

## Growth and drought resilience of four native tree species suitable for reforestation of Brazil's Atlantic Forest

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Deforestation of tropical forests has been a critical issue affecting climate change mitigation and biodiversity conservation. Reforestation strives to remedy this situation, yet it is futile as long as deforestation of primary forests continues. Since deforestation is partly motivated by the demand for valuable tropical wood, reforestation should focus not only on planting native tree species, but specifically on a high diversity of native tree species with high-quality wood. However, the eco-physiological information required for growing such species is limited, and their resilience to drought events is unknown. Here, we focused on four native tropical wood tree species identified as suitable for Brazil's Atlantic Forest reforestation. Growth, carbon assimilation, water-use and xylem hydraulics were studied in seedlings of the two legume species *Dalbergia nigra* and *Plathymenia foliolosa* and the two non-legume species *Cariniana legalis* and *Zeyheria tuberculosa*. Seedlings were monitored weekly for 9 consecutive weeks, three to five weeks of which under induced drought. Growth and carbon assimilation were 25–65 per cent higher in the legume vs. non-legume species. In turn, non-legume species mostly avoided the drought by stomatal closure, producing a 50 per cent higher water-use efficiency (WUE) compared with the legume species. The average water potential at 50 per cent stomatal conductivity ( $\Psi_{gs50}$ ) for legume species was  $-2.6$  MPa, whereas for non-legume species it was  $-0.85$  MPa. Still, each species showed a unique set of responses, indicating different growth strategies under mesic and xeric conditions. Our results indicate a divergence among legume and non-legume species, driven by a trade-off between plant productivity (carbon assimilation and growth) and plant safety (stomatal regulation and WUE). All in all, the four species of juvenile potted plants demonstrated a high capacity for recovery from drought, which supports their potential role in future reforestation under climate change.

### Introduction

Deforestation of tropical forests is among the most critical environmental issues of the 21st century, with direct impacts on climate change mitigation and biodiversity conservation (Da Silva and Tabarelli, 2000). Cutting down of native, mature and even primeval forests is motivated by agricultural applications such as livestock farming and to produce fodder for animals. Another primary driver is the increasing demand for precious tropical wood. Some of the greatest forest losses was and is occurring in Brazil's Atlantic Forest (called Nhe'ery by the Guarani indigenous people), one of the world's biggest rainforests. Five centuries ago, it covered up to 150 million ha and has now been reduced to 16.5 million ha, ~11 per cent of its original size (Ribeiro *et al.*, 2009). Furthermore, 80 per cent of the remaining Atlantic Forest is fragmented into patches smaller than 50 ha. Hence, half of the complete forest area is less than 100 m away from a forest edge. Considering

that many animal species depend on a large core-area to survive (Aleixo, 1999; Harris and Pimm, 2004; Laurance, 2007; Gardner *et al.*, 2007; Barlow *et al.*, 2007a, b) and avoid edge areas (Hansbauer *et al.*, 2008; Lopes *et al.*, 2009), the capacity of today's Atlantic Forest to support its original biodiversity is heavily compromised. The Brazilian Atlantic Forest is one of the most highly biodiverse environments on earth due to its unique and highly heterogeneous environmental conditions (Myers *et al.*, 2000; Martini *et al.*, 2007). These include latitudinal and longitudinal gradients of over 30°, elevations ranging from 0 to 2900 m asl, diverse soil climatic gradients and annual precipitation sums ranging from ~1000 to ~4000 mm (Ribeiro *et al.*, 2011b). The Atlantic Forest is generally separated into four main types according to the characteristics of the trees: (1) evergreen forest, which does not have any dry season and an average temperature of 22–25°C. (2) Semi-deciduous and (3) deciduous forests both having a 2–5-month dry season and average temperatures between 22 and 25°C. (4)

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*Araucaria* forest, which is wet year-round and has a cooler temperature, ranging between 12 and 22°C (Colombo and Joly, 2010).

To reverse the deforestation of the Atlantic Forest and other forests, reforestation programmes are being implemented around the world. Simultaneously, the demand for precious tropical wood is increasing steadily (Montagnini and Jordan, 2005). Therefore, an emerging approach for reforestation is to establish forests with a high diversity of native tree species with high-quality wood (Rolim *et al.*, 2019; Figure 1). Integration of such native species in commercial wood plantations has been tested successfully for decades (Rodrigues *et al.*, 2009) and corresponding experiences can support Atlantic Forest reforestation programmes. Increased use of native tree species with high-quality timber for reforestation can achieve two goals in a single step, namely, (a) to remediate areas once forested and (b) to reduce the need for further deforestation of primary natural forests, by planting trees of valuable tropical wood which can meet the demand for high-quality tropical timber (Sist *et al.*, 2021). Planting native species can also benefit the ecosystem through connectivity restoration and by increasing gene flow between highly fragmented populations, leading to elevated effective population size and higher genetic diversity (Thomas, 2011). De Assis Barros *et al.* (2022) show that protected areas suffer less from deforestation than non-protected areas. We assume that if native species are planted under proper management and protection, there would be an increase in forest cover despite the risk of an increased interest in harvesting the trees with high-wood quality.

To assure the success of reforestation programmes in the tropics with native species, seedlings of native, commercially important tree species must be grown in a greenhouse and re-introduced to the field. However, unlike other commercial tree species grown in plantations (e.g. Eucalypt, Pine), silvicultural and eco-physiological knowledge about native species is largely lacking. Such information becomes crucial considering that conditions on the ground are changing rapidly before the background of climate change, including for example higher frequency of hotter and longer drought periods (Mendivelso *et al.*, 2014; Lyra *et al.*, 2018).

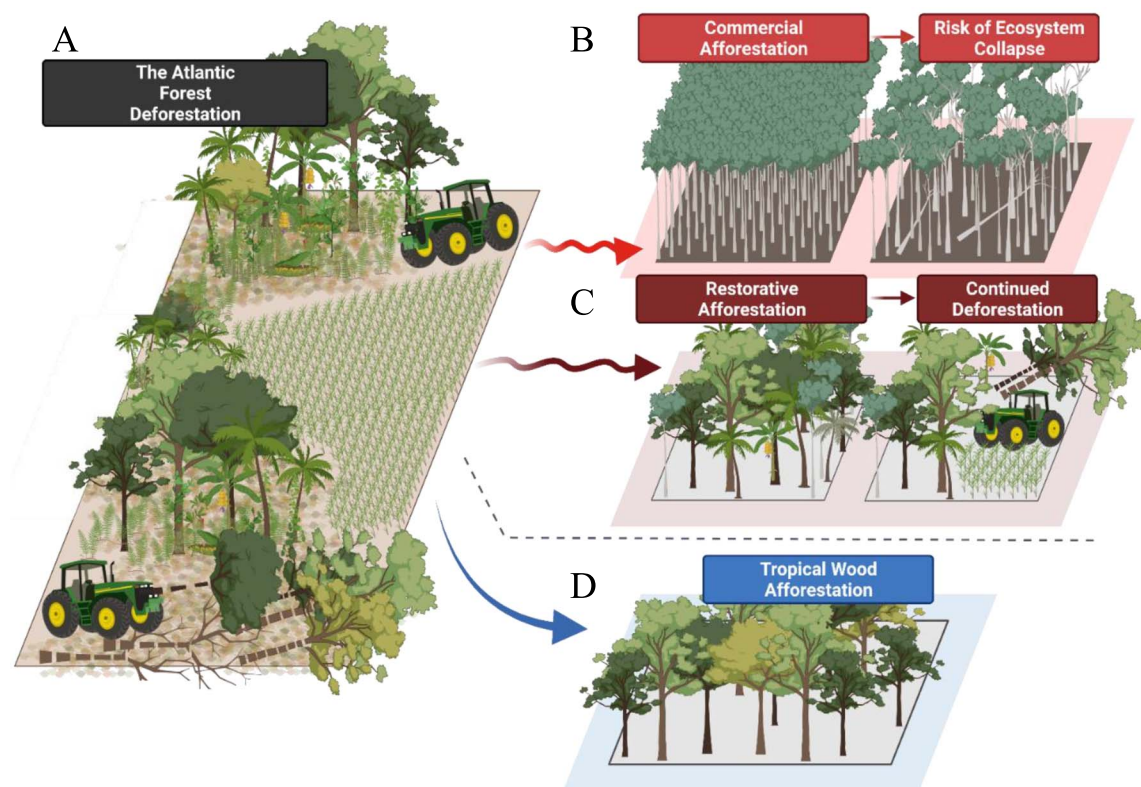
A major axis of functional variation among tree species of the Atlantic Forest is the divergence between fast-growing, short-lived, early successional (pioneer) species and slow-growing, long-lived, late-successional (non-pioneer) species (Shimamoto *et al.*, 2014). Many of the Leguminosae species belong to the former type. A good mixture of these two types of tree species ensures that biomass increases and carbon sequestration in reforestation continues over six or more decades (Shimamoto *et al.*, 2014). Studying an Atlantic Forest reforestation with 20 different native tree species, 2.5 years after planting, pioneer species showed higher survival rates, height and aboveground biomass than non-pioneer species (Campoe *et al.*, 2014). Legume tree species showed higher survival than non-legume, but similar height and aboveground biomass. Carbon assimilation was significantly higher among pioneer species, and similar across legume and non-legume species (Campoe *et al.*, 2014).

There are also differences in drought resistance strategies among tree species. Two common strategies are isohydric and anisohydric behaviour, describing the ability of the tree to cope

with water deficiency by stomatal regulation. To some extent, tree drought resistance is controlled by the vulnerability of the species' xylem to embolism (Klein *et al.*, 2014, 2018) at low water potentials. Values of 50 and 88 per cent embolism ( $P_{plc50}$ ,  $P_{plc88}$ ) are key indicators for plant water condition. Indeed, in two forest drought experiments in the Amazon Forest, tree species with higher vulnerability to embolism in the xylem had higher mortality, regardless of their successional type (Powell *et al.*, 2017). Across tropical forest ecosystems, pioneer tree species have higher hydraulic vulnerability than non-pioneer species (Oliveira *et al.*, 2021).

Due to its high-water availability, the tropical rainforest biome is characterized by tree species of high vulnerability to embolism and a mean  $P_{plc50}$  of  $\sim -2.8$  MPa found in 69 angiosperm tree species from different families (Choat *et al.*, 2012). Accordingly, among 10 Atlantic Forest tree species,  $P_{plc50}$  was measured to range from  $-0.4$  to  $-2.5$  MPa, and water potential at midday ranged between  $-0.4$  and  $-2.7$  MPa (Di Francescantonio *et al.*, 2020). However, some Amazon Forest canopy tree species were found to be more drought resistant than previously thought and reached a mean  $P_{plc50}$  of  $\sim -4$  MPa, similar to the values observed for temperate and Mediterranean forests (Ziegler *et al.*, 2019). In addition, a tree-ring study of seven legume tree species of the Atlantic Forest showed a diversity of growth responses to inter-annual differences in precipitation, and overall, a capacity of trees to continue growing under drought conditions (Macedo *et al.*, 2021). However, it can be argued that these tree species have not yet been exposed to harsh drought episodes as observed in more seasonal biomes (Klein *et al.*, 2014). Indeed, when precipitation was lower than average for a number of consecutive years in the Atlantic Forest, tree growth declined (Venegas-González *et al.*, 2018) and similar behaviour was observed in Bolivian forests (Mendivelso *et al.*, 2014). With climate change, some regions of the Atlantic Forests are projected to suffer up to a 50 per cent reduction in precipitation (Lyra *et al.*, 2018). Therefore, knowing which species will be more resilient to this new reality is crucial for planning restoration efforts.

Here, we present an investigation of the physiological mechanisms of tree growth, carbon assimilation and water-use in four key, native, high-quality wood-producing tree species of the Atlantic Forest. We examine two species of the Leguminosae including *Dalbergia nigra*, which is defined as an early to late secondary species (Pacheco *et al.*, 2013) and *Plathymenia foliolosa*, an early secondary species (de Moraes Junior *et al.*, 2019). The other two examined species belong to the family of Bignoniaceae and include *Zeyheria tuberculosa* – an early secondary species (Pagano and Scotti, 2010; Barroso *et al.*, 2021) and Lecythidaceae, *Cariniana legalis* – a late secondary species (Souza *et al.*, 2004). All four species have already been used in alternative reforestation approaches based on native species. The growth, carbon assimilation and water-use processes were measured using state-of-the-art techniques under both optimal and drought conditions. We quantified the effect of drought on growth by comparing growth rates before, during and following an induced drought period, and calculating drought resistance, recovery and resilience. In addition, micro-computer tomography (CT) was used to detect drought-induced xylem embolism. Based on the scientific literature on other Atlantic Forest tree species, we hypothesized that: (i) the higher carbon assimilation



**Figure 1** Deforestation of Brazil's Atlantic Forest and its alternative solutions. Cutting down native and primeval forests is motivated by clearing for agriculture and increasing demands for precious tropical wood (A). In many areas, reforestation is realized in the form of commercial plantations (B), lacking ecological restoration and risking ecosystem collapse. Restorative afforestation (C) maintains ecosystem integrity, yet deforestation continues due to sustained demands for tropical wood. Here we propose tropical wood afforestation with native species (D) to serve both reforestation and as a source for tropical wood. Created with BioRender (<https://biorender.com/>).

expected in the early successional species compared with the late-successional species is retained under drought. (ii) Due to its successional stage as an early secondary species and its diverse geographical distribution (Figure 2), *Plathymania* will exhibit the lowest stomatal control, and hence a more anisohydric behaviour compared with other species.

## Materials and methods

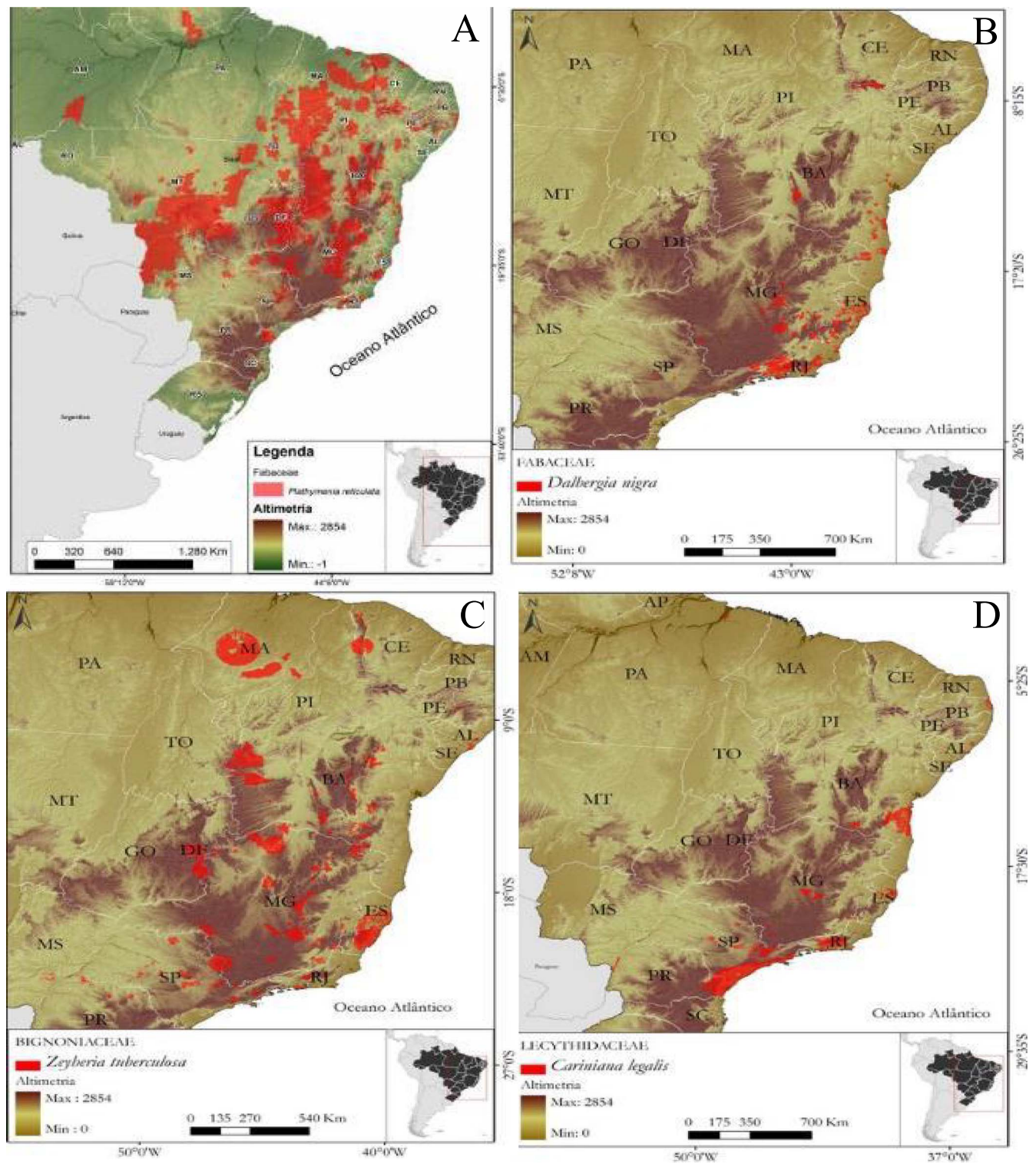
### Species selection and plant material

We studied four tree species: *P. foliolosa*, *D. nigra*, *Z. tuberculosa* and *C. legalis*. For simplicity, we will refer to each of the four species by its genus name in the following, i.e. *Plathymania*, *Dalbergia*, *Zeyheria* and *Cariniana*. These four species were chosen out of a group of 15 species identified by the Brazilian government as critical to ecological research objectives (Rolim et al., 2019). *Dalbergia*, commonly known as Brazilian rosewood, is a species of the Atlantic Forest that is distributed in southeastern Brazil (Figure 2; Ribeiro et al., 2011a; Costa et al., 2015). It has one of the most highly prized woods in Brazil. This led to a massive cutting of the tree. It is currently listed as 'Vulnerable' on the IUCN Red List. The *Plathymania* is distributed in the Atlantic Forest, but also occurs in the more inland Cerrado biome (Figure 2). There is a controversy about whether the *Plathymania* tree genus has one

or two species (i.e. *P. reticulata*, *foliolosa*; Lacerda et al., 2002; Warwick and Lewis, 2003). Its wood is rot-resistant and is widely used as structural timber. *Zeyheria* is endemic to Brazil, but its habitat has been widely devastated by encroaching agriculture, ranching and other developments. This, combined with charcoal production, is causing a decline in this species (Souza et al., 2017). It also produces high-quality wood used in construction, fences and to produce tools (Freitas-Silva et al., 2021). The *Cariniana* is one of the biggest trees in Brazil. The Atlantic Forest is its phyto-geographic domain and is geographically distributed in northeastern, southeastern and southern Brazil (Smith et al., 2016). Its wood is used for general construction purposes and carpentry (Guidugli et al., 2010). This demand and habitat loss endanger this species (Aragão et al., 2017).

### Greenhouse experiment setup, meteorology and soil moisture

The study was conducted between 19 October and 29 December 2020 at the greenhouse facility of the Weizmann Institute of Science, Rehovot, Israel (31°90'N; 34°80'E). The seeds of all four species were collected from a wide area around Espírito Santo and Bahia States (Brazil) and brought to Israel. Seeds were sown without any pretreatment into sowing trays and placed in semi-controlled glass greenhouses. Germination was



**Figure 2** Tropical wood tree species tested for reforestation of Brazil's Atlantic Forest. Maps showing the geographical distributions (red) of the four species: (A) *Plathymeria reticulata*. (B) *Dalbergia nigra*. (C) *Zeyheria tuberculosa* (D) *Cariniana legalis*. Distribution maps are from <http://cncflora.jbrj.gov.br/portal/>.

the fastest in *Plathymeria* but remained at 22 per cent after 2 weeks (Supplementary Figure S1). *Dalbergia* had the highest germination rates (75 per cent), followed by *Cariniana* (54 per

cent) and *Zeyheria* (39 per cent). The light in the greenhouse was 80 per cent of the ambient light (due to decay through the glass), the temperature was  $20 \pm 5^\circ\text{C}$  and humidity was increased to

~70 ± 20 per cent using a fogger (Supplementary Figure S2; Temperature and humidity data were collected using EasyLog USB Version 7.6.0.0 installed in the greenhouse). The seeds were irrigated every 2–3 days to keep the soil moist. Thirty-five days later, the seedlings were transferred into 5-L pots containing 50/50 peat and tuff mixture (tuff particle size of 4–8 cm) for another 2.5 months. Then, nine seedlings were taken from each species for each of the two treatments (control, drought). Unfortunately, water leakage from the greenhouse roof reached a small number of seedlings; hence, data from these individuals were excluded from the analysis. Therefore, we have several missing measurements in the drought treatment. Seedlings were organized in the greenhouse in blocks (Figure 3) to ensure no spatial biases among species and treatments. The pots were irrigated with a drip system following a dynamic irrigation plan. We calculated that to simulate an annual rainfall amount of 1500 mm, as is common in many parts of the Atlantic Forest, irrigation should be translated to 4.3 L week<sup>-1</sup> per pot, supplied in 60–80 min drip irrigation given in 3–4 days intervals. We started the experiment with 4.3 L week<sup>-1</sup> per pot across all control plants (Supplementary Figure S3). Simultaneously, drought was imposed by a reduction of 90 per cent of this amount to mimic an intense short-term water stress condition. In practice, our irrigation amounts were excessive, so we gradually reduced them to avoid flooding in control plants on the one hand and induce drought in drought plants on the other hand. Species-specific water-use patterns meant that irrigation amounts were reduced from 4.3 to 2 L week<sup>-1</sup> and from 0.4 L to 0.3 L week<sup>-1</sup> in the legume control and drought groups, respectively. At the same time, irrigation amounts were reduced to 0 L week<sup>-1</sup> in drought non-legume plants and 1 L week<sup>-1</sup> in the control treatment. The timing of re-irrigation was determined based on the species-specific pre-drought levels of photosynthesis and water potential. During the re-irrigation of drought plants, their irrigation amounts were increased back to match those in control plants, i.e. 2 L week<sup>-1</sup> in legume and 1 L week<sup>-1</sup> in non-legume plants (Supplementary Figure S3). Once in 2 weeks, seedlings were fertilized with 0.25 mL soluble fertilizer ((4 N-2.5P-6 K) + 2 per cent Ca + 0.5 per cent Mg).

### Leaf gas exchange, water-use efficiency

Leaf gas exchange was measured once a week during the morning hours (8:00–11:30). For 9 consecutive weeks, every week, three to four plants were chosen from each species and treatment and were measured in the same order ( $n = 271$ , 14 observations were deducted from the analysis due to the water leakage). These measurements were performed using a mobile carbon assimilation, infra-red gas analyser system (IRGA; Walz, Effeltrich, Germany). A standard leaf chamber (Walz 3010-S) with a top light emitting diode light source (Walz 3040-L) was set to the constant ambient light intensity for each day of measurements (photosynthetically active radiation ranging between 350 and 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$  between measurement days). The CO<sub>2</sub> level was set to 400 ppm; flow rate was set to 750  $\mu\text{mol s}^{-1}$ ; and the impeller to speed 7; temperature was set as ambient with an offset of 1°C. The IRGA provided instantaneous rates of net assimilation and transpiration, complemented by a list of measurement parameters, including vapour pressure deficit (VPD).

The system used transpiration and VPD to generate stomatal conductance ( $g_s$ ). In turn, the ratio between carbon assimilation and  $g_s$  provided the intrinsic water-use efficiency. In *Plathymenia* and *Dalbergia*, leaves were smaller than the IRGA chamber area, and hence leaf area has to be accounted for. Due to repeated weekly measurements, we could not afford to sacrifice these leaves for area measurement. Instead, we took advantage of the homogenous leaf size in our seedlings and measured leaf area from randomly sampled five leaves, which we photographed with a known scale. Photographs were used to calculate leaf surface area (cm<sup>2</sup>) using image J ([github.com/imagej/imagej1](https://github.com/imagej/imagej1)). We used the measured surface area of all five leaves to normalize the photosynthesis rate per leaf area unit ( $\mu\text{mol CO}_2 \text{ m}^{-2}$  of measured leaf s<sup>-1</sup>).

### Xylem water potential and leaf water relations

Xylem water potential was measured weekly using a pressure chamber (model 1515d PMS Instrument Company, Albany, OR, USA). The measurement was performed over 9 consecutive weeks ( $n = 218$ , 14 observations were excluded from the analysis due to the water leakage described above). From each combination (species and treatment), we took small branches from three to four plants measured at mid-day (12:00–14:30). To calculate the leaf water status, we plotted the stomatal conductance as a function of the xylem water potential for each species. For this, we included only individuals with both stomatal conductance and xylem water potential measured on the same day. Then, from the trendline, we extrapolated the  $\Psi_{g_{s50}}$  (the average water potential at 50 per cent stomatal conductance). We are aware that isohydric behaviour can be reflected in several physiological parameters, such as changes in water potential during the day (e.g.  $\Psi_{\text{predawn}} - \Psi_{\text{mid day}}$ ) or changes in water potential throughout the year. However, here we chose to look at isohydric behaviour as the relationship between stomatal conductivity and water potential, as shown in Klein (2014).

### Xylem embolism

To detect embolism inside xylem vessels, we designed an experiment using an X-ray micro-CT (Zeiss X-ray 209 microscopy, Pleasanton, USA). The micro-CT allowed us to detect embolism over time by scanning the whole seedling. Thirty-five days after sowing, one seedling from each species and treatment was transferred into a 1-L pot (of the same media as above). These seedlings were grown together with the others in the same greenhouse, yet with a different irrigation plan (Supplementary Figure S3). Before scanning, each tree was wrapped in Parafilm and then placed in the micro-CT. We set the parameters of the micro-CT to take 720 projections over a 180°-rotation range, using an optical magnification of  $\times 0.5$  to increase the field of view. Voltage and current were set to 46 kV and 165  $\mu\text{A}$ , respectively. The resulting voxel size ranged between 3.97 and 6.41  $\mu\text{m}$ . We scanned the drought seedlings once a week, and the control seedlings were scanned only at the beginning and end of the experiment. Out of the four species, only *Plathymenia* survived the entire experiment. After the scanning, images were reconstructed according to Vogelgesang *et al.* (2016), and the slice of the same orientation



**Figure 3** Layout of the greenhouse experiment on tropical wood tree species tested for reforestation of Brazil's Atlantic Forest in a semi-controlled glass greenhouse at the Weizmann Institute of Science, Israel (a). Blue circles denote prescribed irrigation (C for control), and orange circles denote irrigation manipulation (D for drought). *P*, *Plathymenia foliolosa*; *D*, *Dalbergia nigra*; *Z*, *Zeyheria tuberculosa*; and *C*, *Cariniana legalis* (b). Numbers denote the replicates. The small circles represent the seedlings for the micro-CT treatment.

on the plant was selected for quantitative analysis in ImageJ/Fiji image-processing freeware, a Java-based distribution of ImageJ ([www.fiji.sc](http://www.fiji.sc); Schindelin et al., 2012; Rueden and Eliceiri, 2019). We assessed the ratio of air-filled vs. water-filled vessels by excluding the pith, the primary xylem and the resin channels, as well as other non-conductive areas as determined by the reference scan. Brightness and contrast were automatically adjusted for each sample to improve the detection of water- vs. air-filled conduits and thus permitting the estimate of percentage loss of conductive area. Differentiation into the air- vs. water-filled vessels was confirmed by dye staining on the same samples analysed by micro-CT.

### Leaf $\delta^{13}\text{C}$

To detect the ratio between  $^{12}\text{C}$  and  $^{13}\text{C}$  in the four tree species, samples were examined during three stages in the experiment – in the beginning, before the end of the dry cycle and after rewatering. At each stage, mature leaves were taken from three to four plants in each species and treatment ( $n = 71$ , 5 observations were deducted from the analysis due to the water leakage). The leaves

were dried for 48 h in a  $60^\circ\text{C}$  oven. Ground tissue samples were weighed to  $1.0 \pm 0.2$  mg and were measured using a combustion module attached to a laser isotopic analyser (Picarro G2131-I, Santa Clara, CA, USA).

### Growth and carbon-use efficiency

Stem length was measured once a week in all seedlings ( $n = 521$ , 23 observations were excluded from the analysis due to the water leakage). Stem diameter was measured in six seedlings of each species, except for *Cariniana*, where all nine seedlings were measured ( $n = 386$ , 14 observations were excluded from the analysis due to the water leakage). Stem measurements (diameter and length) were used to calculate relative growth rates as shown in Hoffmann and Poorter (2002):

$$\text{Relative growth rate (diameter or length)} = \frac{\ln(\text{stem measurement}_2) - \ln(\text{stem measurement}_1)}{t_2 - t_1} \quad (1)$$

Because the experiment was finished without sacrificing and weighing the plants, seedling biomass was calculated from other measurements. First, the wood density of each species was determined. Since we used seedlings, we didn't take the wood density value from the literature but rather calculated it on small branch samples by dividing biomass by volume. Then, the volume of the stem was assessed using the measurement of height (h) and basal radius (R), assuming a cylinder shape.

$$\text{volume} = \pi * R^2 * h \quad (2)$$

Then, we multiplied the volume by the density, to obtain the biomass of each plant. The weekly average biomass was divided by the weekly average assimilation to calculate the carbon-use efficiency (CUE).

### Drought resistance, recovery and resilience

To study tree drought responses, we followed the approach of Lloret *et al.* (2011), developed for tree-ring data and applied it to assimilation rates. Briefly, we calculated the following three components: resistance is the ratio between assimilation during the drought (Dr) and the assimilation during the respective pre-drought (PreDr) period:

$$\text{Resistance} = \frac{\text{Dr}}{\text{PreDr}} \quad (3)$$

Recovery is the ratio between the assimilation in the period after the drought (PostDr) and during drought:

$$\text{Recovery} = \frac{\text{PostDr}}{\text{Dr}} \quad (4)$$

Resilience is the capacity to reach pre-disturbance assimilation levels, and is estimated as the ratio between the assimilation after and before disturbance (Sousa, 1980; Tilman and Downing, 1994):

$$\text{Resilience} = \frac{\text{PostDr}}{\text{PreDr}} \quad (5)$$

### Statistical analysis

Statistical analysis was performed using Jamovi (Version 1.6.23). Although seedlings were organized in the greenhouse in blocks, we could not analyse the data using randomized block design since not all seedlings of all treatment combinations could be measured at the same time. Therefore, we used a set of mixed models to test differences among tree species/treatment/time in carbon assimilation, xylem water potential, water-use efficiency (WUE),  $\delta^{13}\text{C}$  (4 species, 2 treatments, 2–4 replicates of each), and relative growth rate of stem diameter and stem length (5–9 replicates of each species) while including individual plant subjects as random variables. For carbon assimilation and WUE, we also included the time of day of each measurement as a covariate. For xylem water potential, we included the amount of irrigation as an additional covariate. These were followed

by a thorough examination of the simple effects contrasting the differences between the control and drought treatments of specific weeks. To test stomatal conductance as a function of the xylem water potential, we used a generalized linear model, using a negative binomial distribution of the residuals, including xylem water potential as a covariate and species and treatment (control/drought) as fixed factors. We repeated the same analysis for each species separately.

## Results

### Carbon assimilation, relative growth rate and CUE

Overall, our model explained ~50 per cent of the variation in carbon assimilation among tree species (marginal R-squared = 0.539, conditional R-squared = 0.692). Carbon assimilation was higher in the two legume species (Figure 4, Supplementary Table S2; *Plathymentia*, *Dalbergia*;  $4.8 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) than in *Cariniana* ( $4 \pm 0.25 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and more so than in *Zeyheria* (Table 1:  $2.5 \pm 0.18 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Species:  $F_{3,35.6} = 7.754$ ,  $P < 0.001$ ). All species exhibited a reduction in carbon assimilation after ~10 days, which was related to the seasonal cooling that decreased the temperature in the greenhouse to a suboptimal temperature for these tropical species (Supplementary Figure S2). However, despite the drought, there was no significant difference in carbon assimilation between the control and drought plants across all four species ( $\sim 4 \mu\text{mol m}^{-2} \text{s}^{-1}$  for both treatments; Treatment:  $F_{1,36.7} = 0.203$ ,  $P = 0.655$ ). Still, the interaction between treatment and species was significant (Treatment  $\times$  Species:  $F_{3,35.6} = 3.808$ ,  $P = 0.018$ ). Probably since in *Cariniana*, we observed an opposite pattern. Specifically, under the drought treatment, we observed a sharp reduction in carbon assimilation which flattened after ~30 days of drought (contrast day~30:  $t_{150} = -2.134$ ,  $P = 0.034$ ). However, a similar, yet weaker trend was observed for the irrigated treatment. It is also worth mentioning that the greenhouse room temperature dropped by 8°C throughout the experiment, which could explain the total decrease in carbon assimilation in the control treatment. In terms of carbon use for growth, we saw a significantly slower relative growth under drought, compared with the control treatment only in *Dalbergia*, unlike other species that did not differ between treatments (Figure 5, Supplementary Figure S4, S5, S6; Supplementary Table S1). *Cariniana* did not show any response to the drought treatment (Supplementary Table S2; total change in stem length  $1.87 \pm 0.09 \text{ mm}$  and  $1.53 \pm 0.09 \text{ mm}$  and stem diameter:  $14.94 \pm 1.05 \text{ cm}$  and  $13.11 \pm 1.05 \text{ cm}$  in drought and control treatment, respectively). In terms of the use of carbon to produce biomass (CUE), there was a general increase among species with the progression of the experiment (Fig. S7). In all species except for *Dalbergia*, the irrigated plants used a greater (but not significantly) amount of their assimilates for biomass production than the drought-exposed plants (Supplementary Table S2).

### Hydraulic sensitivity to drought and leaf water relations

Our model explained >50 per cent of the variation among tree species in xylem water potential (marginal R-squared = 0.564, conditional R-squared = 0.648). There was a significant difference

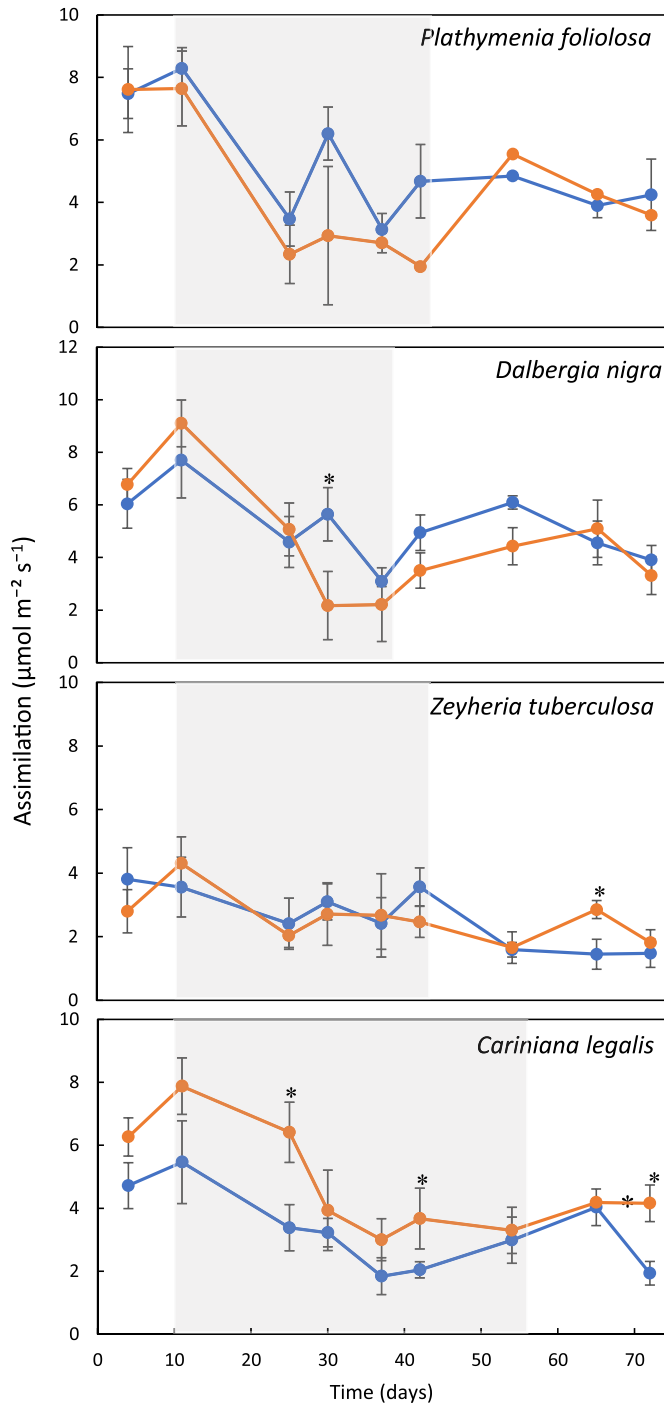
**Table 1** Mixed model results (F-values) for the effects of treatment, species, time and their interactions on sapling assimilation, xylem water potential, WUE,  $\delta^{13}C$  and relative growth rate (diameter and length). The degrees of freedom in the model (Num df), degrees of freedom associated with the model errors (Den df), and *P*-values (*P*) are reported. Significant effects ( $P < 0.05$ ) are denoted in bold.

Parameter	Components	F-value	Num df	Den df	<i>P</i> -value
Assimilation	Treatment	0.203	1	36.7	0.655
	<b>Species</b>	<b>7.754</b>	<b>3</b>	<b>35.6</b>	<b>&lt; 0.001</b>
	<b>Time</b>	<b>24.962</b>	<b>8</b>	<b>156.6</b>	<b>&lt; 0.001</b>
	Hour	0.901	1	42.5	0.348
	<b>Treatment × Species</b>	<b>3.808</b>	<b>3</b>	<b>35.6</b>	<b>0.018</b>
	<b>Treatment × Time</b>	<b>2.661</b>	<b>8</b>	<b>157.5</b>	<b>0.009</b>
	<b>Species × Time</b>	<b>2.306</b>	<b>24</b>	<b>155.2</b>	<b>0.001</b>
	Treatment × Species × Time	0.654	24	153.3	0.888
Xylem water potential	<b>Treatment</b>	<b>4.74003</b>	<b>1</b>	<b>75.9</b>	<b>0.033</b>
	<b>Species</b>	<b>14.83156</b>	<b>3</b>	<b>52.1</b>	<b>&lt; 0.001</b>
	<b>Time</b>	<b>4.30368</b>	<b>9</b>	<b>130</b>	<b>&lt; 0.001</b>
	Irrigation	0.00129	1	102.7	0.971
	Treatment × Species	0.93902	3	50.5	0.429
	<b>Treatment × Time</b>	<b>7.38275</b>	<b>9</b>	<b>130</b>	<b>&lt; 0.001</b>
	<b>Species × Time</b>	<b>2.77711</b>	<b>25</b>	<b>125.7</b>	<b>&lt; 0.001</b>
	Treatment × Species × Time	1.26566	24	126	0.202
WUE	Treatment	0.113	1	198	0.737
	Species	1.862	3	198	0.137
	Time	1.72	8	198	0.096
	Hour	1.014	1	198	0.315
	Treatment × Species	1.833	3	198	0.142
	Treatment × Time	0.346	8	198	0.947
	Species × Time	1.254	24	198	0.201
	Treatment × Species × Time	0.822	24	198	0.706
$\delta^{13}C$	Treatment	0.228	1	26.1	0.637
	<b>Species</b>	<b>9.829</b>	<b>3</b>	<b>26.1</b>	<b>&lt; 0.001</b>
	<b>Time</b>	<b>6.003</b>	<b>2</b>	<b>32.6</b>	<b>0.006</b>
	<b>Treatment × Species</b>	<b>3.014</b>	<b>3</b>	<b>26.1</b>	<b>0.048</b>
	Treatment × Time	1.228	2	32.6	0.306
	<b>Species × Time</b>	<b>3.324</b>	<b>6</b>	<b>28.2</b>	<b>0.013</b>
	Treatment × Species × Time	0.960	6	28.2	0.469
	Treatment	1.06	1	39.3	0.309
Diameter RGR	Species	0.747	3	35.5	0.531
	<b>Time</b>	<b>16.203</b>	<b>7</b>	<b>284.9</b>	<b>&lt; 0.001</b>
	Treatment × Species	1.743	3	42.7	0.173
	Treatment × Time	0.268	7	284.9	0.966
	Species × Time	0.709	21	284.9	0.823
	Treatment × Species × Time	0.336	21	284.9	0.998
	Treatment	3.656	1	58.8	0.061
	<b>Species</b>	<b>3.843</b>	<b>3</b>	<b>58.7</b>	<b>0.014</b>
Length RGR	<b>Time</b>	<b>39.239</b>	<b>7</b>	<b>396.9</b>	<b>&lt; 0.001</b>
	Treatment × Species	0.438	3	58.7	0.726
	Treatment × Time	1.151	7	396.9	0.33
	<b>Species × Time</b>	<b>1.77</b>	<b>21</b>	<b>396.8</b>	<b>0.02</b>
	Treatment × Species × Time	0.758	21	396.8	0.771

in xylem water potential between the control and drought-exposed plants of all species (Figure 6; Table 1: Treatment:  $F_{1,75.9} = 4.74$ ,  $P = 0.033$ ). The different irrigation regimes did not explain much of the variation in xylem water potential

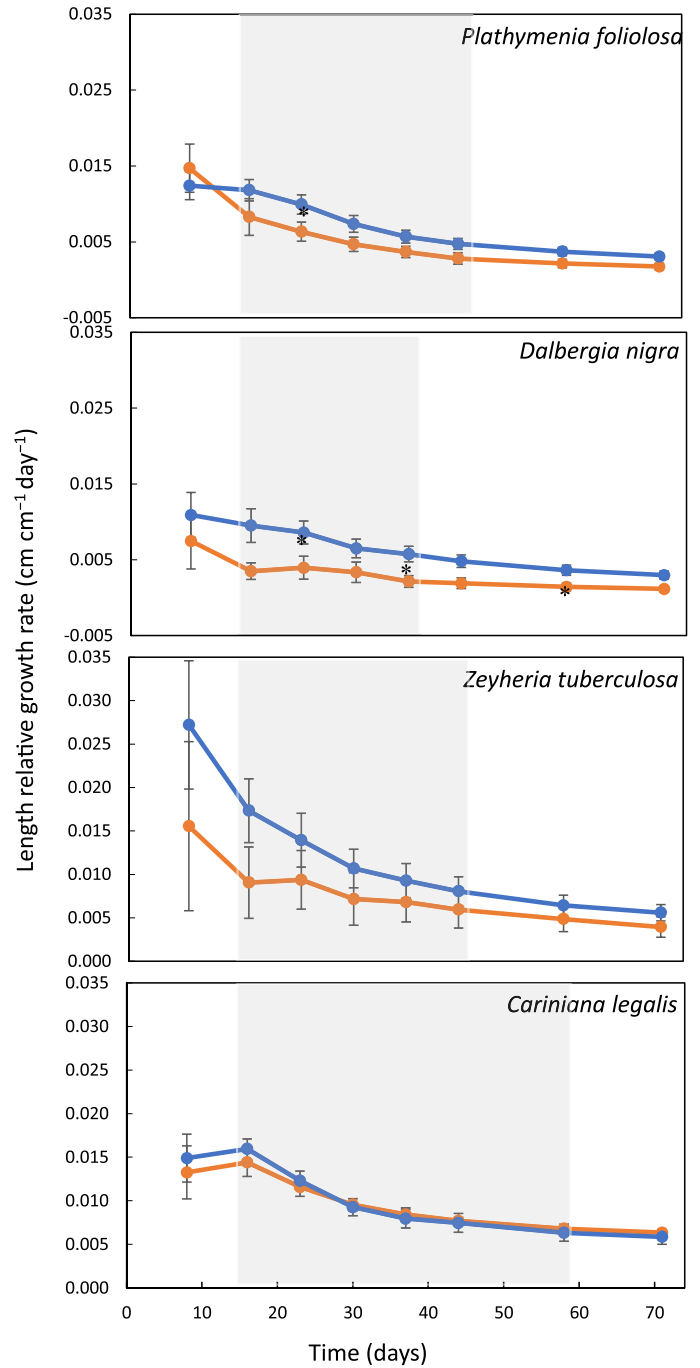
(Irrigation:  $F_{1,102.7} = 0.0012$ ,  $P = 0.917$ ). However, when we added the irrigation regime to the model, we saw that species did not respond significantly differently to the drought treatment, unlike significantly different responses in the model without the





**Figure 4** Carbon assimilation dynamics in tropical wood tree species tested for reforestation of Brazil’s Atlantic Forest. Prescribed irrigation (blue) and irrigation manipulation (orange; with drought denoted by the grey area). Data points are means  $\pm$ SE ( $n=2-4$ ). The single asterisk denotes a significant difference between the control and drought treatments in a specific measurement date: significant effects at the 0.05 significance level are denoted by \*.

irrigation regime (Treatment\*species:  $F_{3,50.5}=0.939$ ,  $P=0.429$ ). Yet, in *Plathymenia*, we observed a sharp reduction in xylem water potential (contrast day  $\sim 30$ :  $t_{10,37}=3.09$ ,  $P=0.011$ ; an



**Figure 5** Length relative growth rate in tropical wood tree species tested for reforestation of Brazil’s Atlantic Forest. Prescribed irrigation (blue) and irrigation manipulation (orange; with drought denoted by the grey area). Data points are means  $\pm$ SE ( $n=4-9$ ). The single asterisk denotes a significant difference between the control and drought treatments on a specific date of measurement: significant effects at the 0.05 significance level are denoted by \*.

average of  $-2.35 \pm 0.22$  MPa and  $-1.36 \pm 0.05$  MPa in drought and control treatment respectively) with a minimum  $-5.20$  MPa after  $\sim 40$  days of drought. We saw a similar reduction for

**Table 2** Generalized linear model ( $\chi^2$ -values) for the stomatal conductance as a function of the xylem water potential. Degrees of freedom associated with the model errors (df), and *P*-value (*P*) are reported. Significant effects (*P* < 0.05) are denoted in bold.

Species	Components	$\chi^2$	df	<i>P</i>
Overall	Treatment	0.0614	1	0.804
	<b><math>g_s</math> vs. xylem water potential</b>	<b>8.0461</b>	<b>1</b>	<b>0.005</b>
	<b>Species</b>	<b>26.3177</b>	<b>3</b>	<b>&lt; 0.001</b>
<i>P. foliolosa</i>	Treatment × Species	3.3287	3	0.344
	<b><math>g_s</math> vs. xylem water potential</b>	<b>8.766</b>	<b>1</b>	<b>0.003</b>
	Treatment	0.743	1	0.389
<i>D. nigra</i>	<b><math>g_s</math> vs. xylem water potential</b>	<b>7.28</b>	<b>1</b>	<b>0.007</b>
	Treatment	1.27	1	0.261
<i>Z. tuberculosa</i>	$g_s$ vs. xylem water potential	3.5127	1	0.061
	Treatment	0.0765	1	0.782
<i>Ceratispa legalis</i>	<b><math>g_s</math> vs. xylem water potential</b>	<b>4.6904</b>	<b>1</b>	<b>0.03</b>
	Treatment	0.0353	1	0.851

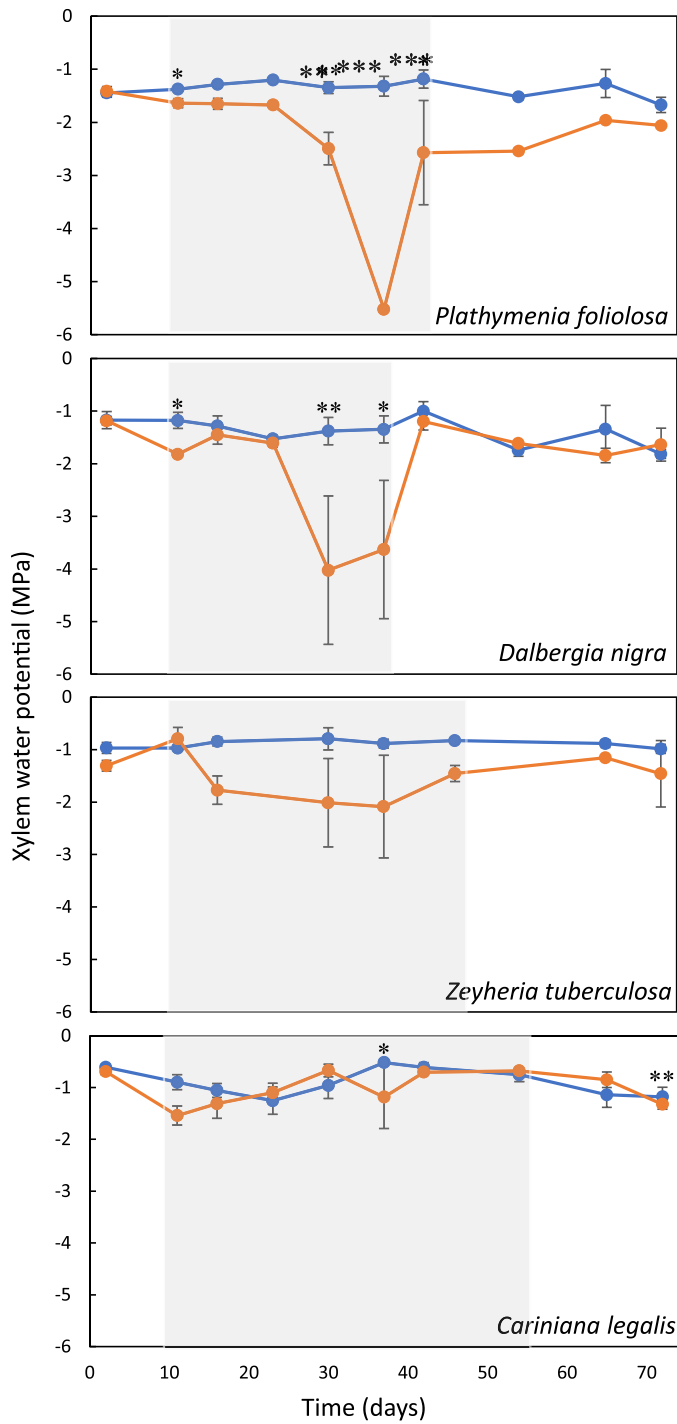
*Dalbergia*, reaching a minimum after ~30 days (contrast day ~30:  $t_{18} = -2.8262$ ,  $P = 0.011$ ). *Zeyheria* had only a moderate decrease in water potential at ~15 days of drought, and *Cariniana* water potential did not respond to drought at all (Average of  $-1.0 \pm 0.08$  MPa and  $-0.86 \pm 0.07$  MPa in drought and control treatment, respectively). In the irrigated plants, micro-CT scans of the xylem of *Plathymentia* showed only a negligible increase in embolism between the two scans taken 2 and 70 days after the experiment began (Figure 7). In contrast, in the scans from the drought-exposed plants, embolism gradually increased during the drought, from <1 per cent on Day 10 to 8 per cent on Day 34. Unexpectedly, an apparent shrinkage of the embolism was observed between the scan of Day 70 and Day 94, which prevailed after rewatering (Figure 7A–C). After ~35 days of drought, embolism slightly increased for another 35 days (~25 after rewatering the plant). Then, until ~50 days after rewatering, we saw a reduction of the embolism to about half of the most expanded range. Rates of embolism were higher in the two other species, increasing steadily from 10 per cent to 33 per cent in *Dalbergia* and from 7 per cent to 27 per cent in *Cariniana* (Figure 7, Fig. S8A–D). The scanned drought-exposed *Zeyheria* plant did not survive. Since we only had one repetition for every species and treatment, we could not analyse this result statistically. About the effect of xylem water potential ( $\Psi_{\text{xylem}}$ ) on the stomatal conductance ( $g_s$ ), overall, water potential ranged between  $-0.44 < \Psi_{\text{xylem}} < -5.52$  MPa at  $g_s$  of  $0$ – $192$  mol  $\text{H}_2\text{O m}^{-2} \text{ s}^{-1}$  (Figures 6 and 8; Supplementary Table S2). Across species, water potential at 50 per cent stomatal conductance ( $\Psi_{g_s50}$ ; we calculate only individuals with both stomatal conductance and xylem water potential measured on the same day) was significantly correlated with  $g_s$  (Table 2; Xylem water potential:  $\chi^2_1 = 8.0461$ ,  $P = 0.005$ ) with an overall  $R^2$  of 0.246. Still, this correlation was different between species (Species:  $\chi^2_3 = 26.31$ ,  $P = <.001$ ). Legume species showed lower  $\Psi_{g_s50}$  than non-legume. In *Dalbergia*,  $\Psi_{g_s50}$  was the lowest, whereas in *Zeyheria* it was the highest (Figure 8;  $-3.3$  and  $-0.8$  MPa, respectively). For the *Cariniana*, there was no clear trendline was found.

### WUE and $\delta^{13}\text{C}$

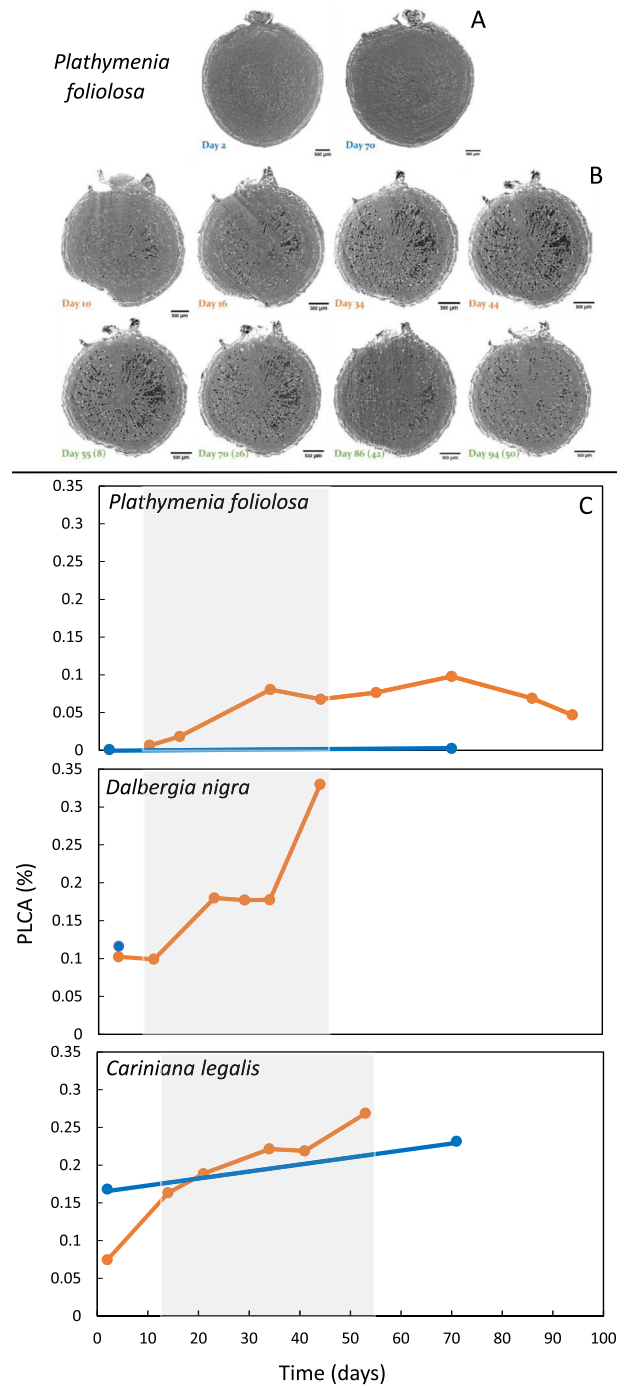
Overall, our model explained ~20 per cent of the variation in WUE among tree species (marginal R-squared = 0.229, conditional R-squared = 0.229). Across all species, WUE fluctuated between 0.05 and  $0.24 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  (Figure 9). Among species, WUE was marginally higher in non-legume than legume species ( $0.119 \pm 0.01 \text{ CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  and  $0.088 \pm 0.003 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  for non-legume and legume, respectively). The latter had stable values along the experiment, with no effect of drought. In contrast, non-legume species showed large fluctuations, with a trend of higher values in drought-exposed than control plants in *Cariniana* in a few of the measurement days (yet these differences were non-significant).  $\delta^{13}\text{C}$  showed a significant difference in leaf tissues across species (Figure 10; Table 1: Species:  $F_{3, 26.1} = 9.829$ ,  $P < 0.001$ ; Fig. S9) and time (Time:  $F_{2, 32.6} = 6.003$ ,  $P = 0.006$ ). Nevertheless, each species responds to the treatment differently (Treatment × Species:  $F_{3, 26.1} = 3.041$ ,  $P = 0.048$ ). Unexpectedly, leaf tissues were slightly enriched with  $^{13}\text{C}$  in control plants compared with the drought plants, yet the difference was non-significant (Treatment:  $F_{1, 26.1} = 0.228$ ,  $P = 0.637$ ; control:  $-28.33\%$ ; drought:  $-28.49\%$ ). Among species, *Zeyheria* and *Cariniana* were more enriched in  $^{13}\text{C}$  compared with the two legume species (Supplementary Table S2: non-legume:  $-27.6 \pm 0.19\%$ , legume:  $-29.1 \pm 0.16\%$ ). This is in line with the higher WUE for non-legume than legume species (Figure 9).

### Drought resistance, recovery and resilience

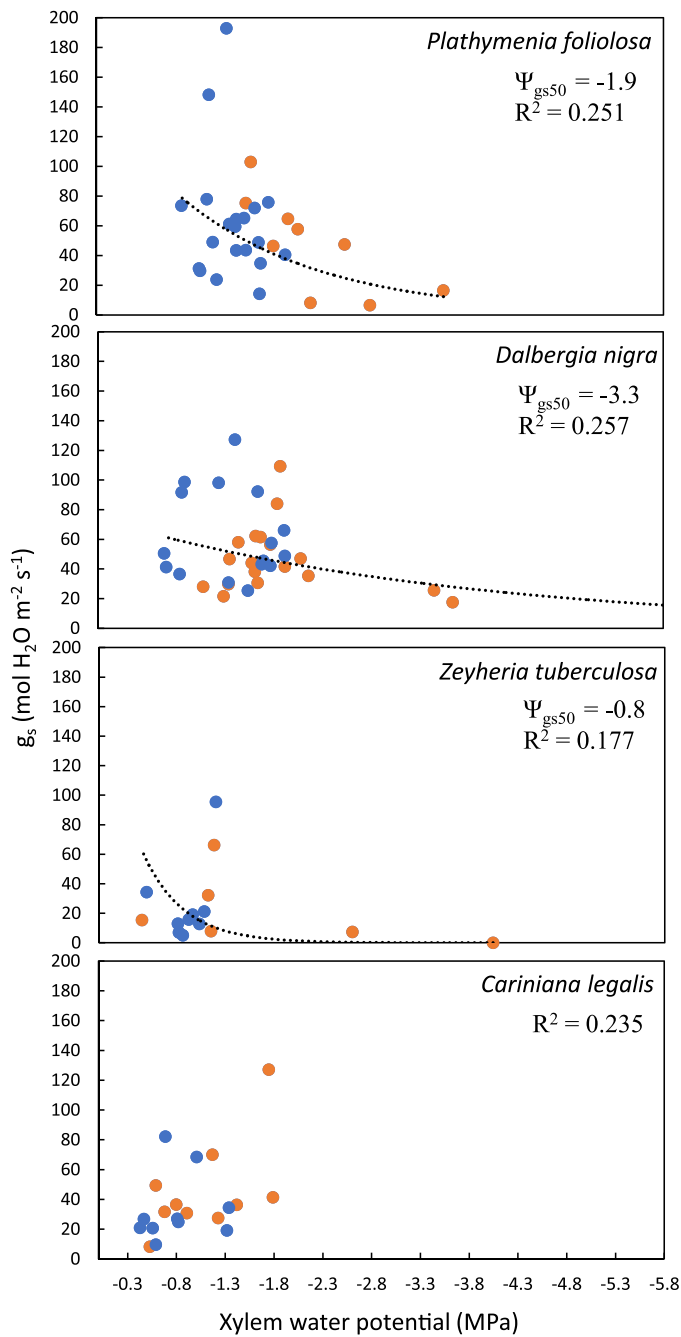
Across species and treatments, drought resistance was the smallest component (Lowest index; Fig. S10), which means that the carbon assimilation rate was lower during the drought period than prior to it (Figure 4). The recovery was high in most species and treatments, which indicates that following re-irrigation, plants assimilated more carbon than during the drought. These trends were consistent across species, but less so in *Zeyheria*, where recovery was meagre (< 1), and the other components were higher than in the other species.



**Figure 6** Xylem water potential dynamics in tropical wood tree species tested for reforestation of Brazil’s Atlantic Forest. Prescribed irrigation (blue) and irrigation manipulation (orange; with drought denoted by the grey area). Data points are means  $\pm$ SE ( $n=1-4$ ). Asterisks denote a significant difference between the control and drought treatments on a specific date of measurement: significant effects at 0.05 and 0.01 are denoted by \* and \*\*, respectively.



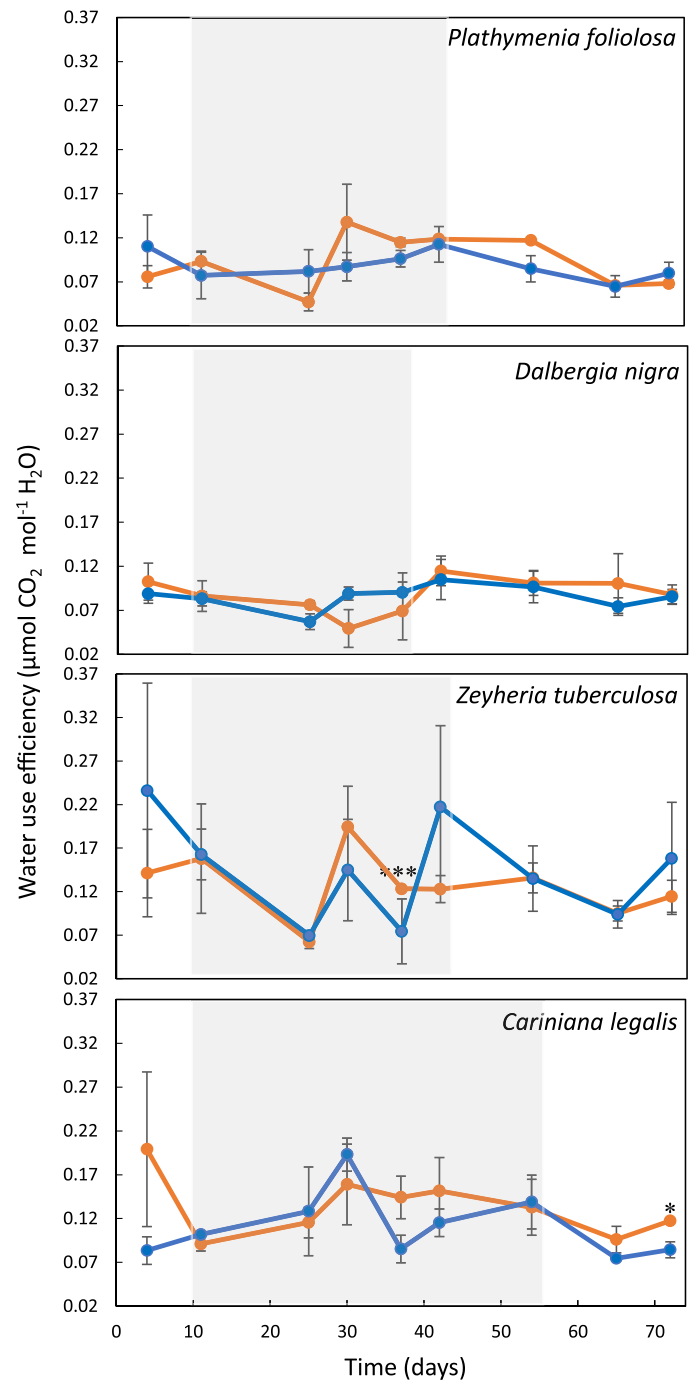
**Figure 7** The effect of irrigation manipulation on the conductive area in the Atlantic Forest native tree species *P. foliolosa*, *D. nigra* and *Ceratispa legalis*. Slices from micro-CT scans showing the embolism dynamics for *Plathymenia* (black dots) of irrigated tree (A; blue colour) and drought-exposed tree (B; orange colour represent the drought period; green colour represent the re-irrigation period). Days are numbered according to the number of days passed since the experiment was initiated. Measured values ( $n=1$ ) are the calculated percentages of embolized vessels under prescribed irrigation (blue) and irrigation manipulation (orange; with drought denoted by the grey area). Slices from micro-CT scans (for *Dalbergia* and *Cariniana*) showing the embolism dynamics are presented in the supplementary.



**Figure 8** Stomatal conductance as a function of the xylem water potential in tropical wood tree species tested for reforestation of Brazil's Atlantic Forest. Prescribed irrigation (blue) and irrigation manipulation (orange). We included only individuals with both stomatal conductance and xylem water potential was measured on the same day. From the trendline (dashed line), we extrapolated the  $\Psi_{gs50}$  (the average water potential at 50 per cent stomatal conductivity).

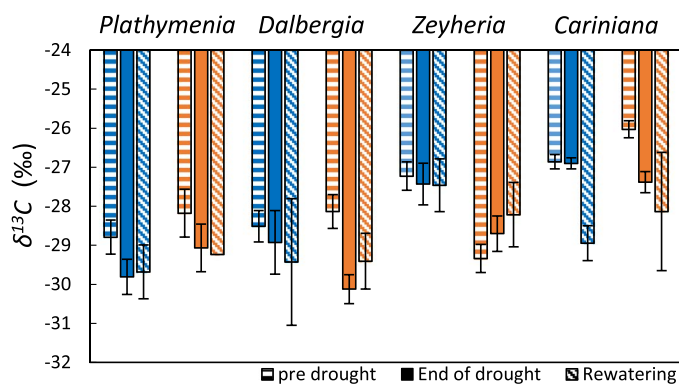
## Discussion

In preparation for enhancing the reforestation of Brazil's Atlantic Forest, while avoiding further deforestation of precious wood (Figure 1), this study examined growth and drought responses



**Figure 9** WUE dynamics in tropical wood tree species tested for reforestation of Brazil's Atlantic Forest. Prescribed irrigation (blue) and irrigation manipulation (orange; with drought denoted by the grey area). Data points are means  $\pm$  SE ( $n = 2-4$ ). The single asterisk denotes a significant difference between the control and drought treatments in a specific measurement date: significant effects at the 0.05 significance level are denoted by \*.

of four native tropical tree species with potential to produce high-quality wood. Each of the species showed a unique set of responses, indicating different growth strategies under mesic and



**Figure 10**  $\delta^{13}\text{C}$  in leaf tissues of tropical wood tree species tested for reforestation of Brazil's Atlantic Forest. Prescribed irrigation (blue) and irrigation manipulation (orange). Measurements were performed before drought (horizontal hatching), before the end of the drought (solid) and during rewatering (diagonal hatching). Bars are means  $\pm$  SE ( $n = 1-4$ ).

xeric conditions. Still, a divergence was identified between the two legume species and the two non-legume species. Based on our results, we reject our first hypothesis that the higher carbon assimilation expected in the early successional species compared with the late-successional species is retained under drought. Growth and carbon assimilation were higher in the legume species compared with non-legume species, only partly matching the successional hierarchy of the species. Our results show that although *Dalbergia* is defined as an early to late secondary species, in our experiment it behaved more like a pioneer species. Similar behaviour of *Dalbergia* has previously been reported by Carlos *et al.* (2018). Also, *Zeyheria* is reported in the literature as an early secondary species with fast growth and high canopy density. Also, this species is known for its ability to grow well in degraded area (Barroso *et al.*, 2021). In this study, *Zeyheria* performed more like a late-successional species. It exhibited low assimilation, high WUE, relatively mild xylem water potential and low stomatal conductance (Figures 4, 6, 8 and 9). The second hypothesis, that due to its successional stage as an early secondary species and its diverse geographical distribution (Figure 2), *Plathymenia* will exhibit the lowest stomatal control – a more anisohydric behaviour, compared with the other species, was as well rejected. The  $\Psi_{gs50}$  of the *Dalbergia* was lower than that of the *Plathymenia* ( $-3.3$  and  $-1.9$  MPa, respectively). Yet, both legumes had lower values (lower stomatal regulation) than the non-legume species ( $-0.85$  MPa, an average for non-legume species). The relatively low  $\Psi_{gs50}$  shown by the legume species has been earlier observed for two other species from seasonal tropical forests in Central America: *Hymenaea courbaril* (legume family) showed  $\Psi_{gs50} = -2.41$  MPa, and *Quercus oleoides* from the Fagaceae family showed  $\Psi_{gs50} = -2.76$  MPa (Klein, 2014).

In our experiment, the *Plathymenia* plant accumulated up to 8 per cent embolism, which was later reversed by xylem refilling (Figure 7), an important yet elusive trait (Klein *et al.*, 2018). The highest embolism rate was measured in *Dalbergia* (33 per cent). It is known from Olson *et al.* (2018) that taller trees tend to have wider conduits, leading to higher vulnerability to xylem embolism. Also, a study conducted with young, mature and old

trees found no clear relationship between the trees' age and vulnerability to embolism (Domec and Gartner, 2003). Other studies found evidence for refilling of embolized tracheids in mature trees (Ogasa *et al.*, 2019; Maruta *et al.*, 2020). Although we poorly understand the mechanism, refilling embolized tracheids might be necessary to compensate for low sapwood growth from year-to-year.

### A productivity-safety trade-off

The divergence between slow-growing, long-lived, late-successional species and fast-growing, short-lived, early-successional species has already been identified in the Atlantic Forest (Shimamoto *et al.*, 2014). Here, we suggest that this divergence is driven by a trade-off between plant productivity (carbon assimilation and growth) and plant safety (stomatal regulation and WUE). The higher assimilation and growth in legume vs. non-legume species observed here are in line with observations in other Atlantic Forest species (Campoe *et al.*, 2014). Such a fast-growth strategy requires high stomatal conductance, and inescapably exposes the tree to low water potentials under drought, in turn yielding low WUE (Figure 9) and low  $\delta^{13}\text{C}$  (Figure 10). In contrast, our non-legume species *Zeyheria* and *Cariniana* mostly avoided the drought by stomatal closure (Figure 8), while assimilating and growing at a slower pace (Figure 4, Supplementary Figure S4; Supplementary Table S2). When the stomatal regulation on photosynthesis is strong, the discrimination against  $^{13}\text{C}$  is reduced, accordingly the expected enriched  $^{13}\text{C}$  values for non-legume vs. legume species (Battipaglia *et al.*, 2013; Figure 10). It appears that the vigour of *Plathymenia* and *Dalbergia* was not jeopardized by drought due to their high drought tolerance, and for the *Plathymenia*, the observed ability to refill embolized xylem (Figure 7). Overall, all four species demonstrated a high capacity for recovery from drought (Fig. S10). This is perhaps the most encouraging result of our experiment, considering their potential role in future reforestation under climate change.

### Species-specific growth and drought resilience strategies

In addition to the general patterns explained above, each of the four species showed unique responses to drought. In *Cariniana*, despite its isohydric behaviour as shown by the low xylem water potential values during the experiment ( $-0.8 \pm 0.07$  MPa and  $-1.0 \pm 0.08$  MPa for control and drought respectively), the assimilation throughout the experiment was higher than expected for a late secondary species. In a former study on 24 Atlantic Forest tree species, *C. legalis* trees were the largest among the species with a high growth rate (Lisi *et al.*, 2008). Here, seedlings of this species displayed isohydric-like behaviour. They maintained high water potential despite the drought (Figure 6), and their assimilation was higher without irrigation (Figure 4). The latter peculiarity has already been observed in another Atlantic Forest tree species, *Tapirira guianensis* of the Anacardiaceae (Souza *et al.*, 2010). The exact mechanisms underlying the responses of *Cariniana* are yet to be resolved, but their utility for reforestation programmes is high. Responses of the early secondary species in our experiment, *Z. tuberculosa*,

were more typical of late secondary species. Our observations of low assimilation and growth in this species are in line with former observations in the study already mentioned above by Lisi *et al.* (2008): unlike *Cariniana*, *Zeyheria* had the lowest growth among the 24 species. On the other hand, *Zeyheria* had the highest  $\Psi_{gs50}$  ( $-0.8$  MPa) and highest drought resistance in our study (Figure 8, Fig. S10), which could relate to its lower assimilation (Figure 4). In the long run, a previous study shows that growth of *Zeyheria* under drought in the field was inhibited more than that of six other species of the Bolivian tropical dry forest (Mendivelso *et al.*, 2014).

### Hydraulic resistance of *Plathymenia*

Our experiment started over a controversy between the existing paradigm of a suspected high xylem vulnerability in tropical rainforest species (Choat *et al.*, 2012) and particularly in the Atlantic Forest (Di Francescantonio *et al.*, 2020), and new evidence indicating a relatively low xylem vulnerability (Ziegler *et al.*, 2019) and high drought resistance (Macedo *et al.*, 2021) in these species. Here, we show that, to some extent, both paradigms hold truth. Water potential was never lower than  $-2$  MPa in *Cariniana*, and only slightly lower than that in *Zeyheria*. At the same time, the legume species studied here reached low water potentials, and *Plathymenia* approached  $-5.52$  MPa. The potentially high hydraulic capacity of *Plathymenia* observed here matches higher survival rates and growth rates than most of the 25 tree species tested for carbon offset plantations in the field (de Moraes Junior *et al.*, 2019). *Dalbergia* showed mildly lower performance than *Plathymenia* in our experiment. This agrees with former observations that *D. nigra* had the lowest growth rate among five legume tree species (Costa *et al.*, 2015) and that its growth was reduced by low water and nutrient availability (Pontara *et al.*, 2016). Indeed, *Dalbergia* had higher hydraulic vulnerability (Figure 7, Fig. S8A, B) than *Cariniana* and *Zeyheria*. Considering the higher water potentials of *Zeyheria*, and more so, of *Cariniana*, their xylem seems rather vulnerable, reaching up to 27 per cent embolism in the latter (Figure 7, Fig. S8C, D).

### Implications for reforestation

Tropical wood from the Atlantic Forest has been exploited for generations, leaving only a small fragment of a once grand forest. The continued supply of these precious woods requires their cultivation, a process typically spanning over decades of trials and preparations. Alternatively, eco-physiological knowledge can expedite successful cultivation by informing forest practices and management. For example, our results suggest planting *Plathymenia* in drier sites, and considering the relatively high growth rate of *Cariniana* in forest planning, despite its classification as late successional species. One of the four species in our experiment, *Zeyheria*, showed a different performance than expected based on its successional stage. Multiple biotic and abiotic parameters above and below ground can affect the variation between slow- and fast-growing trees. Therefore, a tree species can grow fast in one setting and slower in another (Gull *et al.*, 2019). For example, some species evolved to grow below the canopy, and exposure to light in this stage can affect growth

(Lovelock *et al.*, 1994; Demmig-Adams and Adams, 1996). Overall, our observations are encouraging regarding the potential use of the four species in reforestation, even considering a hotter and drier future. *Dalbergia* seedlings were more drought-sensitive, and *Zeyheria* seedlings were lower in performance than the others. Nevertheless, our aim was not to simply grade species by their suitability, but rather to promote the use of all four, along with additional native species, to ensure high biodiversity, high productivity and a successful reforestation.

### Study limitations

In this experiment, we did not measure below ground biomass or other carbon sinks (e.g. root exudation; respiration). Therefore, the differences in carbon biomass partitioning above and below ground among the four species are unknown. Another key factor of tree growth is the interaction that many tropical plant species have with arbuscular mycorrhizal fungi (AMF; Koziol and Bever, 2015), which mediate nutrient supply such as phosphate (Smith and Read, 2010). AMF can also provide advantages to the plant when affected by some abiotic and biotic stresses including drought and herbivory. Nonetheless, the relation between AMF-plant association and its effect on the successional stage of the plant is still debated (Koziol and Bever, 2015). In our experiment, native AMF species were missing, so their potential effects on seedling development are unknown. Moreover, since our experiment was on seedlings planted in pots, there is a clear limitation in mimicking the conditions the trees would experience in their natural habitat, e.g. multiple stressors. Specifically, planted forests are potentially more prone to pest attacks than the highly diverse native tropical forests where pathogens have more difficulties in finding suitable host trees. Given these limitations, we would not presume that our results from experimenting with seedlings are directly transferable to mature trees in the field. Yet, seedling establishment is a key bottleneck for successful reforestation, and hence of direct relevance to the field (Pozner *et al.*, 2022). To this end, germination rates and dynamics are also reported here (Supplementary Figure S1). Moreover, the application of drought in pots typically induces faster and harsher drought than in the field (Tsamir-Rimon *et al.*, 2021), and the drought duration of 3–5 consecutive weeks was longer than reported for some sites in the Atlantic Forest, but not all.

### Conclusions

Major findings of our eco-physiological study of native tropical tree species are that: (1) legume tree species had higher growth and carbon assimilation than non-legume tree species and were more anisohydric. (2) This divergence was driven by a trade-off between plant productivity (carbon assimilation and growth) and plant safety (stomatal regulation and WUE). (3) Still, growth strategies under mesic and xeric conditions were mostly species-specific. And (4) common to all four species is a high capacity of recovery from drought, which supports their potential role in future reforestation under climate change.

## Supplementary data

Supplementary data are available at *Forestry* online.

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## Conflict of interest statement

The authors declare no conflict of interest.

## Author contributions

A.Y. performed the study designed by T.K. A.Y. and T.K. wrote the paper jointly. S.L.L. helped with statistical analysis. F.M., B.M. and R.S. helped formulating the research motivation, provided the seeds and gave comments on an earlier version of the paper.

## Data availability

All data used in this study is reported in the paper.

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