



## Potassium fertilization increases water-use efficiency for stem biomass production without affecting intrinsic water-use efficiency in *Eucalyptus grandis* plantations



Patricia Battie-Laclau<sup>a</sup>, Juan Sinforiano Delgado-Rojas<sup>b</sup>, Mathias Christina<sup>c</sup>, Yann Nouvellon<sup>c,e</sup>, Jean-Pierre Bouillet<sup>b,c</sup>, Marisa de Cassia Piccolo<sup>a</sup>, Marcelo Zacharias Moreira<sup>a</sup>, José Leonardo de Moraes Gonçalves<sup>b</sup>, Olivier Roupsard<sup>c,f</sup>, Jean-Paul Laclau<sup>b,c,d,\*</sup>

<sup>a</sup> Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, CEP 13400-970 Piracicaba, SP, Brazil

<sup>b</sup> Departamento de Ciências Florestais, Escola Superior de Agricultura Luis de Queiroz, Universidade de São Paulo, CEP 13418-900 Piracicaba, SP, Brazil

<sup>c</sup> CIRAD, UMR Eco&Sols, 2 Place Viala, 34060 Montpellier, France

<sup>d</sup> Departamento de Ciência Florestal, Universidade Estadual de São Paulo "Júlio de Mesquita Filho", CEP 18610-300 Botucatu, SP, Brazil

<sup>e</sup> Departamento de Ciências Atmosféricas, IAG, Universidade de São Paulo, CEP 05508-900 São Paulo, SP, Brazil

<sup>f</sup> CATIE, Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba 30501, Costa Rica

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### ABSTRACT

Adaptive strategies to improve tree water-use efficiency (WUE) are required to meet the global demand for wood in a future drier climate. A large-scale throughfall exclusion experiment was set up in Brazil to study the interaction between water status and potassium (K) or sodium (Na) availability on the ecophysiology of *Eucalyptus grandis* trees. This experiment focused primarily on the changes in aboveground net primary production, stand water use, phloem sap and leaf  $\delta^{13}\text{C}$ , net  $\text{CO}_2$  assimilation and stomatal conductance. The correlations between these response variables were determined to gain insight into the factors controlling water-use efficiency in tropical eucalypt plantations. The intrinsic WUE in individual leaves (the ratio of net  $\text{CO}_2$  assimilation to stomatal conductance) was estimated at a very short time scale from the leaf gas exchange. Sap flow measurements were carried out to assess the WUE for stemwood production (the ratio of wood biomass increment to stand water use).

Averaged over the two water supply regimes, the stemwood biomass 3 years after planting was 173% higher in trees fertilized with K and 79% higher in trees fertilized with Na than in trees with no K and Na addition. Excluding 37% of the throughfall reduced stemwood production only for trees fertilized with K. Total canopy transpiration between 1 and 3 years after planting increased from about 750 to 1300  $\text{mm y}^{-1}$  in response to K fertilization with a low influence of the water supply regime. K fertilization increased WUE for stemwood production by approx. 60% with or without throughfall exclusion. There was a strong positive correlation between phloem sap  $\delta^{13}\text{C}$  and short-term leaf-level intrinsic WUE. Whatever the water and nutrient supply regime, the gas exchange WUE estimates were not correlated with WUE for stemwood production. Phloem sap  $\delta^{13}\text{C}$  and leaf  $\delta^{13}\text{C}$  were therefore not valuable proxies of WUE for stemwood production. The allocation pattern in response to nutrient and water supply appeared to be a major driver of WUE for stemwood production. In areas with very deep tropical soils and annual rainfall <1500 mm, our results suggest that breeding programs selecting the eucalypt clones with the highest growth rates tend to select the genotypes with the highest water-use efficiency for wood production.

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### 1. Introduction

In the future, climate changes are likely to result in a reduction in rainfall in most tropical regions where fast-growing tree plantations have been established (IPCC, 2013; Hawkins and Sutton,

\* Corresponding author at: CIRAD, UMR Eco&Sols, 2 Place Viala, 34060 Montpellier, France.

E-mail address: [laclau@cirad.fr](mailto:laclau@cirad.fr) (J.-P. Laclau).

2012), which will affect tree growth and patterns of water use (Wu et al., 2011). As high productivity implies high levels of water use, these planted forests are likely to be particularly affected by severe drought periods (Allen et al., 2010). Given the general increase in world demand for wood products (FAO, 2014), adaptive strategies providing both high growth potential and tolerance to water deficit are urgently needed to manage productive planted forests. Throughfall exclusion experiments using plastic panels to prevent a percentage of the total canopy throughfall from reaching the soil have been undertaken to examine the tree response to drought in temperate (e.g. Hanson et al., 2001) and tropical forests (e.g. da Costa et al., 2010). However, large-scale throughfall exclusion experiments have never been carried out in tropical planted forests to study the physiological adjustment mechanisms of trees in response to a combination of nutrient availability and water stress (Wu et al., 2011).

Tree water-use efficiency (WUE) is a critical parameter used for evaluating tree performance and exploring options for saving water (Monclus et al., 2006; Cernusak et al., 2007; King et al., 2013; Lévesque et al., 2014). Greater understanding of the mechanisms driving tree WUE is required for adapting management practices in areas subject to water shortage. Water-use efficiency is a conceptually simple parameter that, in general terms, defines the ability of the ecosystem to capture carbon and produce biomass as a function of water use. Measuring WUE is, however, methodologically challenging because this trait can be estimated in various ways and on various spatial and temporal scales (Hsiao, 1973; Binkley et al., 2004; Ripullone et al., 2004; Seibt et al., 2008). At a very short time scale, the intrinsic WUE in individual leaves ( $WUE_i$ , the ratio of the net  $CO_2$  assimilation,  $A$ , to the stomatal conductance,  $g_s$ ) can be calculated using measurements of the instantaneous gas exchange through the leaves (Osmond et al., 1980). Leaf WUE can also be estimated at longer time scale using the isotope signature of the carbon incorporated in the leaves over their deployment (leaf  $\delta^{13}C$ , proxy of integrated  $CO_2$  assimilation over stomatal conductance), assuming a strong positive correlation between leaf  $\delta^{13}C$  and  $WUE_i$  as observed in cereals (Farquhar and Richards, 1984) and trees (Ponton et al., 2002; Monclus et al., 2006; Cernusak et al., 2007). However, the time series of leaf  $\delta^{13}C$  cannot be used on its own as a reliable indicator of changes in plant WUE without independent estimates of gas exchange and environmental conditions occurring over leaf construction (Seibt et al., 2008). The phloem sap  $\delta^{13}C$  (proxy of crown  $CO_2$  assimilation over tree water use) has been used as an integrative indicator of short term changes (few last days) in WUE at canopy level (Cernusak et al., 2003, 2007, 2013; Keitel et al., 2003, 2006; Merchant et al., 2010; Rascher et al., 2010). As phloem sugar concentration has been found to be closely correlated with phloem sap  $\delta^{13}C$ , phloem sugar concentration has been proposed as a reliable surrogate for phloem sap  $\delta^{13}C$  and, therefore, for WUE in eucalypt trees (Tausz et al., 2008). At stand scale, water-use efficiency for stemwood production, defined as the ratio of stemwood biomass increment to water transpired over the same period, is a highly integrative indicator taking into account all events occurring during biomass accumulation (Law et al., 2002). Because intrinsic WUE in individual leaves and WUE to produce wood may respond differently to environmental conditions (Lindroth and Cienciala, 1996; Binkley et al., 2004; Niu et al., 2011), WUE must be studied at various scales to provide more information on the sources of spatio-temporal variations.

WUE is implicitly sensitive to environmental conditions and consequently to environmental changes. Water and nutrient availability strongly affect growth as well as resource use efficiency and biomass partitioning in planted forests (Binkley et al., 2004; Stape

et al., 2004; Beer et al., 2009; White et al., 2014). An increase in resource availability is likely to increase tree productivity and WUE for wood production by shifting the  $A:g_s$  ratio in favor of  $A$  (increasing  $WUE_i$ ) and/or by shifting biomass partitioning to aboveground tree components (Litton et al., 2007; Ryan et al., 2010). Whereas a water deficit often leads to an increase in  $WUE_i$  through stomatal closure (Bréda et al., 2006; Ainsworth and Long, 2005), it tends to lead to a decrease in WUE for wood production by increasing the fraction of the  $CO_2$  assimilated that is allocated to the roots (Litton and Giardina, 2008; Franklin et al., 2012). Olbrich et al. (1993) showed that large differences in WUE for wood production among four *Eucalyptus grandis* clones growing at the same site in South Africa were the result of differences in growth rates rather than transpiration rates. However, there are few comprehensive field studies combining measurements of WUE at different scales with different water supply regimes in tree plantations (White et al., 2009a, 2014; Albaugh et al., 2013). Ways of improving tree WUE in areas subject to water deficit must be found, which requires a quantitative understanding of the physiological responses to water stress (Dvorak, 2012; Marguerit et al., 2014). Nutrient supply may improve WUE in plants subject to water shortages (Cakmak, 2005). Potassium (K) and sodium (Na) fertilizations increased  $WUE_i$  in cacao plants (Gattward et al., 2012) and olive trees (Erel et al., 2014). Although high concentrations of salt in soils significantly reduce the yields of agricultural crops (Munns, 2005), Na may replace K for various physiological functions (Wakeel et al., 2011; Kronzucker et al., 2013; Erel et al., 2015). In a *E. grandis* plantation on highly weathered tropical soils, K and Na supply increases tree growth, wood production, leaf gas exchange and stomatal sensitivity to water deficit of trees (Battie-Laclau et al., 2014a,b), and reduces the fraction of carbon allocated belowground (Epron et al., 2012). Na supply alleviates the functional and structural limitations on  $CO_2$  assimilation rates in *E. grandis* trees growing in K-deficient soils (Battie-Laclau et al., 2014b), as also shown recently for olive trees (Erel et al., 2014). K and Na supply might, therefore, be an appropriate means of improving WUE for wood production where there is a shortage of water. However, the effects of K and Na availability on the mechanisms controlling WUE for wood production have yet to be determined.

Within the *Eucalyptus* genus, the highly productive *E. grandis* species is most commonly planted worldwide in moist, warm subtropical regions (Harwood, 2011). This study set out to gain insights into the effects of K and Na availability on the WUE of *E. grandis* trees under contrasting water supply regimes. We tested the hypotheses that (1) fertilizations that increase tree growth increase WUE for stemwood production by increasing both intrinsic WUE (the ratio of the net  $CO_2$  assimilation to the stomatal conductance in individual leaves) and aboveground biomass partitioning for stemwood production, and (2) WUE at leaf and canopy levels can be predicted from leaf and phloem sap  $\delta^{13}C$ , as well as from sugar concentrations in phloem sap. However, the first hypothesis was only tested for the control treatment and K-fertilized trees as sap flow and consequently, WUE for wood production, were not measured for Na-fertilized trees.

## 2. Materials and methods

### 2.1. Study area

The experiment was conducted 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 monthly temperature was 15 °C during

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