org/10.1111/nph.15027.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178, 719–739.

Mello, S.L.d.M., de Moraes Gonçalves, J.L., Gava, J.L., 2007. Pre-and post-harvest fine root growth in *Eucalyptus grandis* stands installed in sandy and loamy soils. For. Ecol. Manage. 246, 186–195.

Menichetti, L., Ekblad, A., Kätterer, T., 2015. Contribution of roots and amendments to soil carbon accumulation within the soil profile in a long-term field experiment in Sweden. Agric. Ecosyst. Environ. 200, 79–87.

Meyer, N., Welp, G., Rodionov, A., Borchard, N., Martius, C., Amelung, W., 2018. Nitrogen and phosphorus supply controls soil organic carbon mineralization in tropical topsoil and subsoil. Soil Biol. Biochem. 119, 152–161.

Moroni, M.T., Worledge, D., Beadle, C.L., 2003. Root distribution of *Eucalyptus nitens* and *E. globulus* in irrigated and droughted soil. For. Ecol. Manage. 177, 399–407.

Nardini, A., Casolo, V., Dal Borgo, A., Savi, T., Stenni, B., Bertoncin, P., Zini, L., McDowell, N.G., 2016. Rooting depth, water relations and non-structural carbohydrate dynamics in three woody angiosperms differentially affected by an extreme summer drought. Plant Cell Environ. 39, 618–627.

Nepstad, D.C., de Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., da Silva, E.D., Stone, T.A., Trumbore, S.E., Vieira, S., 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372, 666.

Nouvellon, Y., Laclau, J.-P., Epron, D., Le Maire, G., Bonnefond, J.-M., Gonçalves, J.L.M., Bouillet, J.-P., 2012. Production and carbon allocation in monocultures and mixed-species plantations of *Eucalyptus grandis* and *Acacia mangium* in Brazil. Tree Physiol. 32, 680–695.

Olmo, M., Lopez-Iglesias, B., Villar, R., 2014. Drought changes the structure and elemental composition of very fine roots in seedlings of ten woody tree species. implications for a drier climate. Plant Soil 384, 113–129.

Ostonen, I., Püttsepp, Ü., Biel, C., Alberton, O., Bakker, M., Lõhmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A., Pronk, A., 2007. Specific root length as an indicator of environmental change. Plant Biosyst. 141, 426–442.

Pate, J., Arthur, D., 1998. δ 13 C analysis of phloem sap carbon: novel means of evaluating seasonal water stress and interpreting carbon isotope signatures of foliage and trunk wood of *Eucalyptus globulus*. Oecologia 117, 301–311.

Pierik, R., Testerink, C., 2014. The art of being flexible: how to escape from shade, salt, and drought. Plant Physiol. 166, 5–22.

Pierret, A., Maeght, J.-L., Clément, C., Montoroi, J.-P., Hartmann, C., Gonkhamdee, S., 2016. Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research. Ann. Bot. 118, 621–635.

Pinheiro, R.C., de Deus Jr, J.C., Nouvellon, Y., Campoe, O.C., Stape, J.L., Aló, L.L., Guerrini, I.A., Jourdan, C., Laclau, J.-P., 2016. A fast exploration of very deep soil layers by Eucalyptus seedlings and clones in Brazil. For. Ecol. Manage. 366, 143–152.

Radville, L., McCormack, M.L., Post, E., Eissenstat, D.M., 2016. Root phenology in a changing climate. J. Exp. Bot. 67, 3617–3628.

Rasse, D.P., Rumpel, C., Dignac, M.-F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant Soil 269, 341–356.

Rumpel, C., Kögel-Knabner, I., 2011. Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. Plant Soil 338, 143–158.

Ryan, M.G., Stape, J.L., Binkley, D., Fonseca, S., Loos, R.A., Takahashi, E.N., Silva, C.R., Silva, S.R., Hakamada, R.E., Ferreira, J.M., 2010. Factors controlling Eucalyptus productivity: how water availability and stand structure alter production and carbon allocation. For. Ecol. Manage. 259, 1695–1703.

Saleska, S.R., Didan, K., Huete, A.R., Da Rocha, H.R., 2007. Amazon forests green-up during 2005 drought. Science 318 612-612.

Scartazza, A., Moscatello, S., Matteucci, G., Battistelli, A., Brugnoli, E., 2015. Combining stable isotope and carbohydrate analyses in phloem sap and fine roots to study seasonal changes of source–sink relationships in a Mediterranean beech forest. Tree Physiol. 35, 829–839.

Schenk, H.J., Jackson, R.B., 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. J. Ecol. 90, 480–494.

Schmidt, M.W., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49.

Solomon, S., Plattner, G.-K., Knutti, R., Friedlingstein, P., 2009. Irreversible climate change due to carbon dioxide emissions. Proc. Natl. Acad. Sci. 106, 1704–1709.

Strand, A.E., Pritchard, S.G., McCormack, M.L., Davis, M.A., Oren, R., 2008. Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319, 456–458.

Taylor, J., Wilson, B., Mills, M.S., Burns, R.G., 2002. Comparison of microbial numbers and enzymatic activities in surface soils and subsoils using various techniques. Soil Biol. Biochem. 34, 387–401.

Teixeira, P.C., Novais, R.F., Barros, N.F., Neves, J.C.L., Teixeira, J.L., 2002. *Eucalyptus urophylla* root growth, stem sprouting and nutrient supply from the roots and soil. For. Ecol. Manage. 160, 263–271.

Tierney, G.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Fitzhugh, R.D., Driscoll, C.T., Yavitt, J.B., 2003. Environmental control of fine root dynamics in a northern hardwood forest. Glob. Change Biol. 9, 670–679.

Vries, F.T.d., Brown, C., Stevens, C.J., 2016. Grassland species root response to drought: consequences for soil carbon and nitrogen availability. Plant Soil 409, 297–312.

Wildy, D.T., Pate, J.S., 2002. Quantifying above-and below-ground growth responses of the western Australian oil mallee, *Eucalyptus kochii* subsp. plenissima, to contrasting decapitation regimes. Ann. Bot. 90, 185–197.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Clim. Change 3, 292.

Zadworny, M., Jagodziński, A.M., Łakomy, P., Ufnalski, K., Oleksyn, J., 2014. The silent shareholder in deterioration of oak growth: common planting practices affect the long-term response of oaks to periodic drought. For. Ecol. Manage. 318, 133–141.

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 Environ. 41, 2589–2599.