



Combining *Eucalyptus* wood production with the recovery of native tree diversity in mixed plantings: Implications for water use and availability[☆]

Nino Tavares Amazonas^{a,*}, David I. Forrester^b, Rafael Silva Oliveira^c, Pedro H.S. Brancalion^a

^a Universidade de São Paulo, Escola Superior de Agricultura Luiz de Queiroz, Departamento de Ciências Florestais, Laboratório de Silvicultura Tropical, Avenida Pádua Dias, 11. CEP 13.418-900, Piracicaba, SP, Brazil

^b Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

^c Department of Plant Biology, Institute of Biologia, University of Campinas, Caixa Postal 6109, CEP 13.083-970, Campinas, SP Brazil



ARTICLE INFO

Keywords:

Atlantic Forest Restoration Pact
Ecophysiology
High diversity mixed plantation
Leaf water potential
Soil volumetric water content
Stomatal conductance

ABSTRACT

Mixed forest plantations now emerge as an alternative to traditional plantations in the tropics and represent ecological gains associated with production, wood quality and nutrient cycling. Mixed plantations with higher diversity may also be advantageous concerning their use of soil water. To shed light onto water-related issues of mixing *Eucalyptus* and a high diversity of tropical native trees, we explored the following questions: What is the impact of high diversity mixed plantations of *Eucalyptus* intercropped with native trees on soil water? How does the mixture affect the physiology of water use in native trees? Firstly, we tested the hypothesis that stands of *Eucalyptus* mixed with a high diversity of native trees consume less water compared to *Eucalyptus* monocultures, by measuring the temporal dynamics of soil water. Secondly, we tested how mixing with *Eucalyptus* affects the hydraulic performance of fast- and slow-growing native species in these forestry systems. This is the first time a large experiment has been implemented to compare the effects of monospecific *Eucalyptus* plantations, native species mixtures and mixed plantations of *Eucalyptus* and native species on soil water dynamics under controlled conditions in terms of site, age, soil type, topography and climate. We found that high diversity mixed plantations of *Eucalyptus* and native trees use less soil water, than *Eucalyptus* monocultures. However, the soil under the mixtures was drier than in native species stands. The mixing with *Eucalyptus* affected the hydraulic performance of native species by decreasing the leaf water potential and stomatal conductance of the fast-growing species, suggesting that fast-growing species performance may be especially constrained by competition for water from *Eucalyptus*. These findings have important implications for forest management and ecological restoration in the tropics. They will help to further develop silvicultural options to adapt to climate change and improve plantation forestry by using mixed plantations for production purposes or rehabilitation of degraded lands.

1. Introduction

New silvicultural systems have been developed to meet the growing demand for forests of multiple uses (Lamb, 2005), including the emergent need to achieve environmental benefits allied to production (Stanturf et al., 2014). Mixed forest plantations now emerge as an alternative to traditional silviculture in the tropics, conferring ecological gains associated with production, wood quality, nutrient cycling and water use efficiency (Bouillet et al., 2013; Forrester, 2015; Forrester et al., 2006; Kelty, 2006; Piotto, 2008). These systems are more resilient and aggregate benefits associated with carbon-pool stability and other ecosystem services (Hulvey et al., 2013), but are often only preferred

when their productivity is higher than that of monocultures. Higher productivity in mixtures is often achieved by combining a nitrogen fixing tree (e.g. *Acacia* species) with non-legume trees used for wood production, to take advantage of the higher nutrient inputs supplied (Bouillet et al., 2013). However, two-species mixed plantations designed for wood production make minimal contributions to biodiversity conservation. This may be increased with the offer of economic incentives associated with the additional values of these systems, such as payments for ecosystem services like biodiversity conservation, carbon storage, or water regulation, to compensate for lower yields (Brancalion et al., 2012).

The high productivity of *Eucalyptus* plantations, the most important

[☆] This article is part of a special issue entitled “Current advances in plant water-relations research, implications for forest management and restoration stemming from the Ecosummit 2016 conference”, published in the Journal of Forest Ecology and Management 418, 2018.

* Corresponding author.

E-mail addresses: namazonas@gmail.com (N.T. Amazonas), david.forrester@wsl.ch (D.I. Forrester), rafaelsoliv@gmail.com (R.S. Oliveira), pedrob@usp.br (P.H.S. Brancalion).

commercial genera in the tropics (Del Lungo et al., 2006), is associated with a high demand for water (Whitehead and Beadle, 2004). Water supply is a key resource determining the productivity of *Eucalyptus* plantations in some regions (Stape et al., 2010) and climate change may negatively affect the hydraulic performance of trees and plantations in regions where it increases temperatures, decreases precipitation and causes soil moisture drought (IPCC, 2015), ultimately compromising wood production and increasing the susceptibility of these forests to die-off (Allen et al., 2010). *Eucalyptus* can obtain water from deep soil layers (Christina et al., 2017) from the early stages of stand development, but may depend on precipitation and moisture of superficial soil layers at the end of the rotation when deep soil layers have dried out (Nouvellon et al., 2011). Other species have different ecological strategies and demand less water. Increasing species diversity in plantations could thus lead to complementary resource use by trees and a decrease in water demand at the stand level, reducing vulnerability to droughts caused by climate change and resulting in more sustainable wood production.

To examine how the water use and physiological performance of native species are affected by mixing with *Eucalyptus* or a high diversity of tropical native trees, we explored the following questions: What is the impact of high diversity mixed plantations of *Eucalyptus* intercropped with native trees on soil water? How does the mixture affect the physiology of water use in native trees? We tested two hypotheses related to the water use strategies of trees in the tropics, with implications for forest management and restoration. Firstly, we tested the hypothesis that stands of *Eucalyptus* mixed with a high diversity of native trees consume less water compared to *Eucalyptus* monocultures, by measuring the temporal dynamics of soil water. We expected intermediate values of soil water content in mixtures compared to *Eucalyptus* monocultures (drier soils) and native species stands (wetter soils). Secondly, we examined whether the mixing with *Eucalyptus* affects the hydraulic performance of fast- and slow-growing native species, by assessing the leaf water potential and the stomatal conductance of model species. We expected to find a decreased hydraulic performance of native trees. There is a widespread concern in society about the impact of *Eucalyptus* monoculture plantations on the conservation of water resources, and natural forests that grow more slowly are believed to have smaller impacts. Reliable information on water use by native and exotic trees derived from controlled experiments is, however, limited. This is the first time a large experiment has been implemented to compare the effects of monospecific *Eucalyptus* plantations, native species mixtures and mixed plantations of *Eucalyptus* and native species on soil water dynamics under controlled conditions in terms of site, age, soil type, topography and climate.

2. Material and methods

2.1. Study site

The experimental site is located in Aracruz, ES, Brazil, (19°49'12"S, 40°16'22"W), within the Atlantic Forest region, managed by Fibria Celulose S.A. The site has a flat relief with a typical Yellow Argisol (Ultisol) presenting a sandy/medium/clayey texture. The region has a tropical climate with a dry winter (Aw) (Köppen, 1936) and a hot wet summer, with annual average temperature of 23.4 °C and annual average rainfall of 1,412 mm (Alvares et al., 2013). Historically, the region experiences a water deficit from February to September (Sentelhas et al., 2013). Precipitation was markedly lower during the period we measured soil moisture compared to historical averages (Supplementary Fig. 1). The weather data from the meteorological station of the seedling nursery located approximately 12 km from the experimental site is shown in Supplementary Fig. 2.

2.2. Experimental design and characteristics of the forests

The experiment had a randomized block design, with three treatments and five blocks (15 plots). Each plot consisted of 10 rows of 24 trees, including two outer rows as borders. Each effective plot measured 18 m × 60 m (1080 m²) and included six rows of 20 trees. The three treatments included a *Eucalyptus* monoculture (hereafter EUC); a mixed plantation of *Eucalyptus* intercropped with 30 native tree species, in alternating single rows (hereafter MIX); and native species plots consisting of 10 native pioneer species (instead of *Eucalyptus*) intercropped with the same 30 native tree species, in alternating single rows (hereafter NAT). In the mixture or native species treatments, half of the seedlings were *Eucalyptus* or 10 native pioneers, and the other half were seedlings from 30 native tree species (diversity group) common to both treatments. The site was planted in July 2011 using a 3 m × 3 m spacing at a density of 1,111 trees ha⁻¹. The *Eucalyptus* used was a clone of *E. grandis* × *E. urophylla*. All seedlings were planted at the same time using the same silvicultural techniques that are commonly used in *Eucalyptus* plantations in the region (fertilization according to the nutritional demands of *Eucalyptus* to local soil conditions, weed control using glyphosate spraying, and ant control using insecticide baits). All treatments had the same spacing in between rows and trees within rows. To control for the variability of neighborhood effects, each native species was planted in the same position within all plots. The list of species used in each treatment is shown in Supplementary Table 1. We used inventory data to estimate aboveground woody biomass as a proxy for production. At 57 months after plantation, we measured the diameter at breast height (DBH) at 1.3 m and total height of all live trees. For multi-stemmed individual trees, we measured the largest five stems. To estimate the aboveground biomass of native trees, we used equations published for native species growing in restoration sites of similar age (Ferez et al., 2015). For *Eucalyptus* biomass, we used equations developed by Rocha (2014). *Eucalyptus* monocultures produced the greatest biomass (93.2 Mg ha⁻¹), followed by mixtures (85.2 Mg ha⁻¹; 81.6 from *Eucalyptus* and 3.6 from native trees in the diversity group) and native species plots (9.3 Mg ha⁻¹; 5.6 from pioneers and 3.7 from trees in the diversity group).

2.3. Soil volumetric water content

Soil volumetric water content was measured weekly for one year (from May 2015 through June 2016) in 30 positions, two in each plot, including the three treatments and covering all seasons. We installed tubes and used a portable device (Diviner 2000, Sentek) to measure soil volumetric water content (Sentek Pty Ltd., 2009) for every 10-cm soil layer down to 1.3 m.

2.4. Xylem water potential and stomatal regulation

Two native species with contrasting growth rates were chosen as model species for the ecophysiological traits, each of which had high survival rates and equal numbers of individuals (only one native tree missing). We chose two Fabaceae to reduce the effect of genetic distance on physiological behavior. *Paubrasilia echinata* Lam. is a slow-growing, late-successional species, while *Mimosa artemisiana* Heringer & Paula is a fast-growing species with traits common to early-successional tree species. We measured two individuals per plot (20 trees of each species). *Eucalyptus* trees were too tall to measure using the resources available for this study. We measured the DBH of all individuals of these species used for the measurement of ecophysiological traits at age 47 months to relate DBH differences between treatments (mixing effect) to differences in hydraulic performance. We compared xylem water potential (Ψ_{xylem}) and stomatal conductance (g_s) of the model species intercropped with *Eucalyptus* with trees in native species plots. We estimated xylem water potential (MPa) using a pressure chamber (model 600, PMS Instrument Company), by measuring the water

potential of leaves detached from small branches (< 2 cm diameter) in the outer part of the middle third of the crown, facing south and shaded. Leaf water potential tends to vary considerably within complex canopies because of contrasting light conditions, so our leaf sampling was designed to estimate the xylem water potential of trees instead of leaf water potential. To estimate the predawn xylem water potential, a branch was enclosed with a black plastic bag in the evening before the measurement, to avoid nocturnal stomatal opening, and detached from the tree just before measurement. We used two leaves per individual for water potential measurements. We measured stomatal conductance (g_s ; $\text{mmol/m}^2 \text{s}^{-1}$) using a portable Leaf Porometer (Decagon Devices, Inc.) for leaves from the outer part of the middle third of the crown, facing north and not shaded. We marked two leaves per individual attached to the branches and used the same leaves to make repeated measures of stomatal conductance. Leaf sampling was designed to estimate the g_s of leaves under stressful conditions. We built daily curves for these variables using measurements made every two hours (from 6 am to 4 pm and predawn at 4 am) in days without rain in June 2015 and January 2016, the historical dry and wet seasons, respectively.

2.5. Statistical analysis

We tested if stands of *Eucalyptus* mixed with a high diversity of native trees consume less water compared to *Eucalyptus* monocultures by modeling soil volumetric water content as a function of treatment and depth as fixed factors, and time (year, month, day) and position (block, plot, tube) as nested random factors with an autocorrelation structure. To compare means, we built an Analysis of Variance model having soil water as a function of treatment and depth. Then, we performed a post hoc test (Tukey, $\alpha = 0.05$) using the package *agricolae* (de Mendiburu, 2017). We tested if the mixing affects the physiology of water use of trees by modeling leaf water potential and stomatal conductance using, first, treatment and species as fixed factors and date, block and time of measurement as nested random factors; and then separately per species entering treatment as a fixed factor and date, block and time of measurement as nested random factors. We visually inspected residual plots to assure that the assumptions of linearity, normality and homoscedasticity were met. Linear Mixed Models were built using the *lme* function of the package *nlme* (Pinheiro et al., 2016). All analyses were performed in R 3.2.1 (R Core Team, 2016).

3. Results

3.1. Soil volumetric water content

Treatment, soil depth and the interaction between them were highly significant factors that explained soil water ($p < .0001$; Supplementary Table 2; Supplementary Table 3). Soil volumetric water content increased with depth and was lowest in *Eucalyptus* monoculture, intermediate in mixtures and highest in native species stands (Table 1). This pattern was stronger during drier months and occurred across the whole soil profile (0–130 cm) and during most of the year (Figs. 1; 2). The temporal change in volumetric soil water contents across different depths in each treatment are shown in Supplementary Fig. 3.

Table 1

Soil water content in three treatments from the experimental area in Aracruz, state of Espírito Santo, Brazil.

Treatment	Soil water content (%)
<i>Native species</i>	12.19 A
<i>Mixed</i>	11.91 B
<i>Eucalyptus</i>	10.99 C

Means followed by different letters are significantly different (Tukey; $\alpha = 0.05$; DF Error: 17,160).

3.2. The mixing effect and the physiology of water use in model species

Native trees mixed with *Eucalyptus* grew less than their counterparts that were intercropped with native pioneers. This effect was statistically significant for the fast-growing, but not for the slower-growing species (Table 2). The survival rate of *P. echinata* was 100% in both treatments. *M. artemisiana* had a survival rate of 100% in the mixed plantation and 90% in native species stands.

We found contrasting xylem water potential values between species ($p < 0.0001$) and treatments ($p = 0.0294$). The fast-growing species *M. artemisiana* showed less negative leaf water potential than *P. echinata* in the two periods measured, June 2015 and January 2016. Daily variation also contrasted between these species, with greater differences in xylem water potential observed for *P. echinata* during the day. Generally, the lowest potentials were observed around midday and both species showed lower values when intercropped with *Eucalyptus* (except for *M. artemisiana* at 10 am in the first period). Values at 06:00 am were usually higher than predawn measures (Fig. 3).

Stomatal conductance was different between species ($p < 0.0001$) but not between treatments ($p = 0.4608$). *P. echinata*, the slow-growing species, had more similar values of stomatal conductance between the measurement periods and varied less during the day, while *M. artemisiana* showed the greatest differences both within days and across measurement periods (Fig. 4). Considering treatments, *P. echinata* showed similar stomatal regulation with a tendency to higher conductance when intercropped with *Eucalyptus*. *M. artemisiana* tended to lower conductance in mixtures (Fig. 4).

4. Discussion

In support of our first hypothesis, our results showed that mixed plantations of *Eucalyptus* and a high diversity of native trees had a lower impact on soil water than *Eucalyptus* monocultures. However, the soil under the mixtures was still drier than that of native species stands. Despite the favorable results considering soil water content under mixtures, our physiological measurements demonstrated that *Eucalyptus* negatively affected the hydraulic performance of native tree species. This is consistent with the general finding that more productive stands use more water (Law et al., 2002) and that when mixtures are less productive than monocultures they generally also use less water (Forrester, 2015). That is, the transpiration and consequently soil water use of a stand appears more likely to depend on its productivity, species identity and the species functional traits than tree species diversity *per se* (Kunert et al., 2012; Lübke et al., 2015).

It is important to note that *Eucalyptus* plantations can take up water from soil depths up to 10 m (Christina et al., 2017), however, we monitored soil water down to 1.3 m, and part of the interaction between *Eucalyptus* and the native species may have occurred deeper within the soil profile. Despite this limitation, we emphasize the importance of superficial soil water for fast-growing species of this genus especially from the age of around three years towards the end of the rotation, when *Eucalyptus* may depend on precipitation after most water in the deep soil layers has been depleted (Nouvellon et al., 2011). Even earlier in stand development, the proportion of water acquired from deep soil layers is generally low when water is available in shallower layers (Christina et al., 2017). Moreover, a global analysis of root distribution showed that most of the roots in tropical forests are concentrated in the first 1–1.5 m of the soil, including as much as 78% in the first 50 cm (Jackson et al., 1996). There are, however, studies indicating that the use of water from deep soil layers can be important in tropical forests (Nepstad et al., 1994); although this capacity is limited (Markewitz et al., 2010; Romero-Saltos et al., 2005).

Xylem water potential and leaf stomatal conductance may change in response to mixing (Gebauer et al., 2012; Jonard et al., 2011) and species growing in mixtures have been found to experience increased or decreased water stress, depending on the species they are mixed with

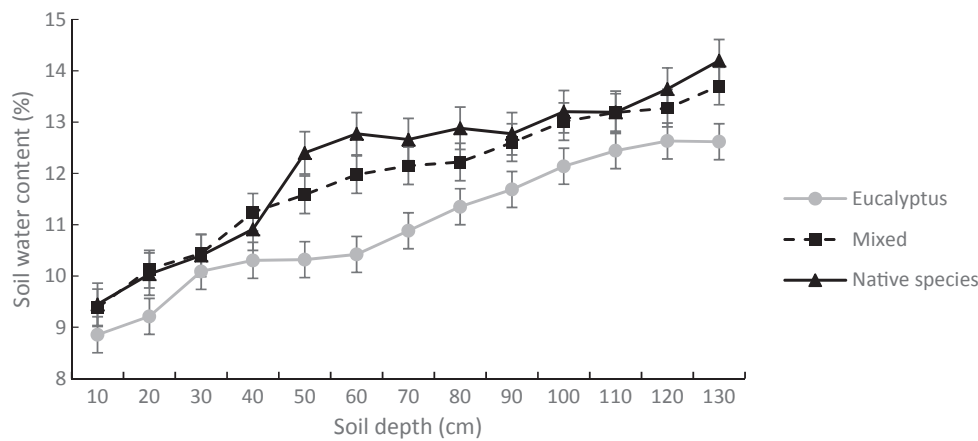


Fig. 1. Average soil moisture differences among three types of forestry system implemented in Aracruz, ES, Brazil. Each point represents annual averages \pm standard error for every 10-cm layer from 0 to 130 cm.

(Gebauer et al., 2012; Forrester et al., 2006). Low soil moisture may decrease xylem water potentials and force plants to close their stomata to avoid water loss, which in turn can lead to decreased photosynthetic rates and ultimately to decreased biomass production and growth. Taking advantage of the lower competition in the mixtures we studied, *Eucalyptus* produced 88% of the aboveground biomass produced by *Eucalyptus* monocultures, even though the mixtures contained only 50% of the number of *Eucalyptus* trees. That is, the replacement of half of the *Eucalyptus* seedlings by native species increased diversity while significantly reducing water consumption (8.4% difference in soil moisture) disproportionately to the reduction in overall aboveground biomass production (12%). Despite the advantages related to increased biodiversity and lower water consumption, and even though there may be some degree of niche separation and competitive reduction in the mixtures (Vandermeer, 1989), the ecological interactions were also associated with a negative mixing effect on the growth and physiology of native species.

The negative mixing effect was higher for the faster growing native species. These species may have a correspondingly high demand for water than the slower growing species, which makes the faster growing native species more constrained by competition for water, or other resources, from *Eucalyptus*. The growth reduction is in accordance with the observed changes in the water use physiology of our model native species, which had lower leaf water potential in mixtures. In one extreme, the growth of *P. echinata* (a slow growing species) was not significantly affected by *Eucalyptus* and had equivalent performances in both treatments, consistent with a conservative water-balance strategy to avoid water losses, without compromising growth. At the other extreme, *M. artemisiana* (a fast-growing species) experienced a large negative mixing effect, associated with more pronounced changes in the physiology of water use. Especially in the drier period, its pre-dawn leaf water potential was as low as -0.6 MPa, suggesting that leaves did not rehydrate overnight. The tendency of *M. artemisiana* to reduce g_s in

Table 2

The mixing effect on the DBH of model species.^{a,b} The control for native species are native species plots and the control for *Eucalyptus* are monocultures.

Species	Treatments		Mixing effect	p-value
	Mixture	Controls		
	DBH (cm)			
<i>Eucalyptus</i>	16.2 \pm 0.1	12.9 \pm 0.2	+25.0%	< 0.0001
<i>Mimosa artemisiana</i>	14.9 \pm 1.6	21.0 \pm 0.6	-28.9%	0.014
<i>Paubrasilia echinata</i>	2.2 \pm 0.3	2.4 \pm 0.2	-7.8%	0.673

^a Results are presented as means \pm standard error.

^b p-values from Welch's t test are shown.

mixtures may have occurred in response to lower soil water content. These patterns were probably caused by greater water uptake by *Eucalyptus* in mixtures than by native pioneers in native species plots, thereby significantly reducing the water potential in the rooting zone of *M. artemisiana*.

Eucalyptus mixed with *Acacia* has been found to increase the vertical segregation and increase the density of *Acacia* fine roots in deep soil layers (Laclau et al., 2013). Even though a similar niche separation is possible in our experiment, the physiological changes observed are probably also related to water limitation experienced by native species growing in the presence of *Eucalyptus*. Despite the marked differences in soil moisture and leaf water potential, the high variance in stomatal conductance led only to a non-significant tendency of lower values in the mixtures.

The adoption of forestry systems that consume less water have direct implications for watersheds important for water yield and may result in greater yields than those from catchments with higher proportions of *Eucalyptus* monocultures. At the catchment scale, the combination of the proportion of the area occupied by plantations, the

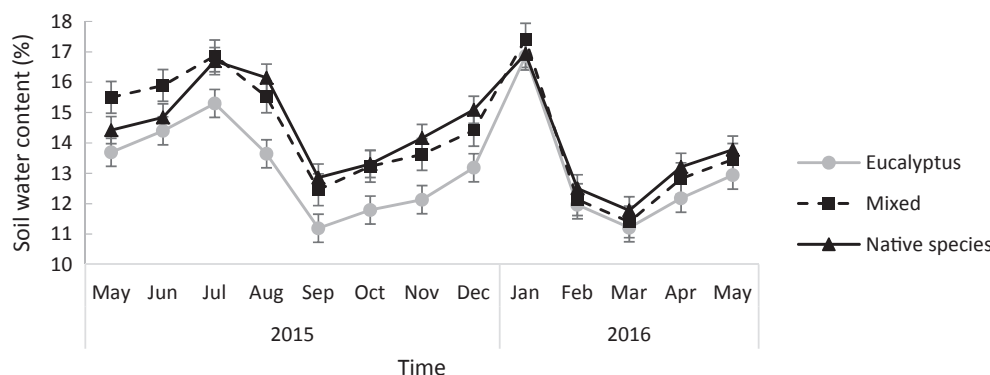


Fig. 2. Annual variation of soil moisture among three types of forestry system implemented in Aracruz, ES, Brazil. Values are averages \pm standard error for every month across the whole profile.

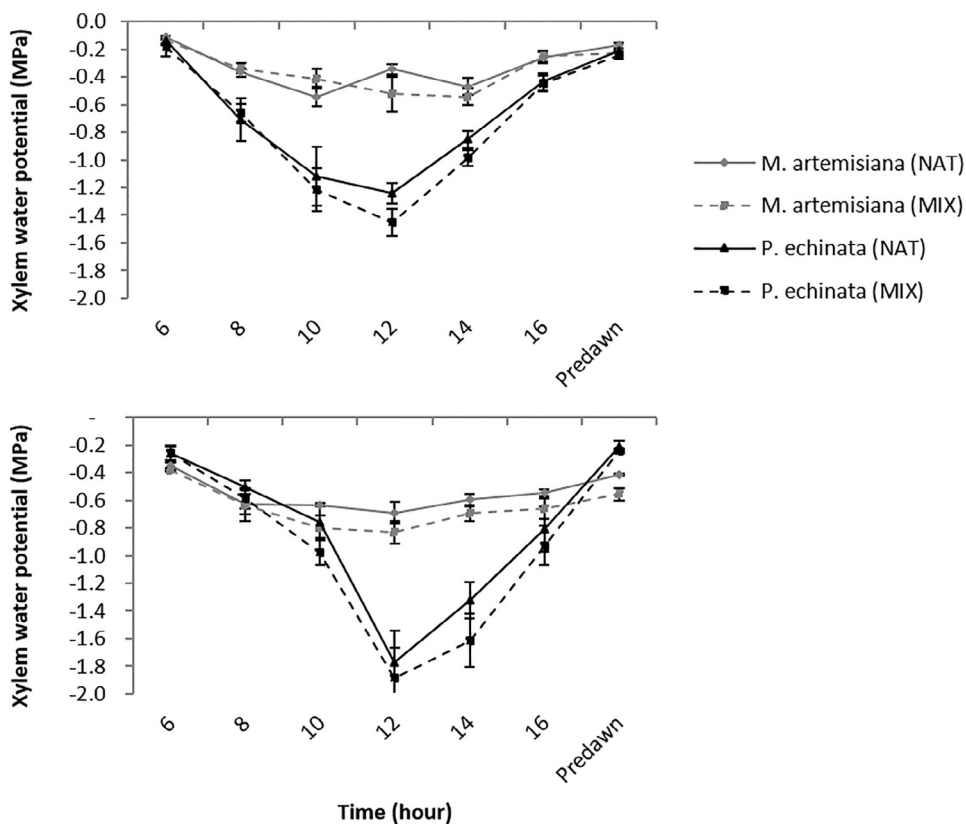


Fig. 3. Diurnal variation in xylem water potential of *Mimosa artemisiana* and *Paubrasilia echinata* intercropped with native pioneers (NAT) or *Eucalyptus* (MIX). Top: historical dry season (June 2015); bottom: historical wet season (January 2016). There was a dry spell during measurements in the wet season.

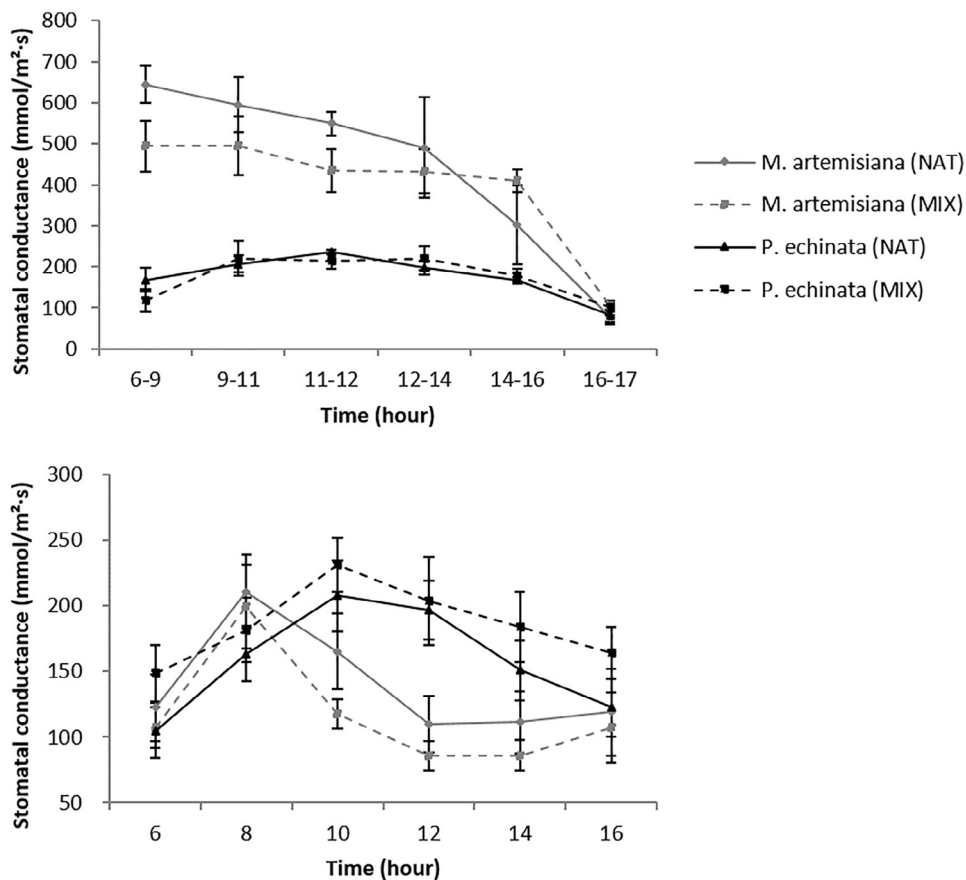


Fig. 4. Diurnal variation in stomatal conductance of *Mimosa artemisiana* and *Paubrasilia echinata* planted intercropped with native pioneers (NAT) or *Eucalyptus* (MIX). Top: historical dry season (June 2015); bottom: historical wet season (January 2016). There was a dry spell during measurements in the wet season.

growth rate of species planted and their water use efficiency is a key element influencing the impact of forests on water yield (Forrester et al., 2010; White et al., 2014). Therefore, fast-growing species like *Eucalyptus* which often have high water use efficiency, can be used to produce more wood, while using less water and less land area, than slower growing and less water use efficient species (Forrester et al., 2010; White et al., 2014). This high water use efficiency combined with the lower water use of the native species may be combined by using mixtures. Beyond these characteristics, the use of mixed forests, may reduce the vulnerability of plantations to droughts since the water content of soils is higher, at least in these young stands. In the design of new forestry systems, it is important to consider the growth rate and the strategies of water use by different tree species, such as their ability to drop leaves and escape competition for water during the dry period. Also, other important traits to consider while designing plantations are related to the hydraulic characteristics of species, because trees with hydraulic systems that confer higher embolism resistance may result in more resistant forest communities (Rowland et al., 2015).

When trees transpire more, they use more of the water available in the soil and less water is left for infiltration and groundwater store. Considering the predictions of climate change in the near future, with the dry season expected to become drier and longer, this new silvicultural system can be considered as an alternative to *Eucalyptus* monocultures in regions important for water production. We tested this system in Brazil, which is an important global player in *Eucalyptus* silviculture, tree species biodiversity conservation (Beech et al., 2017) and in tropical forest restoration (Aronson and Alexander, 2013; Calmon et al., 2011; Holl, 2017). The country has ambitious restoration objectives and these highly diverse mixed forest intercrops of *Eucalyptus* and native tree species may also be considered when rehabilitation of degraded lands is an option for restoration, representing positive gains for production and conservation.

5. Conclusion

The mixed plantation of *Eucalyptus* intercropped with native species consumed less water than *Eucalyptus* monocultures, but reduced the hydraulic performance of fast-growing native trees and constrained their growth. These findings have important implications for forest management and ecological restoration in the tropics. They may help to further develop silvicultural options to adapt to climate change and improve plantation forestry by using mixed plantations for production purposes and rehabilitation of degraded lands. Further research is necessary to test similar systems in other regions, while adapting the design and species composition in relation to the natural distributions of the native species. In addition, a complete hydrological study that includes measurements in deep soil layers, direct measurements of tree transpiration and catchment water yield would provide a more comprehensive understanding of how mixed forests influence water production.

Acknowledgements

We would like to thank Fibria Celulose S.A. for the extensive collaboration in this research; Bruno Bordron for the friendly review; the editor and two anonymous reviewers for their valuable suggestions in previous versions of this article; several colleagues and workers for their help on field and laboratory activities; the financial support to the project and to Nino Tavares Amazonas through grant #2013/50718-5 and grant #2014/02070-9, São Paulo Research Foundation (FAPESP). PHSB thanks the National Council for Scientific and Technological Development (CNPq - grant #304817/2015-5).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the

online version, at <http://dx.doi.org/10.1016/j.foreco.2017.12.006>.

References

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, Ted, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684. <http://dx.doi.org/10.1016/j.foreco.2009.09.001>.
- Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. *Meteorol. Zeitschrift* 22, 711–728. <http://dx.doi.org/10.1127/0941-2948/2013/0507>.
- Aronson, J., Alexander, S., 2013. Ecosystem restoration is now a global priority: time to roll up our sleeves. *Restor. Ecol.* 21, 293–296. <http://dx.doi.org/10.1111/rec.12011>.
- Beech, E., Rivers, M., Oldfield, S., Smith, P.P., 2017. GlobalTreeSearch: the first complete global database of tree species and country distributions. *J. Sustain. For.* 36, 454–489. <http://dx.doi.org/10.1080/10549811.2017.1310049>.
- Bouillet, J.-P., Laclau, J.-P., Gonçalves, J.L.d.M. Voigtlaender, M., Gava, J.L., Leite, F.P., Hakamada, R., Mareschal, L., Mabilia, A., Tardy, F., Levillain, J., Deleporte, P., Epron, D., Nouvellon, Y., 2013. *Eucalyptus* and *Acacia* tree growth over entire rotation in single- and mixed-species plantations across five sites in Brazil and Congo. *For. Ecol. Manage.* 301, 89–101.
- Brancalion, P.H.S., Viani, R.A.G., Strassburg, B.B.N., Rodrigues, R.R., 2012. Finding the money for tropical forest restoration. *Unasylva* 63, 41–50.
- Calmon, M., Brancalion, P.H.S., Paese, A., Aronson, J., Castro, P., da Silva, S.C., Rodrigues, R.R., 2011. Emerging threats and opportunities for large-scale ecological restoration in the Atlantic forest of Brazil. *Restor. Ecol.* 19, 154–158. <http://dx.doi.org/10.1111/j.1526-100X.2011.00772.x>.
- Christina, M., Nouvellon, Y., Laclau, J.P., Stape, J.L., Bouillet, J.P., Lambais, G.R., le Maire, G., 2017. Importance of deep water uptake in tropical eucalypt forest. *Funct. Ecol.* 31, 509–519. <http://dx.doi.org/10.1111/1365-2435.12727>.
- Del Lungo, A., Ball, J.B., Carle, J.B., 2006. Global Planted Forests Thematic Study: Results and Analysis. Rome.
- Ferez, A.P.C., Campoe, O.C., Mendes, J.C.T., Stape, J.L., 2015. Silvicultural opportunities for increasing carbon stock in restoration of Atlantic forests in Brazil. *For. Ecol. Manage.* 350, 40–45. <http://dx.doi.org/10.1016/j.foreco.2015.04.015>.
- Forrester, D.I., 2015. Transpiration and water-use efficiency in mixed-species forests versus monocultures: effects of tree size, stand density and season. *Tree Physiol.* 35, 289–304. <http://dx.doi.org/10.1093/treephys/tpv011>.
- Forrester, D.I., Bauhus, J., Cowie, A.L., Vanclay, J.K., 2006. Mixed-species plantations of *Eucalyptus* with nitrogen-fixing trees: a review. *For. Ecol. Manage.* 233, 211–230. <http://dx.doi.org/10.1016/j.foreco.2006.05.012>.
- Forrester, D.I., Theiveyanathan, S., Collopy, J.J., Marcar, N.E., 2010. Enhanced water use efficiency in a mixed *Eucalyptus globulus* and *Acacia mearnsii* plantation. *For. Ecol. Manage.* 259, 1761–1770. <http://dx.doi.org/10.1016/j.foreco.2009.07.036>.
- Gebauer, T., Horna, V., Leuschner, C., 2012. Canopy transpiration of pure and mixed forest stands with variable abundance of European beech. *J. Hydrol.* 442–443, 2–14. <http://dx.doi.org/10.1016/j.jhydrol.2012.03.009>.
- Holl, K.D., 2017. Restoring tropical forests from the bottom up. *Science* (80-). 355, 455–456. < <http://doi.org/10.1126/science.aam5432> > .
- Hulvey, K.B., Hobbs, R.J., Standish, R.J., Lindenmayer, D.B., Lach, L., Perring, M.P., 2013. Benefits of tree mixes in carbon plantings. *Nat. Clim. Change* 3, 869–874. <http://dx.doi.org/10.1038/nclimate1862>.
- IPCC, 2015. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. Intergovernmental Panel on Climate Change, Geneva.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H. a., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108, 389–411. < <http://doi.org/10.1007/BF00333714> > .
- Jonard, F., André, F., Ponette, Q., Vincke, C., Jonard, M., 2011. Sap flux density and stomatal conductance of European beech and common oak trees in pure and mixed stands during the summer drought of 2003. *J. Hydrol.* 409, 371–381. <http://dx.doi.org/10.1016/j.jhydrol.2011.08.032>.
- Kelty, M.J., 2006. The role of species mixtures in plantation forestry. *For. Ecol. Manage.* 233, 195–204. <http://dx.doi.org/10.1016/j.foreco.2006.05.011>.
- Köppen, W., 1936. Das geographische System der Klimate. *Handbuch der Klimatologie*. In: Köppen, W., Geiger, R. (Eds.), *Handbuch Der Klimatologie*. Gerbrüder Bornträger, Berlin, pp. 1–44.
- Kunert, N., Schwendenmann, L., Potvin, C., Ho, D., 2012. Tree diversity enhances tree transpiration in a Panamanian forest plantation 135–144. < <http://doi.org/10.1111/j.1365-2664.2011.02065.x> > .
- Laclau, J., Nouvellon, Y., Reine, C., Gonçalves, J.L., De, M., Krushe, A.V., Jourdan, C., le Maire, G., Bouillet, J.P., 2013. Mixing *Eucalyptus* and *Acacia* trees leads to fine root over-yielding and vertical segregation between species. *Oecologia* 172, 903–913. <http://dx.doi.org/10.1007/s00442-012-2526-2>.
- Lamb, D., 2005. Restoration of degraded tropical forest landscapes. *Science* (80-). 310, 1628–1632. < <http://doi.org/10.1126/science.1111773> > .
- Law, B., Falge, E., Gu, L., Baldocchi, D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A., Falk, M., Fuentes, J., Goldstein, A., Granier, A., Grelle, A., Hollinger, D., Janssens, I., Jarvis, P., Jensen, N., Katul, G., Mahli, Y., Matteucci, G., Meyers, T., Monson, R., Munger, W., Oechel, W., Olson, R., Pilegaard, K., Paw U, K., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation.

- Agric. For. Meteorol. 113, 97–120. [http://dx.doi.org/10.1016/S0168-1923\(02\)00104-1](http://dx.doi.org/10.1016/S0168-1923(02)00104-1).
- Lübbe, T., Schuldt, B., Coners, H., Leuschner, C., 2015. Species diversity and identity effects on the water consumption of tree sapling assemblages under ample and limited water supply. *Oikos* 1–12. <http://dx.doi.org/10.1111/oik.02367>.
- 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. <http://dx.doi.org/10.1111/j.1469-8137.2010.03391.x>.
- de Mendiburu, F. 2017. *Statistical Procedures for Agricultural Research*.
- 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, 666–669. <http://dx.doi.org/10.1038/372666a0>.
- Nouvellon, Y., Stape, J.L., le Maire, G., Epron, D., Gonçalves, J.L.M., Bonnefond, J.-M., Campoe, O., Loos, R., Bouillet, J.-P., Laclau, J.-P., 2011. Factors controlling carbon and water balances on fast growing Eucalyptus plantations. In: IUFRO Eucalyptus Conference. Porto Seguro, Bahia, pp. 43–46.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2016. Linear and Nonlinear Mixed Effects Models.
- Piotto, D., 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. *For. Ecol. Manage.* 255, 781–786. <http://dx.doi.org/10.1016/j.foreco.2007.09.065>.
- R Core Team, 2016. R: A Language and Environment for Statistical Computing.
- Rocha, J.H.T., 2014. Reflexos do manejo de resíduos florestais na produtividade, nutrição e fertilidade do solo em plantações de Eucalyptus grandis. Universidade de São Paulo, Tese.
- Romero-Saltos, H., Sternberg, L. d. S.L., Moreira, M.Z., Nepstad, D.C., 2005. Rainfall exclusion in an eastern Amazonian forest alters soil water movement and depth of water uptake. *Am. J. Bot.* 92, 443–455. < <http://doi.org/10.3732/ajb.92.3.443> > .
- Rowland, L., da Costa, A.C.L., Galbraith, D.R., Oliveira, R.S., Binks, O.J., Oliveira, A.A.R., Pullen, A.M., Doughty, C.E., Metcalfe, D.B., Vasconcelos, S.S., Ferreira, L.V., Malhi, Y., Grace, J., Mencuccini, M., Meir, P., 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* 528, 119–122. <http://dx.doi.org/10.1038/nature15539>.
- Sentek Pty Ltd., 2009. Diviner 2000 User Guide Version 1.5. Sentek Pty Ltd., Stepney.
- Sentelhas, P.C., Marin, F.R., Ferreira, A.S., Sá, E.J.S., 2013. Banco de dados climáticos do Brasil. Município de Linhares, ES [WWW Document]. < <http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=&COD=54> > .
- Stanturf, J.A., Palik, B.J., Dumroese, R.K., 2014. Contemporary forest restoration: a review emphasizing function. *For. Ecol. Manage.* 331, 292–323. <http://dx.doi.org/10.1016/j.foreco.2014.07.029>.
- Stape, J.L., Binkley, D., Ryan, M.G., Fonseca, S., Loos, R.A., Takahashi, E.N., Silva, C.R., Silva, S.R., Hakamada, R.E., Ferreira, J.M. de A., Lima, A.M.N., Gava, J.L., Leite, F.P., Andrade, H.B., Alves, J.M., Silva, G.G.C., Azevedo, M.R., 2010. The Brazil Eucalyptus potential productivity project: influence of water, nutrients and stand uniformity on wood production. *For. Ecol. Manage.* 259, 1684–1694. < <http://doi.org/10.1016/j.foreco.2010.01.012> > .
- Vandermeer, J., 1989. *The Ecology of Intercropping*. Cambridge University Press, New York.
- White, D.A., McGrath, J.F., Ryan, M.G., Battaglia, M., Mendham, D.S., Kinal, J., Downes, G.M., Crombie, D.S., Hunt, M.E., 2014. Managing for water-use efficient wood production in Eucalyptus globulus plantations. *For. Ecol. Manage.* 331, 272–280. <http://dx.doi.org/10.1016/j.foreco.2014.08.020>.
- Whitehead, D., Beadle, C.L., 2004. Physiological regulation of productivity and water use in Eucalyptus: a review. *For. Ecol. Manage.* 193, 113–140. <http://dx.doi.org/10.1016/j.foreco.2004.01.026>.