Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests

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Abstract. Whilst the relationships between growth strategies and leaf traits are well established in functional plant ecology, little attention has been paid to root traits in very deep soil layers. The objective of our study was to compare the vertical velocity of the above- and belowground exploration of the environment for one of the fastest-growing tree species. Fine roots were studied in a chronosequence of intensively-managed *Eucalyptus* plantations established on highly weathered soils. Here we show that the root front depth was accurately predicted at 85% of mean tree height for stands <20 m in height, in the absence of any physical or chemical barrier. Tree height and root front growth velocities peaked at 0.59 and 0.55 m month^{-1} respectively 9–10 months after planting, and decreased steadily thereafter. Fast root front displacement might provide a competitive advantage to fast-growing species in forests established on deep soils. Our study may contribute to the debate on the environmental impact of short-rotation plantation forests in the Tropics.

Key words: Brazil; environment exploration; *Eucalyptus grandis* W. Hill ex Maiden; extension; growth; plantation; root front; synchrony; tree; velocity.

Citation: Christina, M., J.-P. Laclau, J. L. M.Gonçalves, C. Jourdan, Y. Nouvellon, and J.-P. Bouillet. 2011. Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. Ecosphere 2(3):art27. doi:10.1890/ES10-00158.1

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INTRODUCTION

Deep-rooted trees have been found in many tropical regions and may largely influence the tropical climate system, supplying water during droughts (Kleidon and Heimann 2000, Saleska et al. 2007). However, the dynamics of the root front in very deep soil layers have never been investigated throughout tree growth in tropical and subtropical regions. Such information is becoming essential in the context of climate change and accelerated land use conversions between native forests, pastures, crops and fast-growing forest plantations, since deep-rooted plants may contribute significantly to the hydrological cycle of native biomes in tropical regions (Oliveira et al. 2005). Sensitivity analyses for Amazonia have shown that the prediction accuracy of general circulation models is highly dependent on realistic characterizations of fine root distribution (Kleidon and Heimann 2000). Moreover, experimental evidence from a set of forested ecosystems shows that rising atmospheric [CO_2] may lead to deeper rooting distributions (Iversen 2010). Fine root growth at depth is likely to increase the resilience of forests

ecosystems to climate change, providing access to water pools stored in deep soil layers during rainfall seasons. Although process-based models are largely dependent on reliable estimations of water availability, the ability of trees to take up water in very deep soil layers throughout their development is still poorly known (Jackson et al. 2000, Tatarinov and Cienciala 2006). A relationship making it possible to assess the volume of soil explored by fine roots from aboveground trees attributes (extensively studied) would then be highly valuable to improve current tree growth models on deep tropical soils.

A general tendency towards synchrony between above- and belowground biomass accumulation throughout plant development is well documented (Gedroc et al. 1996, Cairns et al. 1997). However, little attention has been paid to the relationships between the vertical extension of shoots and roots throughout plant growth. This pattern reflects plant strategies to explore their environment and is dependent on the development of fine roots representing a very low fraction of total plant biomass. Based on a review of the available literature, Stone and Kalisz (1991) found that at least 22 tree species grow roots more than 10 m deep, with record depths of about 60 m for *Juniperus monosperma* and *Eucalyptus* sp. trees. However, most of the studies in tropical woody ecosystems did not sample the deepest roots. Meta-analyses have suggested that the maximum rooting depth is underestimated in tropical woody ecosystems and have highlighted the need to sample soils down to the root front in tropical shrublands and forests (Schenk and Jackson 2002a, 2002b).

Root front dynamics may be difficult to assess for particular tree species in natural ecosystems as a result of the necessity to use quantitative molecular techniques to measure the amount of non-target species roots in each particular sample (Lang et al. 2010). Mono-specific plantation forests managed with complete weeding are thus an interesting model to gain insight into the relationships between vertical above- and belowground growth rates for trees established on deep soils (Coll et al. 2008). The area occupied by plantation forests has been expanding at an annual rate of 2.0–2.5 million ha over recent decades (FAO 2006). Most recent plantation expansion has been based on exotic species managed in short rotations in tropical and subtropical regions. *Eucalyptus* is the most widely planted genus in tropical regions, covering about 20 million hectares. Whilst a review of the literature indicated that the Gross Primary Production (GPP) of world forests ranges from 973 to 3551 g C m^{-2} yr^{-1} (Luyssaert et al. 2007), the GPP of Brazilian eucalypt plantations can be > 4000 g C m^{-2} yr^{-1} (Ryan et al. 2010). Our study was carried out in one of the most productive world's forests to gain insight into the belowground growth strategy making it possible to reach such high biomass productions. These plantations are set to provide a growing share of world wood supplies in the future, helping to reduce the pressure on native forests. However, the consequences of large commercial plantations on landscape hydrology and soil carbon sequestration remain controversial (Cossalter and Pye-Smith 2003, Jackson et al. 2005, Vanclay 2009). Most of Brazilian eucalypt plantations are set up in pastures, a long time after the clear cut of native forests (Lima et al. 2006). Our study may contribute to the debate on the environmental impact of eucalypt plantations since the replacement of shallow-rooted pastures with low water requirements by deep-rooted trees with high transpiration rates may influence both water resources and soil carbon storage. A major deep-soil link between the water and carbon cycles in Amazonia suggests that land use changes between forest and pasture may affect carbon storage in highly weathered tropical soils (Nepstad et al. 1994). A large share of soil carbon is stored below the first metre in tropical evergreen forests, and introducing deeply rooted vegetation into shallow-rooted systems might store carbon at depth (Jobbágy and Jackson 2000). Fine root turnover in a considerable volume of soil, as well as harvesting and replanting trees every 6–7 years in these short-rotation forests, might lead to the release of not insubstantial amounts of fresh carbon in deep soil layers.

We put forward the hypothesis that the well-documented synchrony between shoot and root biomass accumulations is valid for the vertical extension of shoots and roots throughout the growth of fast-growing tropical plantations in the absence of any physical and chemical barrier in the soil. Our objective was to gain insight into the

dynamics of the root front throughout the development of fast-growing tropical trees.

MATERIALS AND METHODS

Study site

The study was conducted in southern Brazil (23°02′ S, 48°38′ W) close to the Itatinga city (São Paulo state). The mean annual rainfall over the 15 years prior to this study was 1367 mm and the mean annual temperature was 20°C. The soils were deep Ferralsols developed on Cretaceous sandstone, with a clay content ranging from 16% in the A_1 horizon to about 25% down to a depth >15 m. The mineralogy was dominated by quartz, kaolonite and oxyhydroxides, with acidic soil layers containing very small amounts of available nutrients before the experiment was set up (sum of base cations < 0.3 cmolc kg^{-1}, whatever the soil layer). A soil analysis relative to the mineralogy, exchangeable elements, and soil texture showed the absence of any physical or chemical barrier for eucalypt roots down to a depth > 15 m (Maquère 2008). All seedlings received standard commercial plantation fertilization, which was non-limiting for growth in this soil type (120 kg N ha^{-1}, 33 kg P ha^{-1}, 100 kg K ha^{-1}, 2 t ha^{-1} of dolomitic lime, and micronutrients). Successive herbicide applications in each stand led to an absence of understorey thereby avoiding confusion between the roots of *Eucalyptus* trees and of other plants.

Chronosequence

Half-sib family seedlings were planted after clear cutting a single *Eucalyptus grandis* W. Hill ex Maiden plantation, representing the whole rotation: 5-, 18-, 30-, 42- and 71-month-old plantations (logging age) were sampled. The area of each sampled stand ranged from 828 to 1152 m^2. They were situated in a 200 m radius, on the top of a hill (slope < 3%), and their silviculture was identical (spacing of 3 m × 2 m, same fertilization, complete weeding). The mean height of all the stands was close to the height growth curve of the oldest stand of the sequence that had been inventoried every 6–12 months over the rotation (Fig. 1). The mean annual GPP over the full rotation in the oldest stand of the chronosequence was estimated at approximately 4500 g C m^{-2} yr^{-1} (unpublished data).

Field sampling

The stumps from the previous rotation were killed after harvest to prevent resprouting. The area was kept free of other plants by successive herbicide applications during a >2 year inter-rotation period, which made it possible to distinguish living from dead root (even in the 5-month-old stand). Fine roots (<2 mm in diameter) were sampled at each age by soil coring at one distance (0.4, 0.9 or 1.5 m) from 3 trees with the same basal area as the mean of the stand, along a diagonal between trees in adjacent rows (Fig. 2). These trees were >7 m apart from each another in each stand (>15 m from stands of other ages). Excavation of the three largest superficial roots for these 3 trees in each stand revealed a length of <6.5 m (data not shown). Fine roots sampled at each soil coring position belonged then to different trees and the 3 samples at a specific depth in each stand were considered independent. Soils were sampled every metre with a cylindrical auger (diameter 7 cm), except for the upper metre where four samples were collected (depths of 0–0.16, 0.17–0.33, 0.34–0.66 and 0.67–1 m). Easily identifiable fine roots were separated by hand picking in the field, then the soils were brought to the laboratory for thorough quantification of extremely fine roots. Soil coring down to 10 m in an area of the same plot where trees had not yet been planted showed that the delay >2 years between clear cutting and fine root sampling in all the stands was sufficient to distinguish without any doubt between living roots and dead roots from the previous rotation. We were especially careful to avoid contamination of the soil samples collected at depth by roots from the upper layers. After sampling the soils down to a depth of 2 metres, we dug further to enlarge the diameter of the hole and we installed a 2-metre long plastic tube with a diameter of 20 cm to avoid surface soil falling further down. Moreover, we only considered soil blocks from the inner part of the auger and all fragmented soil pieces likely to come from upper soil layers were systematically discarded. The root front was defined at each sampling position as the depth of the layer where the deepest root was observed. Soils were systematically collected a further 2 metres down at each sampling position and the absence of roots below the layer identified as the root front
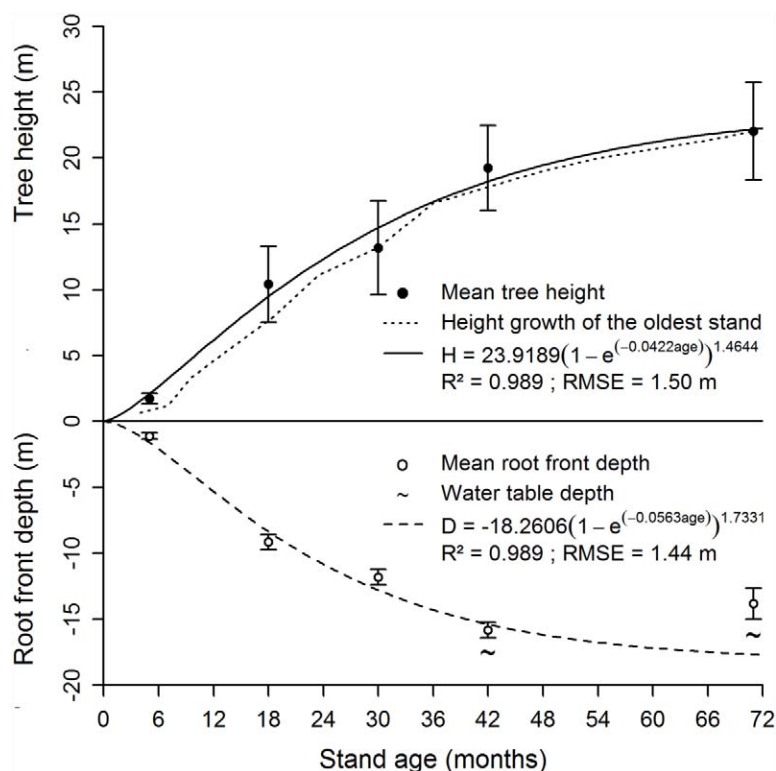
Fig. 1. Tree growth in height (H) and depth (D) over a full rotation. Non-linear regressions were computed from measurements in the 5-, 18-, 30-, 42- and 71-month-old plantations of the chronosequence (excluding the 71-month-old stand for the root front). The height growth curve of the oldest stand of the sequence measured every 6–12 months over the rotation is indicated. Bars represent standard deviations ($n = 139, 191, 155, 136$, and 140 for tree height at ages 5, 18, 30, 42 and 71 months, respectively, and $n = 3$ for the root front depth in each stand). The tilde symbols at 42 and 72 months of age indicate the depth of the water table.

was carefully checked.

Tree height was measured on the same date as root sampling, excluding two external buffer rows in each stand. A 10-cm graduated pole was used in the 5- and 18-month-old stands and a Vertex III device (± 25 cm) at ages 30, 42 and 71 months. Soil water contents were monitored with 6 TDR probes installed at a depth of 3.0 m and 4 probes installed at a depth of 10.0 m. Two pits were dug manually down to a depth of 3.0 m before planting the oldest stand of the chronosequence and 3 TDR probes (Trase Soilmoisture, USA) were horizontally buried in an undisturbed area at different distances from trees, from the upward wall of each trench. Another pit was dug manually down to a depth of 10.0 m in the same stand when it was 43 months of age, and 4 probes were buried horizontally at different distances from trees. The trenches were back

filled with soil horizons in their natural arrangement after installation. Probe calibration was checked by gravimetric soil water content and bulk density measurements. Volumetric soil water contents were measured weekly from April 2004 to August 2010 (except during periods of equipment failure).

Laboratory measurements

Soil samples collected in the field were weighed and uniformly mixed, and sub-sample weights of whole cores were observed in the laboratory to identify extremely fine roots that had not been detected in the field. The fresh mass of soil observed in the laboratory was 50, 80, 100, 150, 200, 300, 400, 500, 600, 700, 800, and 900 g for soil samples collected at depths of 0–0.16, 0.17–0.33, 0.34–0.66, 0.67–1.00 m, then every metre down to 10 m, respectively. Below a depth of 10
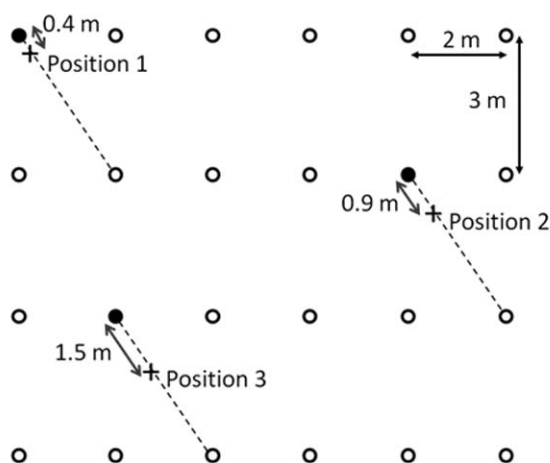
CHRISTINA ET AL.

Fig. 2. Schematic representation of the 3 soil coring positions in each stand of the chronosequence. Three trees with the same basal area as the mean of the stand (filled circles) were selected at each age.

m the totality of the soil collected was carefully observed. All the fine roots in the sub-samples were washed free of soil with tap water using a sieve with a mesh size of 550 μm and separated carefully by hand. Living roots were sorted according to criteria such as a living stele, bright colour and resilient aspect. All living fine roots separated from each soil sample were scanned (400 dpi), and root lengths were estimated with WinRHIZO Version Pro V.2009c software (Regent Instruments, QC, Canada) both for roots separated in the field and in the laboratory. Roots were then dried for 24 hours at 65°C and weighed (±0.1 mg). Soil moisture in each layer was measured from 10 g of soil dried at 105°C up to constant weight. Dry masses and lengths of fine roots separated in the field and in the laboratory (estimated proportionally to the mass of the total soil sample collected versus the sub-sample) were totalized for each soil layer.

Data analysis

Root densities per unit of soil dry weight were converted into root densities per unit of soil volume using soil bulk densities measured in a trench (3 replicates every metre) down to a depth of 10 m, in the oldest stand of the chronosequence (data not shown). Soil texture varied little between the depths of 9 and 15 m (Maquère 2008), and the bulk density of the 9–10 m layer

was used below 9 m. At each sampling position, the maximum depth of fine roots found between the depths of n and $(n+1)$ metres was considered as $(n + 0.5)$ metre. The depth of the water table was measured when mud was collected by the auger and the gravimetric water content was >20%.

Non-linear regressions were computed using a modified Chapman-Richards model (Richards 1959) between stand age (independent variable) and mean tree heights or root front depths (dependent variables) for the plantations of the chronosequence, excluding the 71-month-old stand for the root front. A linear regression was computed between mean tree height in each stand (independent variable) and mean root front depth (dependent variable). This regression was forced through the origin because the intercept was not significant ($P < 0.05$). The Nlin (Gauss-Newton method) and Reg procedures of SAS software version 9.1 were used. Current height and root growth velocities were estimated by deriving the equations of growth curves. We had to make root depth a discreet trait rather than a continuous one to be able to weight and to measure the length of very low amounts of fine roots in deep soil layers. Sampling 1 m-thick soil layers probably reduced the variability between the true root front depths in each stand.

RESULTS

Early vertical tree growth was found to be fast above and below ground, reaching 10.4 m in height and 9.2 m in depth at 1.5 years of age, and 19.2 m in height and 15.8 m in depth at 3.5 years of age (Fig. 1). The root front, as well as height growth, followed a similar pattern up to 42 months of age, when roots reached the vicinity of the water table. From the age of 42 months onwards, the depth of the root front did not increase further. The root front depth was 85% of the stand height in our chronsequence, up to a mean tree height of 20 m (Fig. 3). Thereafter, fine roots reached the vicinity of the water table and the relationship was no longer valid. Height and root front current increments increased sharply the first months after planting and peaked at 0.59 and 0.55 m month^{-1} at 9.0 and 9.8 months of age, respectively. Mean height growth rate was 0.2–0.3 m month^{-1} at age 36 months, and declined to
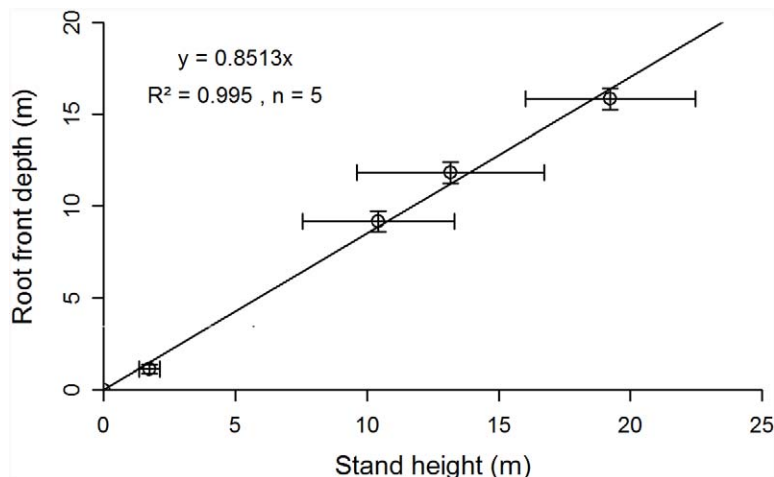
Fig. 3. Linear regression forced through the origin between mean tree height (independent variable) and root front depth (dependent variable) up to 42 months after planting. Bars represent standard deviations ($n = 139$, 191, 155 and 136 for tree height at ages 5, 18, 30 and 42 months, respectively, and $n = 3$ for root front depth in each stand).

<0.1 m month^{-1} in the last months of the rotation.

Fine root length densities (RLDs) decreased by 2–3 orders of magnitude from the upper soil layer to the root front, whatever the stand age (Fig. 4). Below a depth of 5 m, they decreased more sharply 18 months after planting than at the other ages studied. RLDs increased with stand age in soil horizons close to the root front from about 1 cm dm^{-3} at 18 months of age to 10 cm dm^{-3} at 71 months of age. Low standard deviations in Figs. 1 and 3 suggested relatively uniform soil exploration by deep fine roots, and a downward movement of the root front at the same velocity whatever the distance from the trees. Although depths >10 m were already explored by fine roots 30 months after planting, the rooting depth corresponding to 95% of the fine root mass remained at depths <5 m throughout stand growth.

The time-course of volumetric soil water contents in the oldest stand of the chronosequence exhibited large seasonal variations over stand growth at a depth of 3 m and a decrease from 0.23 m^3 m^{-3} to 0.20 m^3 m^{-3} from 44 to 56 months after planting at a depth of 10 m (Fig. 5). Soil water contents were >0.22 m^3 m^{-3} at a depth of 3 m the first year after planting and decreased sharply the second year of growth, down to the minimum values observed throughout the rota-

tion. This pattern indicated that active water withdrawal extended down to a depth of 3 m during dry periods, starting in the second year after planting. The decrease in soil water content at a depth of 10 m from 43 to 56 months after planting showed that water was withdrawn at the end of stand rotation. Standard deviations between probes remained low (<0.04 m^3 m^{-3}) at a depths of 3 m and 10 m throughout the monitoring period, even after the arrival of drainage waters from upper soil layers.

DISCUSSION

Eucalyptus grandis trees rapidly explored a considerable volume of soil at limited carbon cost. Whatever the stand age, roots below a depth of 3 m amounted to $<10\%$ of total fine root mass. Root observations on trench walls down to a depth of 6 m one and two years after planting *Eucalyptus grandis* trees and down to 10 m at 3 and 6 years of age were also consistent with RLD distributions in our study (unpublished data). Root growth in deep soil layers right from the first year after planting suggests strong ontogenetic determinism of deep soil exploration. Large amounts of nutrients were applied by fertilization at the soil surface and the development of fine roots down to a depth of 9 m at 18 months of age could not be accounted for by water or
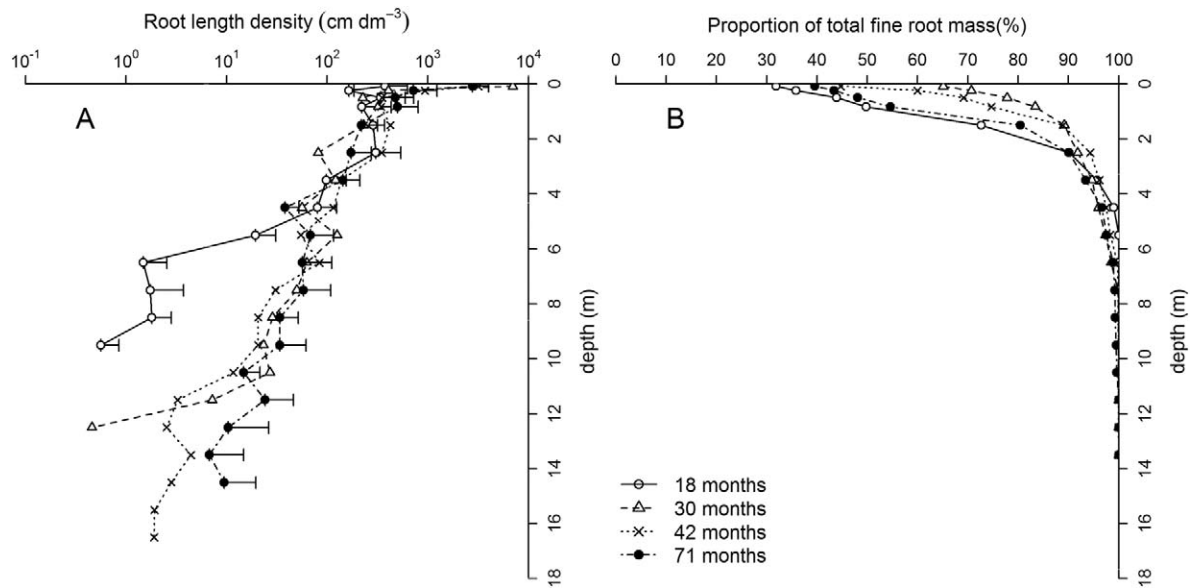
Fig. 4. Root length densities down to the root front (A) and proportions of cumulated fine root masses down to the root front at 18, 30, 42 and 71 months of age (B). Standard deviations in each soil layer ($n = 3$) are indicated by horizontal bars at 18 and 71 months of age only, for the clarity of (A).
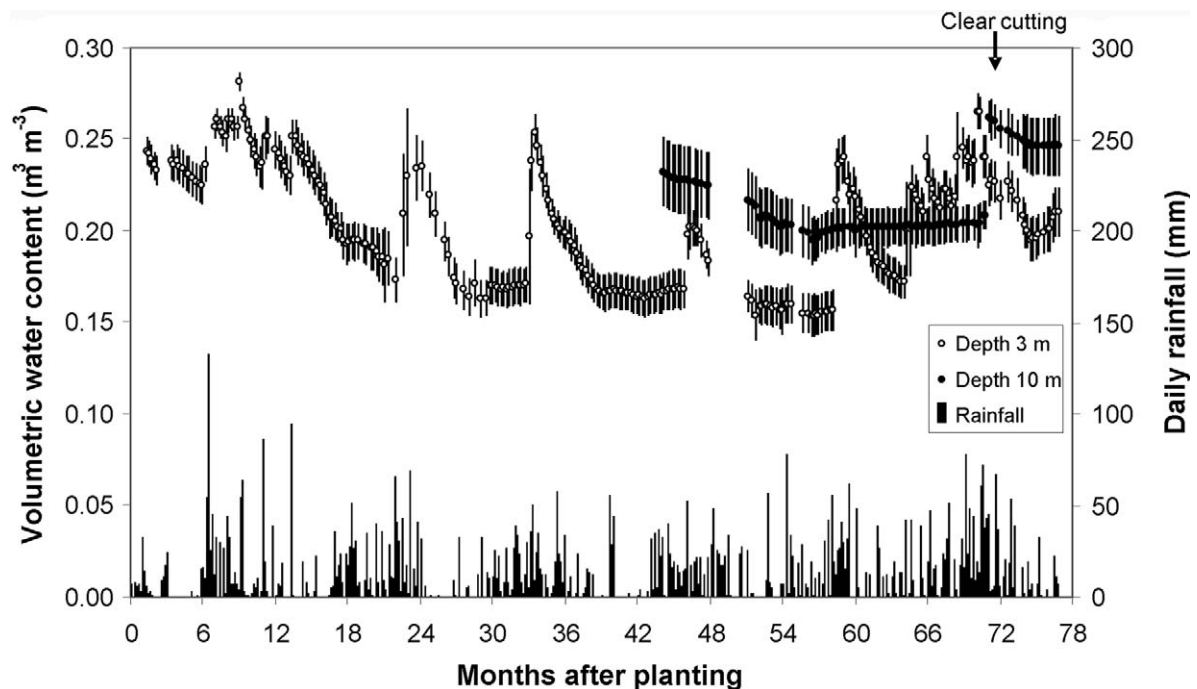

Fig. 5. Time-course of volumetric water contents measured weekly at depths of 3.0 and 10.0 m in the oldest stand of the chronosequence, from planting to the end of the rotation. Standard deviations are indicated by vertical bars ($n = 6$ at a depth of 3.0 m and $n = 4$ at a depth of 10.0 m). Probes at a depth of 10.0 m were installed 43 months after planting. Daily rainfall over the study period is indicated.

nutrient shortages in the top soil. The functional equilibrium hypothesis whereby plants adapt their biomass allocation strategies at depth to edaphic and climatic variations does not seem to apply in these fast-growing tropical plantations. The same behaviour has been observed in sugar cane (Battie-Laclau and Laclau 2009) and soybean crops (Mayaki et al. 1976) planted on deep soils, with root front growth little affected by irrigation. A high ontogenetic constraint of root/ shoot partitioning has been demonstrated for other plant species, even though fine root distribution may also be largely affected by biotic and abiotic factors (Gedroc et al. 1996).

A rapid occupation of space may lead to an advantage for competition in multi-species environments with limited resources, making it possible to take up transient resources (Schenk 2006, Lambers et al. 2008). In their natural habitat, *Eucalyptus grandis* trees are among the dominant species in mixed forests established on deep and well-drained soils (Boland et al. 2006). The rapid exploration of deep soil layers by *Eucalyptus grandis* trees might be a territorial strategy (Schenk et al. 1999), providing access to water below the resource-determined carrying soil capacity. The ontogenetic determinism of deep soil exploration might contribute to the high net primary production of *Eucalyptus grandis* trees established on deep soils in regions prone to dry seasons, despite the high water requirements of this species (Mielke et al. 1999). The capacity to redistribute water between soil layers by hydraulic lift has been demonstrated for *Eucalyptus* species (Burgess et al. 2001) and is likely to influence performance and plant-plant interactions (Dawson 1993). Cation uptake from deep soil horizons in some forest ecosystems (McCulley et al. 2004) might also be involved in the competitive advantage provided by a rapid vertical growth of fine roots (Jackson et al. 2000).

Although leaf traits associated with tree growth strategies are well documented (Reich et al. 2003), the relationships between tree growth and fine root development are still poorly known (Ryser 2006, Withington et al. 2006). Competition for directional vertical resources (light and water) is likely to shape the vertical distribution of resource-acquiring organs (Schenk 2006). Soil water monitoring in southern India over the first 3 years after planting *Eucalyptus camaldulensis*

trees showed that root front displacement was about 2.5 metres per year, roughly equivalent to the annual tree growth in height (Calder et al. 1997). We also observed almost symmetrical vertical tree extension above and below ground with growth rates roughly twice as high. Such synchrony would be worth further attention for other plant species growing in deep soils. The commonly used root trait of 95% rooting depth (Cornilessen et al. 2003, Schenk and Jackson 2002b) remained within the upper 5 m of soil in our study and was unsuitable for representing the important functional role of scarce very deep roots in coping with water deficits in upper soil layers. A clear decrease in soil water content at a depth of 10 m from 43 to 56 months after planting in our study showed that scarce very deep roots may have an important functional role to supply water for tree growth during droughts. A similar pattern has been demonstrated in Amazonian forests (Nepstad et al. 1994).

Large water demands of eucalypt plantations relative to pastures they replace might be largely involved in the reduction of stream flow widely observed after afforestation with *Eucalyptus* species (Jackson et al. 2005) and might influence atmospheric moisture (Vanclay 2009). Our study suggests that the fast root growth in deep soil layers might be an important factor leading to high evapotranspiration rates over the development of these plantations. Eucalypt roots provide access to large amounts of water stored in deep soil layers during rainfall seasons. The fast development of eucalypt roots in deep soil layers may then contributes to reduce the recharge of water tables in comparison with the previous vegetation of pasture characterized by lower water demands and shallower root systems (Nepstad et al. 1994).

ACKNOWLEDGMENTS

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