Potassium fertilization increases hydraulic redistribution and water use efficiency for stemwood production in *Eucalyptus grandis* plantations

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ARTICLE INFO

ABSTRACT

Climate change is expected to increase the frequency of droughts in most tropical regions in the coming decades. A passive phenomenon called hydraulic redistribution (HR) allows some plant species to take up water from deep and wet soil layers and redistribute it in the upper dry layers where other plants and soil biota can benefit from it. In addition, soil fertilization, particularly potassium (K), may also affect drought-adaptive mechanisms and increase water use efficiency (WUE) on poor and acidic tropical soils. The present study aimed at quantifying the role of HR and K fertilization on both wood productivity and WUE for stemwood production (WUE$_p$) of *Eucalyptus grandis* plantations in Brazil under ambient and reduced (−37%) throughfall conditions.

Tree transpiration was measured using trunk sap flow sensors over 21 months, and HR was estimated from the reverse sap flow (RF) observed in shallow roots over 18 months. Tree biomass, hydraulic conductance, soil water storage from surface to the water table (down to 17 m), and leaf photosynthetic capacity were also assessed.

Significant HR was detected over the whole year, even during the rainy seasons. Neither potassium fertilization nor throughfall exclusion affected the velocity of water transported by HR, probably because most trees reached water table. Nonetheless, some photosynthetic capacity parameters, including the maximum photosynthetic rate (A$_{max}$), increased in treatments with K addition. This higher A$_{max}$ combined with an increased sapwood area index, was associated with an increase in water uptake by 30 %–50 % and WUE$_p$ by 300 % relative to K-deficient trees. We postulate that the increase in WUE$_p$ promoted by potassium fertilization was partly driven by an increase in biomass allocation to wood, at the expense of foraging organs (leaves and roots), because K addition alleviated constraints on light and water use. Our results indicate that fertilizing *E. grandis* plantations with K is beneficial to both wood biomass production and WUE$_p$.

1. Introduction

Extreme climatic events such as heavy rainfall, wind storms, and severe droughts are increasing in frequency worldwide as a consequence of climate change (IPCC, 2014; Sherwood and Fu, 2014). Recent climate predictions show that Southeast Brazil will be affected by more frequent heavy rainfall events, higher mean air temperatures and water vapor pressure deficit, and an increase in the length of dry periods (Chou et al., 2012; Salazar et al., 2016). From 2012–2015, the state of São Paulo, in southeast Brazil, suffered a 20–23 % reduction in precipitation, which led to a significant decrease in soil moisture (Getirana, 2016). The increase in the frequency of extreme climatic events will increase the difficulty for plants to acclimate physiologically and morphologically to the rapidly changing climatic conditions, which

will likely result in decreased primary productivity and increased mortality (Choat et al., 2018). Since planted forests play an important role in supplying human needs for wood and paper products, it is important to determine which forest management practices would be more appropriate for trees to grow properly under those new climatic conditions (Noormets and Nouvellon, 2015).

High mortality rates in commercial eucalypt plantations during recent droughts in Brazil (Scolforo et al., 2019a) have highlighted the need to understand the key physiological processes that allow trees to acclimate to recurrent dry summers (Lobell et al., 2011; Gessler et al., 2017). A suitable nutrient application, and in particular potassium (K) fertilization has been shown to have positive effects on plant water and light use efficiency during drought periods (Harvey and van den Driessche, 1997; Cakmak, 2005; Battie-Laclau et al., 2016). Previous studies have evaluated the effect of the interaction between K fertilization and water availability on plant growth, but most of them with non-woody species such as corn and sugarcane (da Silva Moura et al., 2005; Djaman et al., 2013; Mahmood et al., 1999, Martineau et al., 2017). Other studies on woody species like olive trees, were performed on small and potted individuals growing under greenhouse conditions (Arquero et al., 2006). Under field conditions, the only studies addressing the potassium nutrition x drought interacting effects on woody species were conducted on *Eucalyptus grandis* in Brazil (Battie-Laclau et al., 2014; Christina et al., 2015) but were limited to the first three growing seasons after planting. The end of the rotation cycle (that typically lasts 6–7 years) is however a crucial period, when most of the drought-related mortality in Brazilian eucalypt plantations occurs (Scolforo et al., 2019b). This is likely due to decreasing soil water availability and increasing water table depth as stand ages (Christina et al., 2018). Potassium fertilization was shown to increase photosynthesis and tree biomass during the first years after harvest (Battie-Laclau et al., 2014), but it also increased tree transpiration, thus leading to faster soil water depletion and increased plant water stress during the dry seasons (Battie-Laclau et al., 2014). An evaluation of the interaction effect of K fertilization and soil water availability on the water use and water-use efficiency of eucalyptus trees along a whole commercial rotation is thus strongly needed.

Plants have different strategies for surviving during drought periods. Some plant species such as *Eucalyptus* trees can take up water from deep and moist soil layers through deep roots and then transport it up to dry soil layers, where it can be used when transpiration demand increases (Burgess et al., 1998, 2001; Burgess, 2006; Brooksbank et al., 2011). This process is called hydraulic redistribution (HR), or specifically hydraulic lift (HL, Weaver, 1919; Richards and Caldwell, 1987) when water is only moved upward in response to water potential gradients ($\Delta\Psi$) in the soil-plant system, occurring when Ψ_{soil} in shallow soil layers is more negative than Ψ_{soil} in deep soil layers and when stomata are closed (Domec et al. 2004; Scholz et al., 2008; David et al., 2013). Both HR and HL usually occur at night, when leaf transpiration has diminished, and during dry seasons, when soil water content is low in upper soil layers. This process was shown to improve plant growth and survival during droughts (Brooks et al., 2002; Scholz et al., 2008; Bleby et al., 2010). However, few studies directly measured HR and HL on roots with sap flow sensors (Scholz et al., 2002; Brooks et al., 2002; Domec et al., 2010; Bleby et al., 2010; Nadezhdina et al., 2015). All these studies except for Bleby et al. (2010) and Nadezhdina et al. (2015) monitored root sap flow only during the dry season. Bleby et al. (2010) observed reverse flow in tree roots of a semi-arid woodland during the whole year. Monitoring HR over the whole growing season appears therefore important to understand the drivers of tree water use and acclimation to drought.

Subtropical and tropical hardwood plantations are dominated by the *Eucalyptus* genus. Within this genus, the highly productive *E. grandis* is the most planted species worldwide in moist and warm subtropical regions (Gonçalves et al., 2013). A strong effect of rainfall regimes on the productivity of eucalypt plantations has been widely documented

(Stape et al., 2004, 2010; Binkley et al., 2017). Their fast growth is often associated with high water-use, thus raising concerns on their potential impact on water resources. There is therefore much interest in assessing their water-use efficiency (WUE), a highly integrative indicator related to the plantation ability to capture carbon and produce biomass per unit of water use (Farquhar et al., 1989; Law et al., 2002; Mateus et al., 2019). At the stand level, WUE for stemwood production (WUE_p) can be computed as the ratio of stemwood biomass increment to the water transpired over the same period. In fact, in areas with limited water resources, managing planted forests in a way that increases tree WUE_p is a promising avenue to sustain productivity under climate change.

The main goal of our study was to assess the effects of K fertilization on wood production, water use, hydraulic redistribution between soil layers, whole tree hydraulic conductance (K_{tree}) and WUE_p in *Eucalyptus grandis* plantations grown under ambient and reduced rainfall conditions, over the three last years of a commercial rotation (from 4 to 6 years after planting). We hypothesized that (i) HR occurs in the studied *Eucalyptus grandis* plantations, and is more pronounced under reduced soil water availability; (ii) K addition increases HR and; (iii) K addition increases water-use efficiency for stemwood production. While Battie-Laclau et al. (2016) studied the effects of K fertilization and throughfall exclusion on WUE_p over the early growth of the trees in the same experiment, we show in this paper stand water use and WUE_p at the end of the rotation cycle, as well as HR and whole-tree water transport (tree hydraulic conductance; K_{tree}), which were not evaluated in previous studies.

2. Materials and methods

2.1. Experimental design

The experiment was carried out at the Itatinga Experimental Station of the University of São Paulo in Brazil (23°02´S; 48°38´W). Over the previous 15 years, the mean annual rainfall was 1360 mm. The mean temperature was 15 °C during the dry season (from June to September), and 25 °C during the rainy season (from October to May). The experimental site was located on a hilltop (slope < 3 %) at an altitude of 850 m. The soils were very deep (> 15 m) Ferralsols, with a clay content ranging from 14% in the A1 horizon to 23 % in the deep soil layers. The mineral content was dominated by quartz, kaolinite and oxyhydroxides and the soil was acid (pH 4.5–5). Before the experiment, exchangeable K and Na concentrations were on average 0.02 $cmol_c$ kg^{-1} in the upper soil layer and < 0.01 $cmol_c$ kg^{-1} from 5 cm to 1500 cm (Laclau et al. 2010). The rhizosphere biogeochemistry was studied down to a depth of 4 m in this experiment (Pradier et al., 2017), as well the vertical distribution of ectomycorrhizas (Robin et al., 2019). Meteorological data were measured during the whole experiment using an automatic weather station located at the top of a 21 m tower, at 50 m from the experimental plots.

A split-plot experimental design, described in detail in Battie-Laclau et al. (2014), was set up in June 2010 with a highly productive *E. grandis* clone used in commercial plantations by the Suzano Company (Brazil). Two K fertilization regimes ($+/-K$) and two water supply regimes ($+/- W$) were applied in three blocks, thus leading to four treatments and twelve plots. The four treatments were:

-K + W: without K fertilization, and no throughfall exclusion,

+K + W: control, 0.45 mol K m^{-2} applied as KCl and no throughfall exclusion.

-K-W: without K fertilization, and ~37% of throughfall excluded,

+K-W: 0.45 mol K m^{-2} applied as KCl, non-limiting in terms of the availability of K for tree growth (Almeida et al., 2010), and ~37% of throughfall excluded,

The area of each individual plot was 864 m^2, with 144 trees per plot at a spacing of 2 m x 3 m (1667 trees per hectare), except one plot for each treatment that was 50% larger to allow destructive sampling

without disturbing tree growth in the inner plots where measurements were made. The KCl fertilization was applied once, 3 months after planting. All the plots in the experiment were fertilized with other nutrients when the trees were planted (3.3 g m^{-2}, 200 g m^{-2} of dolomitic lime, and micronutrients) and after 3 months (12 g m^{-2}). Field trials at the study site and in nearby areas on the same type of soil showed that the amounts of N, P, Ca, Mg and micronutrients applied in this experiment were not limiting for tree growth (Gonçalves et al., 2008; Laclau et al., 2009).

Throughfall was partially excluded in the -W plots from September 2010 onwards, using panels made of clear greenhouse plastic sheets mounted on wooden frames at heights varying between 0.5 and 1.6 m. Plastic sheets covered 37% of the area in the -W plots leading to a throughfall exclusion of about ~450 mm y^{-1} in the -W plots. Scaffold towers were used to access the crown of four trees in the central part of each plot at block 1 (four towers in total).

2.2. Tree biomass and leaf area index

Tree height and circumference at breast height (H and CBH, respectively) were measured every 6 months on 36 trees per plot (excluding a minimum of three buffer rows to avoid edge effects), except for the last year, when only one inventory was made at the end of the rotation. The aboveground biomass was estimated at 47, 59 and 71 months by sampling eight trees representative of the range of cross-sectional areas in each treatment. The selected trees were felled and measured for total height (H$_t$) and height of the crown base (H$_b$). Then the crown length (L = H$_t$ - H$_b$) was divided into three equal-length sections (lower, middle and upper). The foliage biomass was determined by weighing all the leaves from each of the three crown sections, and randomly subsampling 30 leaves per crown section. Sampled leaves were immediately scanned at 300 dpi and fresh mass was measured. Leaves were then oven dried at 65 °C for three days, and weighed again. The dry weights of the sub-samples were used in conjunction with their measured area to calculate specific leaf area (SLA) for each crown section. The foliage dry weight of each crown section was calculated from the foliage fresh weight and the dry to fresh weight ratio of the sub-samples. The tree leaf biomass (B$_l$) and leaf area (A$_l$) were then estimated as:

$$B_l = \sum_{i=1}^{3} B_i$$

$$A_l = \sum_{i=1}^{3} B_i \, SLA_i$$

where B$_i$ and SLA$_i$ are the foliage dry weight (kg) and SLA (m^2 kg^{-1}) in the ith crown section, respectively.

Live branches, dead branches, stemwood (diameter > 2 cm at the thinner end) and stem bark were collected in the field for all the trees and weighed separately. Subsamples were taken from all the tree compartments (live branches, dead branches, stemwood and bark), dried at 60 °C until constant weight, and the dry biomass of the components in each tree was calculated proportionally.

Treatment-specific allometric relationships were established at each age and applied to the inventory made on the same date to estimate plot-scale above-ground biomass (kg m^{-2}) and leaf area index (LAI, m^2_leaf m^{-2}_ground) from tree attributes (diameter at breast height and height); see Battie-Laclau et al. (2016) for further details on the allometric equations and the fitting procedures.

2.3. Stand transpiration and water use efficiency for biomass production

Trunk sap flow was continuously measured between August 2014 and April 2016 (for 21 months) in 6 trees per treatment using the heat dissipation technique (Granier, 1985). Two sap flow sensors per tree

were installed at 1.3 m above the ground and protected from external temperature variations and water intrusion by a reflective aluminum foil. The sensor output voltage was recorded every 30 s and the 30-min average values stored in data loggers (CR1000, Campbell Scientific Inc., Logan, UT, USA). All sensors were checked every week and replaced if they were physically damaged. Additionally, the sensors were moved to newly drilled holes in another position round the trunk (selected at random) 3 months after installation to prevent sap flow from being underestimated due to fast radial growth. The CBH of all equipped trees was measured monthly. The sap-flow sensor signal was converted to sap flux density (SFD, kg_H$_2$O m^{-2}_sapwood s^{-1}) using the calibration equation determined previously at our site on 18 trees (Delgado-Rojas et al., 2010) and the sapwood area at breast height (A$_s$, m^2). The semi-hourly sap flux (kg_H$_2$O 30 min^{-1}) was then calculated for each tree and then cumulated over the day to compute daily transpiration (kg_H$_2$0 d^{-1}). Then, for each tree fitted with a sap flow sensor in each treatment, the relationship between the daily total transpiration (dependent variable) and CBH^2 (independent variable) was determined by linear regression (SFD = a + b·CBH^2), as in other recent studies (Kunert et al., 2012; Battie-Laclau et al., 2016). The mean R^2 values of all the regressions between daily total transpiration and CBH^2 over the study period were between 0.60 and 0.71 in the four treatments. These regressions were then used to estimate the daily stand transpiration (E, mm day^{-1}) from the CBH of all the trees in each inner subplot (linearly interpolated between 2 measurements of CBH per year), which made it possible to take into account the changes in distribution of CBH in each stand over the study period. Then the water use efficiency for stemwood production (WUE$_p$) was calculated in each inner subplot as the stem-wood biomass produced divided by the total amount of water transpired over the same period. Since tree biomass was measured at times that do not match the beginning or the end of sap flow measurements, stand stemwood biomass for August 2014, April 2015 and April 2016 was calculated using CBH values interpolated between two consecutive inventories, based on the monthly CBH records available for the trees equipped with sap-flow sensors.

The sapwood area at 1.3 m above the ground was determined by pressurizing water dyed with concentrated liquid dye into the trunk section of 8 trees felled at 4, 5 and 6 years in each treatment. The allometric relationships between tree CBH and sapwood area were determined for each treatment and each age and applied to the CBH inventories of all trees of the experiment to calculate sapwood area index (cm^2_sapwood m^{-2}_ground). Sap flow of each tree (SF) was calculated as the product of SFD and sapwood area estimated from successive measurements of CBH over the study period. The sensors were assumed to measure the instantaneous sap velocity integrated over the average sapwood thickness of each tree. It was not necessary to apply a correcting factor to extrapolate sap flow density to whole-tree sap flux (Delzon et al., 2004) because the sapwood areas of the measured trees never exceeded the length of the sap flow sensor (2 cm).

2.4. Root sap flow

To detect the relative influence of transpiration and HR on root sap flow, root SF was monitored from November 2014 to April 2016 (18 months) in six roots per treatment, corresponding to one root in each of the trees selected for monitoring sap flow. The excavated roots were shallow (< 20 cm deep), horizontal and thicker than 1-cm in diameter and sampled at least 2 m away from the tree trunk to make sure that they were located in the upper soil. The space of the root with installed sensors was protected from sunlight and rainfall with a plastic cap covered with a reflective foil.

Root SF was measured with the same thermal dissipation technique used to determine tree transpiration but modified to allow the direction of flow to be detected (Brooks et al., 2002; Domec et al., 2010). A directional probe was installed in each selected root to detect reversal of flow. The heated temperature sensor was 10 mm in length, and it was

inserted into the xylem in the center of the exposed root. Two unheated reference temperature sensors, also 10 mm in length, were placed axially 8 cm up- and downstream from the heater sensor and wired to measure the temperature differences between the heated and unheated sensors. For the directional probe, two thermocouples were inserted 5 mm axially to a depth of 5 mm up- and downstream from the heated probe (Brooks et al., 2002). The movement of the heated water increases the temperature of the thermocouple closest to the trunk relative to that of the distal thermocouple, providing an accurate measure to direction of flow. Sap flow moving toward the tree was indicated as positive, whereas sap flow moving away from the tree (reverse flow) was indicated as negative. The temperature of the reference probe that was determined to be upstream of the direction of flow was used to calculate root *SF* when the direction of the flow was positive, and the downstream reference probe when there was reverse flow. Root sapwood area was determined by injecting dye with water pressure into the section with sensors of each monitored root. The whole section was stained in all roots, indicating that the whole area was sap-conducting. The reverse volumetric flow rate was calculated as the average of RF velocity (i.e., averaging all RF velocity > 0) over each month.

The sensor signal was converted to *SF* (cm^3 cm^{-2} 30 min^{-1}) using the calibration equation determined for stems (Delgado-Rojas et al., 2010), without taking into account sapwood area. These semi-hourly values were summed up over 24 h to obtain a daily value, accounting positive values as regular flow and negative values as reverse flow.

2.5. Leaf and whole tree hydraulic conductance

Leaf water potential was measured monthly from October 2014 to May 2016 (20 months) in each treatment on four of the same trees used for sap flow (total of 16 sampled trees) with a Scholander-type pressure chamber (PMS Instrument Company, Albany, OR, USA). Measurements were carried out on one fully expanded leaf (approximately two months old and accessed through a scaffold tower) sampled in the upper third of the crown of each tree. Predawn leaf water potential (Ψ_{pdwn}) was measured before sunrise between 6h00 and 7h00. On the same day and on the same four trees, midday leaf water potential (Ψ_{md}) and branch water potential (Ψ_{branch}) were measured between 12h00 and 14h00. Ψ_{branch} was determined from leaves covered with a sealed plastic bag and aluminum foil installed the evening before the measurements. Under these conditions, leaves are not transpiring and the leaf water potential is generally agreed to equilibrate to that of the adjacent xylem (Melcher et al., 1998).

Field leaf hydraulic conductance (K_{leaf}) was calculated as $K_{leaf} = E/(\Psi_{branch} - \Psi_{midday})$, where *E* is the value of transpiration measured with sap flow sensors converted to a tree-scale average transpiration per unit leaf area (*E*, in mmol m^{-2} s^{-1}) (Domec et al., 2009). We used the transpiration values from the same day as Ψ_{midday} and Ψ_{branch} were measured, from 12:30 h to 14:00 h. The leaf-specific tree hydraulic conductance (leaf-specific K_{tree}) that represents the leaf-specific hydraulic conductance of the soil to tree to atmosphere continuum was calculated according to Ohm's law (Cochard et al., 1996, Loustau et al. 1998) as $K_{tree} = E/(\Psi_{pdwn} - \Psi_{midday})$. The sapwood-specific K_{tree} was calculated with the same equation than for leaf-specific K_{tree} but normalizing *E* for sapwood area index instead of leaf area index.

2.6. Soil water storage and water table

Soil volumetric water content was measured with three TDR probes per soil layer (CS616 and CS650, Campbell Scientific Inc., Logan, UT, USA) installed at depths of 0.15, 0.50, 1, 1.5, 3, 4.5, 6, and 8 m in each subplot in block 1. In addition, 3 probes CS616 were also installed at 10, 12, 14 and 17 m depth in the subplots of the treatments + K + W and + K-W. Probes were calibrated by gravimetric soil water content and bulk density measurements. Volumetric soil water contents were continuously measured every 30 s from August 2014 to April 2016.

There was a loss of data from February to October 2015 for treatments -K + W and -K-W due to technical problems.

The depth of the water table was monitored at the subplots of + K + W and + K-W in block 1 with piezometers located 18.9 and 19.9 m deep, respectively. Data were collected every hour and showed that the water table varied from 18.01 to 16.52 m in + K + W and from 17.06 to 17.16 m in + K-W, from the beginning to the end of the study.

2.7. Photosynthetic measurements

Photosynthetic net CO$_2$ assimilation rate as a function of intercellular CO$_2$ (C$_i$) concentration (A-C$_i$ curves; Long and Bernacchi, 2003)) was measured on 1- to 2-month-old leaves. Measurements were carried out in four leaves per treatment with a Li-Cor 6400 portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) on May 2016. During field measurements, the CO$_2$ concentration in the gas exchange chamber was reduced from 400 to 300, 250, 200, 150, 100, 75 and 50 µmol CO$_2$ mol^{-1}, and then increased from 50 to 400, 600, 800, 1000, 1300 and 1600 µmol CO$_2$ mol^{-1}. These measurements were carried out at a constant photosynthetic photon flux density (PPFD) of 1600 µmol m^{-2} s^{-1}, ambient relative humidity (60–75 %) and leaf temperature of 25 °C. From these A-C$_i$ curves, the maximum photosynthetic rate at ambient CO$_2$ concentration (400 µmol CO$_2$ mol^{-1}) and saturating PPFD (A$_{max}$), the mesophyll conductance to CO$_2$ (g$_m$), the maximum rate of RubiscO-catalysed carboxylation (V$_{c,max}$), the ribulose bisphosphate (RuBP) regeneration rate controlled by the electron transport rate at saturating PPFD (J$_{sat}$), and the RuBP regeneration rate controlled by the triose phosphate utilization (TPU), as defined by Farquhar et al. (1980) and Harley et al. (1992), were estimated using the Sharkey et al. (2007) curve fitting utility software (version 1.2).

2.8. Statistical analyses

In order to explore the significance of the treatment effects on the studied variables, mixed-effect models were used. The water supply (W), fertilization (F) treatments, as well as stand age, season (wet vs dry), W x F, W x stand age, F x stand age and W x K x stand age were included as fixed effects. Studied variables were stand transpiration, WUE$_p$, LAI, stand transpiration per m^{2}leaf, wood increment per LAI, leaf area per sapwood area ratio, leaf-specific K_{tree}, sapwood, sapwood-specific K_{tree}, daily reverse flow velocity, daily reverse volumetric flow rate, number of days with reverse flow, and number of roots with RF. Blocks and water supply x block were considered as random effects, consistently with the split-plot design of the experiment, and the residuals were modeled by a first-order autoregressive correlation model to account for the correlations between sampling dates. For reverse flow variables, monitored roots and water supply x roots were considered as random effects. In order to evaluate weather treatment modalities had significantly different values for a given variable, post-hoc tests were done. In case of homogeneity of variance, a least significant difference test (LSD) was carried out. If there was no homogeneity, Dunnett's T3 test was performed. A value of 0.05 was used as the level of significance for all tests. All statistical analyses were carried out using the software SPSS Statistics for Windows, version 15.0 (SPSS Inc., Chicago, Ill., USA).

3. Results

3.1. Tree transpiration

While K fertilization greatly increased tree transpiration, the effect of throughfall reduction was not significant (Fig. 1, Table 1). The amounts of water transpired by *Eucalyptus grandis* trees were 30 % to 50 % higher in the plots fertilized with K (+K) than in the unfertilized plots (−K) under ambient precipitation regime (water control treatment; +W) over the studied period (Fig. 1a, Fig. S1, Table S1). Under
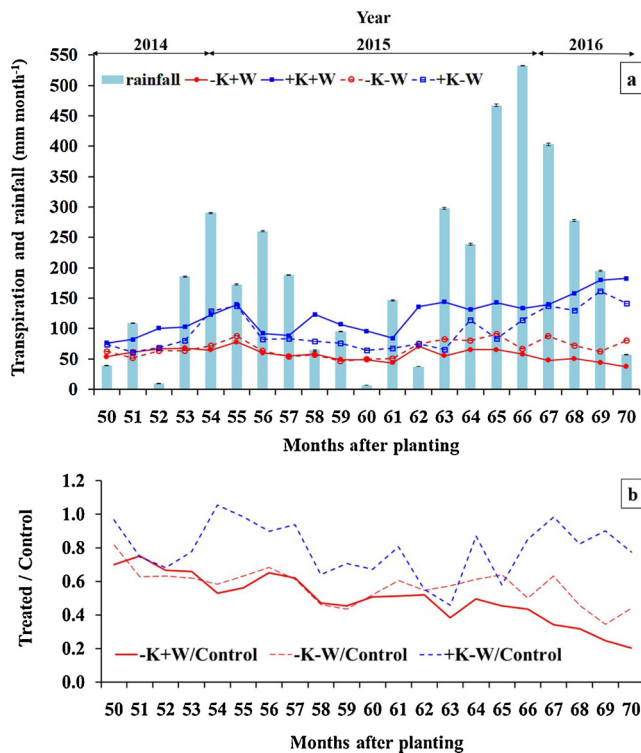
Fig. 1. (a) Monthly rainfall and stand transpiration in *Eucalyptus grandis* plots at the Itatinga experimental site, and (b) ratio between the monthly sap flow measured in treatment plots (- K + W, -K-W, +K-W) and in control plots (+K + W), from August 2014 to April 2016 (50–70 months after planting). Each point in figure "a" is the sum of 30–31 daily values (SE for monthly transpiration were always lower than 0.50 mm and are not shown on the figures). Applied treatments were: K fertilization and undisturbed rainfall as in adjacent commercial plantations (+K + W, control), neither K fertilization nor throughfall exclusion (-K + W), no K application and 37% throughfall exclusion (-K-W), K fertilization and 37% throughfall exclusion (+K-W).

37% throughfall exclusion ($-$W), the amounts of water transpired were similar in plots with and without K addition (Fig. 1a, Table S1). Most of the time, tree transpiration was higher in $+$K$-$W than in $-$K + W, although throughfall was reduced by 37 %. The ratios of monthly transpiration between plots without K fertilization ($-$K) and the control treatment representative of nearby commercial plantations (+K + W) highlighted that: i) transpiration in plots without K fertilization was

always lower than in the $+$K + W plots, and ii) this difference increased over time (Fig. 1b). Stand transpiration was significantly influenced by stand age (Table 1). The ratio of stand transpiration between $+$K$-$W and the control treatment (+K + W) shows that throughfall exclusion decreased the transpiration in plots fertilized with K, especially over dry periods. Stand transpiration was significantly influenced by the seasons (Table 1). At the end of the dry seasons or at the beginning of the wet ones, the ratios of stand transpiration between $+$K$-$W and $-$K treatments were similar (Fig. 1b). It was expected that the amount of water transpired be considerably higher in wet than in dry seasons, but it only happened in $+$ K-W plots. In the other treatments, there were significant differences in transpiration only in some months (P < 0.05) (Table S1). It was observed that in $+$ K + W, transpiration from month 62 to the end of the rotation was significantly higher than in previous months, even in the months of dry season (62 and 63). In all treatments, we detected small amount of night-time trunk water movement over the whole study period (Fig. S2).

3.2. Water use efficiency of Eucalyptus

Tree transpiration was positively correlated to wood increment for $+$ K treatments only (P < 0.05) (Fig. 2a). K deficiency strongly decreased WUE for wood production (WUE$_p$): in -K plots WUE$_p$ was only a quarter of that in $+$ K plots (Fig. 2b). By contrast, WUE$_p$ was not significantly affected by throughfall exclusion whatever the K supply regime (Fig. 2b, Table 1).

Potassium significantly increased leaf area (LAI) and sapwood area index (Table 1) (Fig. S4). Trees in $+$ K plots exhibited higher leaf area to sapwood area ratios than trees in -K (Fig. 3a). On the other hand, those trees fertilized with K showed lower tree water use per unit of leaf area (Fig. 3b), and higher growth efficiency (wood production per leaf area; Fig. 3c), than trees in -K plots. Neither potassium fertilization nor throughfall exclusion had significant effect on leaf or whole-tree hydraulic conductances (K_{leaf} and K_{tree}, respectively; in Fig. 4a–c).

3.3. Root sap flow and hydraulic redistribution (HR) over 18 months

Reverse sap flow in roots (RF, away from the trunk) indicated the occurrence of HR. We detected RF every month for 18 continuous months in the $+$ W plots (Fig. 5, Table S2). Roots in the -W plots showed RF all months except in November and December of both years in -K-W, and December 2015 and February 2016 in $+$ K-W. Those months corresponded to wet periods. We also observed that all monitored roots (6 per treatment) had RF, at least for a few days. In some days with high transpiration rates, we also detected RF during the day

Table 1

P-values for the effects of fertilization regime (F, control, supply of K), water supply regime (W, undisturbed rainfall vs 37% of throughfall exclusion), stand age (age), season (wet vs dry), interaction between water supply and fertilization (F x W), fertilization and stand age (F x age), water supply and stand age (W x age), among water supply, fertilization and stand age (W x F x age) on: stand transpiration, water use efficiency for stem wood production (WUEp), leaf area index (LAI), sapwood area index, leaf area per sapwood area (Al/As), sap flow per leaf area (SF/Al), wood increment per leaf area (wood/Al), daily reverse flow velocity (RF vel), daily reverse volumetric flow rate (RF vol), and number of days with reverse flow (RF days) for *Eucalyptus grandis* trees in a split-plot design.

	F	W	F x W	Age	F x Age	W x Age	F x W x Age	Season
Transpiration	< 0.001	0.695	0.042	< 0.001	< 0.001	0.880	0.011	< 0.001
WUE$_p$	< 0.001	0.208	0.149	< 0.001	< 0.001	0.129	0.148	–
LAI	< 0.001	< 0.001	< 0.001	0.456	0.491	< 0.001	< 0.001	–
Sapwood	0.007	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	–
Al/As	< 0.001	< 0.001	< 0.001	< 0.001	0.006	< 0.001	< 0.001	–
SF/Al	< 0.001	< 0.001	< 0.001	0.010	< 0.001	< 0.001	< 0.001	–
Wood/Al	0.101	0.057	< 0.001	< 0.001	0.011	0.070	0.001	–
RF vel	0.750	0.579	0.844	0.072	0.597	0.634	0.846	0.347
RF vol	0.367	0.758	0.339	0.034	0.418	0.817	0.383	0.126
RF days	0.354	0.141	0.204	0.757	0.257	0.208	0.222	0.002

Transpiration is shown in Fig. 1 and S1, WUE$_p$ in Fig. 2b, LAI and sapwood area in Fig. S4, leaf area per sapwood in Fig. 3a, sap flow per leaf area in Fig. 3b, wood increment per leaf area in Fig. 3c, daily reverse flow velocity in Fig. 5, daily reverse volumetric flow rate in Table S2, and number of days with reverse flow in Table S3. Dash lines means there is no factor "season" for those variables.
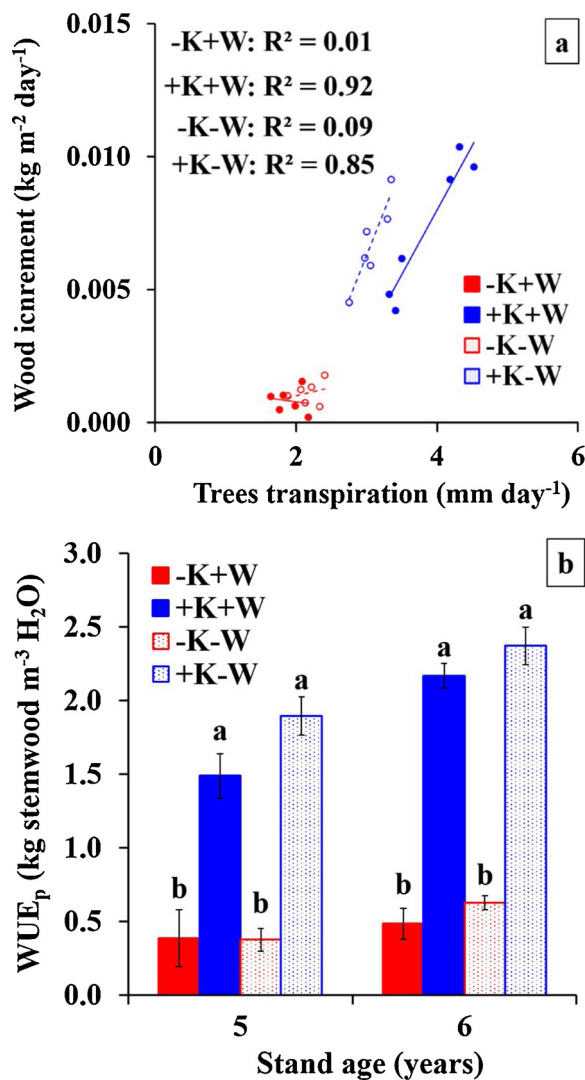
Fig. 2. (a) Mean daily wood increment in relation to mean daily tree transpiration in each plot (3 plots per treatment, and 2 measurement periods), and **(b)** water use efficiency for stem wood production (WUE$_p$) of each treatment for the last two years before harvesting (5th and 6th). Calculations for the 5th year were made without the first three months of the year due to the unavailability of sap flow data. Values are the mean ± SE (n = 3). Within each year, bars with different letters are significantly different (P < 0.05). The treatments were: K fertilization and undisturbed rainfall (+K + W), no K fertilization and undisturbed rainfall (-K + W), no K application and 37% throughfall exclusion (-K-W), K fertilization and 37% throughfall exclusion (+K-W).

in some roots, with sometimes maximum reverse flow occurring even at midday (Fig. S3).

Neither potassium fertilization nor throughfall exclusion significantly affected RF velocity (Table 1). Nevertheless, we observed that during the dry season (months 60–63), and month 70 (low rainfall), when is expected the highest RF of the year, daily RF was always higher in + K plots than in -K plots, and it was generally higher in + W plots than in -W plots (Fig. 5). Such increase in RF velocity during dry periods was especially evident in + K + W.

In order to observe the capacity of roots to transport water away from the trunk, their reverse volumetric flow rates were calculated (Table S2). Neither potassium fertilization nor throughfall exclusion had an effect on the reverse volumetric flow rate (Table 1). Nevertheless, we observed that potassium fertilization tended to increase the reverse volumetric flow rate, especially in dry season (Table S2). The number of days with RF (Table S3) was also not influenced by
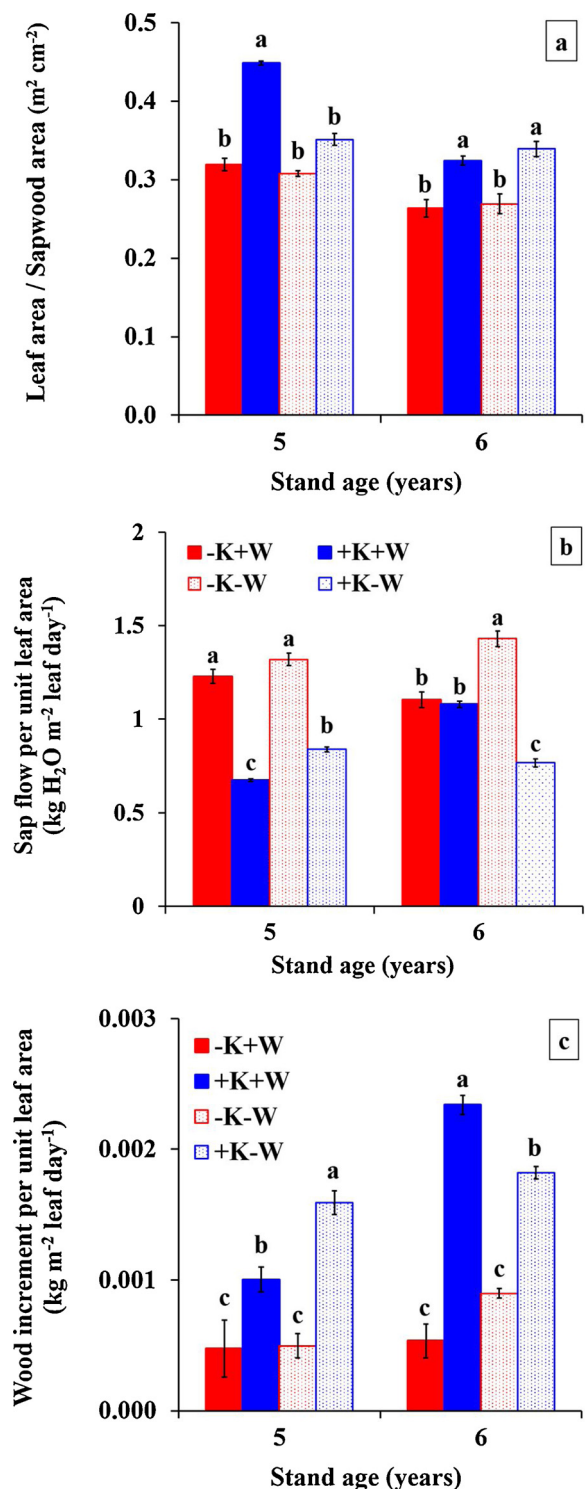

Fig. 3. Water and potassium fertilization effects on **(a)** leaf area index (LAI) per sapwood area, **(b)** daily tree water use, and **(c)** daily wood increment on a leaf area basis 5 and 6 years after planting. Calculations for the 5th year were made without the first three months of the year due to the unavailability of sap flow data. Values are the mean ± SE (n = 3). Within each year, bars with different letters are significantly different (P < 0.05). Applied treatments were: K fertilization and undisturbed rainfall (+K + W), no K fertilization and undisturbed rainfall (- K + W), no K application and 37% rainfall exclusion (-K-W), K fertilization and 37% rainfall exclusion (+K-W).
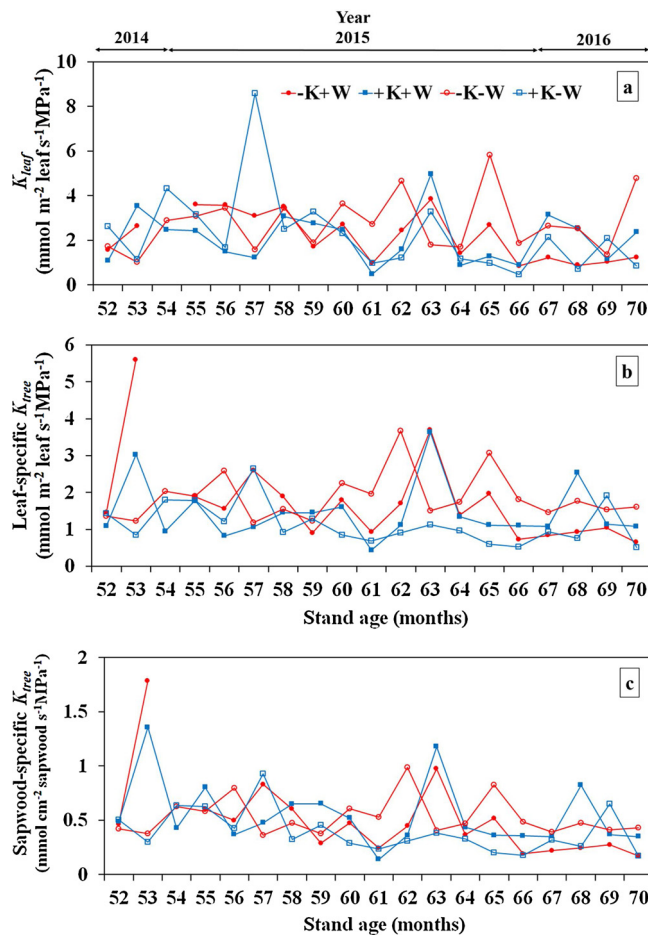
Fig. 4. Effect of water supply and potassium treatments on the seasonal variation in **(a)** leaf hydraulic conductance (K_{leaf}) and **(b)** leaf-specific whole-tree hydraulic conductance (K_{tree}), and **(c)** sapwood-specific K_{tree} of *Eucalyptus grandis* from October 2014 to May 2016 (56 to 72 months after planting). Applied treatments were: K fertilization and undisturbed rainfall (+K + W), no K fertilization and undisturbed rainfall (-K + W), no K application and 37% throughfall exclusion (-K-W), K fertilization and 37% throughfall exclusion (+K-W).
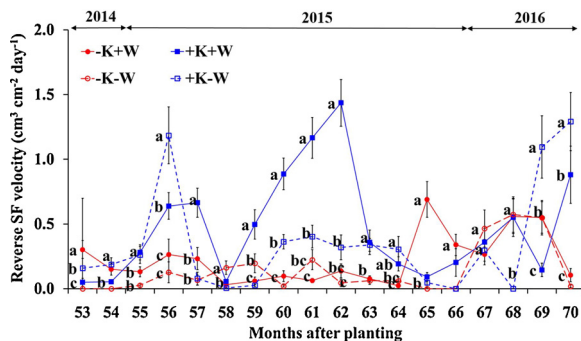

Fig. 5. Average daily reverse sap flow (*SF*) velocity per month in horizontal coarse roots of *Eucalyptus grandis* trees measured in the topsoil between November 2014 and April 2016 in the control (+W) and 37% throughfall exclusion (-W) plots, and with (+K) or without (-K) potassium addition. Values are the mean ± SE (n = 180 or 186). Monthly values with different letters are significantly different (P < 0.05).

potassium or water regime (Table 1). On the other hand, throughfall exclusion seemed to induce a decrease in the number of roots with RF per month (Table S4), since more roots exhibited RF in the + W plots than in -W plots, and so for almost all months except two from the wet

season.

3.4. Soil water and water table dynamics

Soil water storage was higher in the -K plots than in the + K plots, from soil surface to 17 m in depth over the studied period (Fig. 6 a–d). Soil water storage was also higher under + W than under -W. It can be observed the differences in soil water content between treatments increased with soil depth. It can also be observed that from 7 to 17 m in depth, the soil water storage varied over time in -K plots, whereas it was more stable in + K plots.

Water table level was always deeper in the throughfall exclusion plots than in the control plots (Fig. 6e). The deepest level of the water table during the experiment was measured at the end of the dry season (November of 2015) and reached 18 m in + K + W plots and 19 m in + K–W plots. The shallowest level was 16.5 m in + K + W and 17.2 m in + K–W, at the end of the rainy season 2016 (April).

3.5. Photosynthetic efficiency

The maximum photosynthetic rate (A_{max}), V_{cmax}, J_{sat} and TPU were significantly higher in treatments with K fertilization (Table 2). Throughfall exclusion did not significantly affect any parameters derived from the A-C_i curves (P > 0.23). Mesophyll conductance (g_m) was similar in all treatments except in -K + W, where it was significantly lower (Table 2).

4. Discussion

4.1. Occurrence of hydraulic redistribution (HR)

In line with our first hypothesis, HR was observed in the studied *Eucalyptus grandis* plantation. The most unexpected result of this study was the presence of HR over the entire year, even during the rainy seasons, when superficial soil layers were wet (Fig. 6). Just a few studies detected HR after large rain events (Burgess, 2006; Bleby et al., 2010), and hypothesized that it was the consequence of soil moisture variability with some soil patches remaining dry after rainfall events. Interestingly, in some days we observed unexpected HR during the day, which indicates that water potential gradients from shallow soil to leaf during canopy transpiration must be sometimes equivalent or slightly smaller than between soil layers within the rooting zone (Fig. S3). Since canopy transpiration was high at the same period that reverse flow was detected, daytime HR was not caused by cloudy conditions. Specifically, we can hypothesize that daytime HR was probably localized in shallow roots that were highly connected to the deep taproot system. When water potentials gradients in the trunk and in the shallow roots reached equilibrium (probably before noon in Fig. S3), then water moved from deep soil layers to the trunk and then to the leaves, and in the meantime from deep soil roots to shallow roots. Daytime HR was observed in other tree species by Bleby et al. (2010), who suggested that it was caused by a mosaic of patchy dry soil, and the creation of such water potentials gradient but within shallow soil layers. Hultine et al. (2003) also suggested that daytime HR might occur in plants that are highly vulnerable to xylem embolism in order to prevent high loss of conductivity, which could be of importance for *E. grandis* since it has been reported to be less tolerant to drought than sub-humid *Eucalyptus* species (Bourne et al., 2017). Another hypothesis explaining HR during the day when tree transpiration rates were high could be linked to the existence of direct (physical) or indirect (mycorrhizae) mechanical connections between roots from the same tree or, but less likely (Laclau et al. personal communication), from two neighboring trees (Lev-Yadun, 2011; Paula et al., 2015). If those anastomoses involved roots with different absorption rates, then an imbalance flow could have been created between them, thus inducing reverse flow (Warren et al., 2008).

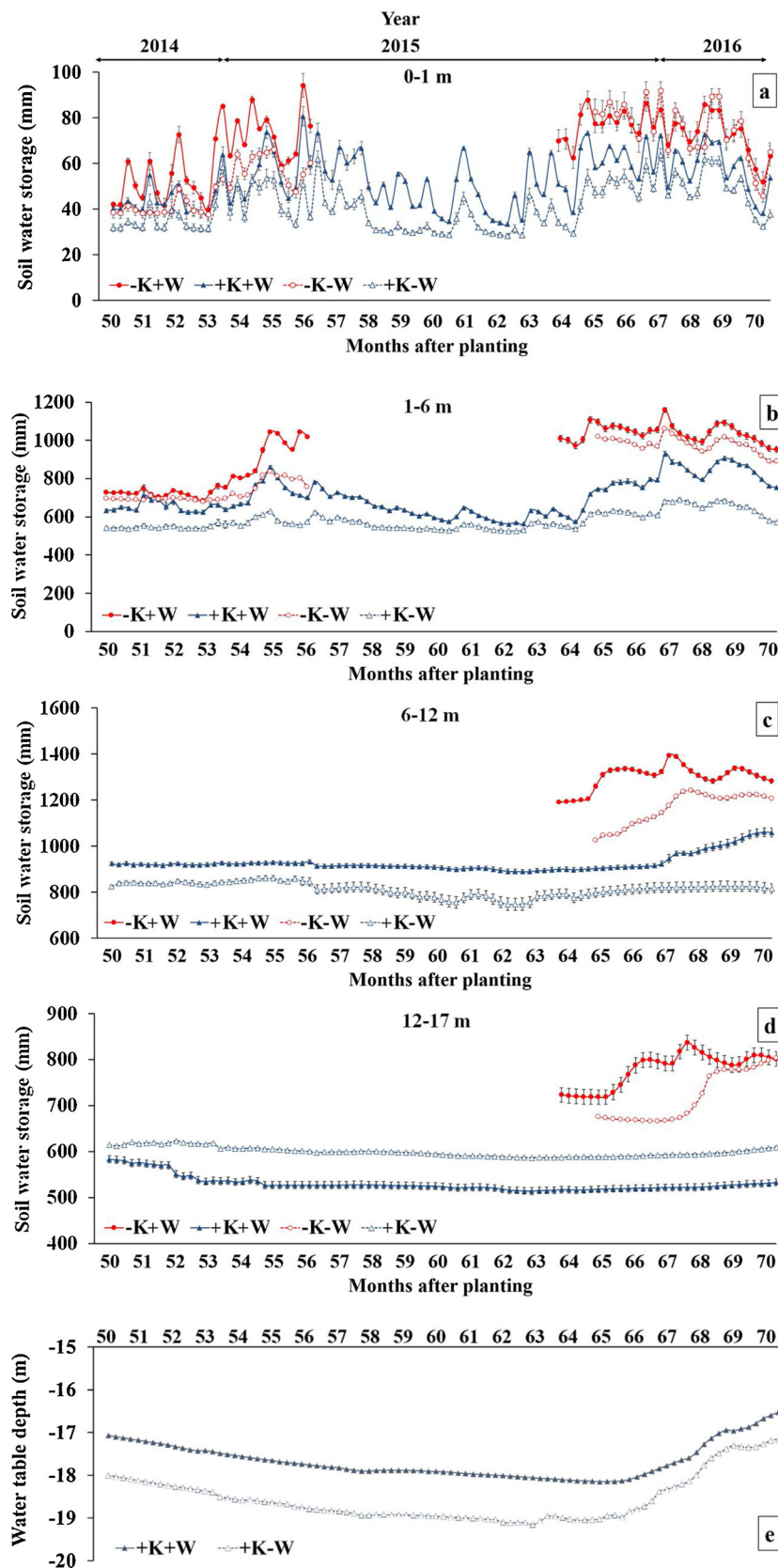Most of the HR measured in this study was probably water

Fig. 6. Soil water storage from August 2014 (month 50) to April 2016 (month 70) in four different soil layers ranging from the soil surface to a depth of 17 m (**a, b, c and d**) in the control (+W) and throughfall exclusion (-W) plots, with (+K) or without (-K) potassium addition. Water table depth over the same period in the + K + W and + K-W plots is shown (**e**). Values are the mean ± SE (n = 3).

Table 2

Effects of potassium (+K) and 37 % throughfall exclusion (-W) on photosynthetic capacity parameters and mesophyll conductance (g_m). Mean values were calculated from the A-Ci curves and normalized at 25 °C.

	Treatment			
	-K + W	+K + W	-K-W	+ K-W
A_{max} (µmol CO_2 m^{-2} s^{-1})	20.1 ± 0.9 b	28.2 ± 2.2 a	19.6 ± 1.7 b	29.3 ± 2.5 a
$V_{c,max}$ (µmol CO_2 m^{-2} s^{-1})	82.1 ± 8.7 ab	100 ± 4.2 a	75.7 ± 7.8 b	103 ± 7.3 a
J_{sat} (µmol CO_2 m^{-2} s^{-1})	102 ± 6.1 b	138 ± 11 a	100 ± 8.6 b	147 ± 12 a
TPU (µmol CO_2 m^{-2} s^{-1})	5.3 ± 0.4 bc	7.6 ± 0.8 ab	4.8 ± 0.5 c	8.1 ± 0.9 a
R_d (µmol CO_2 m^{-2} s^{-1})	1.7 ± 0.01 a	1.7 ± 0.003 a	1.7 ± 0.003 a	1.7 ± 0 a
g_m (µmol CO_2 m^{-2} s^{-1} Pa^{-1})	16.7 ± 7.9 b	30.1 ± 0.1 a	30.1 ± 0.1 a	30.0 ± 0 a

Different letters within a row indicate significantly differences between treatments (P < 0.05).

A_{max}: maximum photosynthetic rate at saturating PPFD; $V_{c,max}$: photosynthetic RuBisCO capacity per unit leaf area; J_{sat}: potential electron transport rate per unit leaf area; TPU: triose phosphate utilization per unit leaf area; Rd: rate of mitochondrial respiration in the light.

hydraulically lifted (hydraulic lift) because top soil layers were drier than deep soil layers (Fig. 6), which likely created soil water potential gradients strong enough to move water up. In addition, for a given soil layers, soil structure and root density were homogeneous and therefore water potential gradients at a given depth were probably small. Consequently, the reverse flow that was measured in the topsoil (Fig. 5) was probably the consequence of water moving from deep to shallow roots and then to the shallow soil.

The results did not agree with our second hypothesis: RF velocity did not significantly increase in plots with potassium fertilization (+K) (Fig. 5). Another unexpected result was that trees under throughfall exclusion (−W) did not exhibit higher reverse flow (RF) than trees without (+W), and RF was even lower in −W in some of the months (Fig. 5, Table S2). We hypothesized that throughfall exclusion would increase the amount of water transported by HR because of a decrease in water storage in superficial soil layers (Fig. 6). Our results could be attributed to the fact that in all treatments, roots reached a permanent source of water by tapping directly into the water table (Johnson et al., 2014; Germon et al., 2019), which could explained why RF in some roots was also sometimes quantified during the day (Fig S3). However, if roots reached the water table, then why did hydraulic lift and redistribution occur? On one hand, we hypothesize that the amount of water they can take up from the water table is limited due to the low root biomass located at that depth (Germon et al., 2019). For that reason, eucalypt trees still need to take up a considerable amount of water from other soil layers, as shown by Christina et al. (2017) at a nearby site. In our study, HR probably helped keep the fine roots of eucalyptus alive during dry seasons, which is important to maintain a high water and nutrients uptake capacity (Richards and Caldwell, 1987; Scholz et al., 2008), and to prevent embolism (Domec et al., 2004; Scott et al., 2008). The maintenance of a wide superficial root system also allows a rapid uptake of soil water after small rainfall events (Burgess et al., 1998; Bleby et al., 2010).

Our results showed that neither potassium fertilization nor throughfall exclusion significantly affected the volumetric capacity of roots for transporting water away from the trunk (Table S2) nor the number of days with RF per month (Table S3). This reinforces the importance of long-term hydraulic redistribution monitoring, in addition to root system trait measurements, for our understanding of water use in forests.

4.2. Water use efficiency for biomass production (WUEp)

Despite a negative rainfall-transpiration balance was reached one month earlier in + K than in -K plots (data not shown), and soil water storage was lower in + K over the studied period (Fig. 6), tree transpiration was always higher under + K than in -K plots, likely as a result of much higher LAI (Fig. S4a), which increases water demand, and higher sapwood area (Fig. S4b), which increases the water

transport capacity of K fertilized trees.

K fertilization promoted an increase in wood production, which was proportionally much higher than the increase in transpiration, thus strongly enhancing water-use efficiency (Fig. 2b). In fact, our WUE_p values in plots with + K, even with 37% throughfall exclusion, were similar to the values observed in other *Eucalyptus* plantations without water deficit (Forrester et al., 2010; Maier et al., 2017). This result indicates not only that potassium increased WUE_p, but also that a decrease of throughfall until 37 % did not significantly affect that efficiency.

The annual tree transpiration did not increase over the period of six years in any treatment (the first three years are published in Battie-Laclau et al., 2016), and WUE_p slightly increased in the second half of the rotation with respect to the first in plots with potassium fertilization. Therefore, after six growing seasons, we observed that: 1) K fertilization enhanced WUE_p over time, and that 2) throughfall exclusion had no effect on WUE_p. We postulate that the increment in WUE_p may result from a preferential partitioning of biomass toward stemwood, at the expense of roots or leaves. At the same study site in Brazil, Epron et al. (2012) showed that K fertilization increased both wood production and the fraction of carbon allocated aboveground in *E. grandis* plantations at the end of the rotation. According to the optimal partitioning theory (OPT), plants allocate additional biomass to the organ that takes up the resource that most limits growth (Bloom et al., 1985). Field studies showed that plants allocate relatively more carbon to shoots under light limitation and to roots under water and/or nutrient limitation (Lapenis et al., 2013; Doughty et al., 2014; Girardin et al., 2016). A change in the partitioning of biomass in favor of stemwood in the studied *Eucalyptus* stands fertilized with K was likely because of two reasons. First, K fertilization increased leaf longevity (Battie-Laclau et al., 2013) and decreased limitations in the use of light through an increase in the photosynthetic efficiency (Table 2), so trees with + K allocated less biomass in leaves at the end of the rotation. In fact, K fertilization increased the ratio between wood increment to leaf area (Fig. 3c). Second, trees did not need to allocate too much biomass belowground because roots probably reached water table. Root biomass production in *Eucalyptus* growing on deep Ferralsols under tropical climate is usually high in the first years of growth (Laclau et al., 2013; Pinheiro et al., 2016), which probably contributed to decrease water supply limitation at the end of the rotation in our plantation.

5. Conclusions

Hydraulic redistribution (probably lift) occurred in the *Eucalyptus grandis* plantation during the last two years of the rotation cycle, with or without potassium fertilization and 37% throughfall exclusion, and even after large rain events. Neither potassium fertilization nor throughfall exclusion affected the velocity of water transported by HR, probably because most trees reached water table. Potassium

fertilization increased the water use efficiency for stemwood production. This increase was associated to an increase in the photosynthetic efficiency, LAI and sapwood area index, but not leaf nor whole-tree hydraulic conductance. Even if potassium fertilization can lead to higher risk of hydraulic dysfunction in *Eucalyptus* under extreme water deficit, hydraulic redistribution can help fertilized trees to grow during dry periods. Our results indicate that fertilizing *E. grandis* with potassium is beneficial to increase both wood biomass production and WUE$_p$, even with a 37% decrease in throughfall, when the deepest roots have access to water stored in the subsoil.

Authors' contributions

JPL, JPB and YN conceived the experiment and provided the study site. JPL, JPB, YN, CHAJ and VA got funding. VA and JDR implemented the methodologies with the assistance of JPB, CHAJ and YN. VA and JDR made data collection. VA made data curation and processing under the supervision of JCD, JDR and JG. VA made statistical analyses under the supervision of JG. VA wrote the original draft of the manuscript and all authors review and edited it. All authors have read and approved the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.envexpbot.2020.104085.

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