



Drought resistance traits predict tree species performance in a humid tropical landscape, but their importance shifts between managed cover types

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ABSTRACT

In the humid tropics, the substitution of forest cover by open pastures generates hotter and dryer conditions limiting the establishment of native plants. In this context reforestation of pastures using fast-growing tree species is commonly used to improve the environmental conditions, however, contrary to expected this strategy may lead to drier soil conditions due to the elevated transpiration rates of large trees, overall generating landscape mosaics with high variation in light and water availability. Despite the high sensitivity of tree species from the humid tropics to drought, efforts to predict species performance in reforestation campaigns have been focused mostly on carbon gain traits, while ignoring the drought resistance traits. In this study we addressed the hypothesis that both carbon gain and drought resistance traits are good predictors of growth rate and survival of species under contrasting vegetation cover types in a managed landscape. To test this hypothesis, the growth and survival over 38 months, and 17 physiological and morphological leaf traits related to carbon economy and drought resistance were measured in ten tree species planted in pastures and tree plantations. Plantations showed higher soil water depletion than pastures and the relative growth rate and survival of species were higher in pastures. Carbon economy and drought resistance traits together predicted interspecific growth rate and survival; however, the importance of functional traits as predictors depended on the cover type. Carbon acquisition traits (Am and AFE) were the best predictors in pastures, while drought resistance traits (RWC_{ulp} , LDMC and ϵ) had the lowest magnitude of interspecific variation, but were the best predictors in plantations. This suggests that, despite its restricted variation, drought tolerance traits may be of paramount importance in defining tree performance and long-term success of managed species in the humid tropics, particularly under fast-growing tree cover types. This study shows that soil water might act as a limiting factor on plant performance in managed landscapes in the humid tropics, and challenges the common assumption that using a low diversity of fast-growing and highly resource-demanding species is the best strategy to reforest abandoned pastures and improve the environmental conditions for other species.

1. Introduction

As humid tropical forest become degraded by human activities, reforestation has been widely considered an important approach to restore the structure and function of these ecosystems (Lamb et al. 2005; Chazdon 2008; Keenan et al. 2015). Under scenarios where forest cover has been completely lost (i.e. abandoned pastures), a limited number of fast-growing and highly productive species have been

traditionally used to increase forest cover, shade out grasses and improve the environmental conditions to facilitate colonization by other species (Lamb et al., 2005). However, this low-diversity planting strategy may lead to undesirable effects, such as the homogenization of vegetation cover and drier soil conditions due to elevated transpiration rates of fast-growing trees (Shi et al., 2012; Lacombe et al., 2016), potentially limiting the regeneration of native species. This potential shortcoming calls for the detailed study of habitat conditions and the

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capacity of new trees to establish and prosper under plantations compared to open pastures.

Tropical humid ecosystems are characterized by high annual rainfall, however, periods of water shortage can occur as consequence of rainfall distribution thorough the year and the interannual differences linked to El Niño events (De Souza and Ambrizzi, 2002; Wohl et al., 2012), exposing trees to water stress that can affect growth and survival (Engelbrecht et al., 2006; Novoplansky et al., 2001; Westerband et al., 2019). In addition, these natural periods of water shortage for plants can be intensified depending on the vegetation cover types, particularly in those human managed landscapes. For example, clear-cutting the tropical humid forest to establish pastures for cattle leads to hotter conditions, with a reduction in air moisture and an increase in evaporative demands (Keenan and Kimmins, 1993). Likewise, livestock activity during long periods causes an increase in soil erosion and compaction, which in turn reduces infiltration and groundwater recharge, with a consequent tendency towards soil drying (Martínez and Zinck, 2004; Scheffler et al., 2011). On the other hand, a common view is that the harsh conditions of open abandoned pastures in the humid tropics can be ameliorated by the quick generation of a forest cover by using fast-growing and resource exploitative species. However, strikingly, evidence shows that tree plantations of fast-growing species established in abandoned pastures are highly water-consuming (Wolf et al., 2011; Zhang et al., 2001; Shi et al., 2012); therefore, the water availability for plant uptake in the periods of low precipitation is likely more reduced in such reforested areas as compared to pastures.

Recently, ecological restoration in the humid tropics has been done by planting native tree species in order to recover biodiversity and ecosystem functions (action hereafter named community enrichment); however, many attempts have failed, in part owing to a lack of understanding of these species' resource use and stress tolerance, as well as, the lack of key functional traits useful in predicting growth and survival of species (Funk et al., 2008). Since light is widely recognized as the most important factor for plant performance in the humid tropics, the characterization of light environment and the analysis of functional traits related to light use and carbon economy have been extensively used to assess resource use strategies and predict potential growth and survival of tree species. For example, maximum photosynthetic rate, leaf nitrogen content, leaf nitrogen use efficiency and specific leaf area have been proposed as indicators of species growth rate under high light conditions (Kitajima, 1994; Kobe, 1999; Sanchez-Gomez et al., 2006; Lestari and Nichols, 2017), while light compensation point, dark respiration and leaf density have been used as indicators of species shade tolerance (Reich et al., 1998; Niinemets and Valladares, 2006). However, plants from the humid tropics have shown to be more sensitive to soil water shortage than species from other ecosystems (Bartlett et al., 2012; Zhu et al., 2018a). Previous studies have found that even short dry periods are sufficient to induce drought stress and mortality in a wide range of species, mostly at the seedling stage, since their small and shallow root systems cannot tap into deeper and moister soil layers. (Gilbert et al., 2001; Engelbrecht et al., 2005; Engelbrecht et al., 2007; Comita and Engelbrecht, 2009). In this context, it is reasonable to think that functional responses related solely to light requirements and carbon economy of species do not adequately predict growth and survival of tree species planted in human managed landscapes in the humid tropics.

Some functional traits related to the dehydration tolerance of leaf tissues have been found to be indicators of tree drought tolerance. The leaf turgor loss point ($\pi_{t_{lp}}$), the water potential at which leaf cells lose turgor pressure and close stomata (Cheung et al., 1975; Bartlett et al., 2012) is widely used to describe the plant drought tolerance (Bartlett et al., 2012; Maréchaux et al., 2015; Zhu et al., 2018a). This trait vary strongly among species from the humid tropics (Maréchaux et al., 2015) and is coordinated to other drought tolerance mechanisms as the vulnerability to cavitation (Bartlett et al., 2016; Brodribb et al., 2003; Bucci et al., 2004; Zhu et al., 2018a) and the ability for stomatal control

(anisohydric vs isohydric behavior) to maintain plant water status (Brodribb et al., 2003; Meinzer et al., 2016). Besides, it has been associated with carbon economy traits like specific leaf area (SLA), leaf density (LD), Leaf life span (LL) and maximal photosynthetic rate (A_m) (Zhu et al., 2018a). Leaves with higher concentrations of osmolytes that loss turgor at more negative water potentials ($\pi_{t_{lp}}$) are able to sustain stomatal conductance and photosynthesis under drought stress (Blackman et al., 2009; Mitchell et al., 2013; Zhu et al., 2018a), suggesting that the maintenance of cell turgor has a fundamental role in the regulation of carbon balance, as well as, in plant growth and survival of individuals under drought conditions. Other functional traits associated with the leaf water relations such as the relative water content at turgor loss point ($RWC_{t_{lp}}$) and the modulus of elasticity (ϵ) have also been proposed as important indicators of plant drought tolerance (Bartlett et al., 2012). These parameters contribute to maintaining the hydration and the structural integrity of leaf cells (Bartlett et al., 2012; Scoffoni et al., 2014; Binks et al., 2016). However, the relationship between the drought tolerance traits at the leaf level and the individual performance (survival and growth) in field conditions are still scarcely tested (Zhu et al., 2018b).

Proposing effective restoration strategies to maintain biodiversity in human managed landscapes require the understanding of plant physiological responses to environmental gradients generated by the anthropogenic use, as well as, identify which trait combinations may allow species to sustain growth and survival. The question of how carbon economy and drought tolerance traits predict growth and survival of tropical species planted in human managed landscapes has received little attention, and the ecological implications for forest management have not yet, to our knowledge, been addressed. In this study we evaluate the plant performance of tropical tree species planted in anthropogenic cover types with contrasting environmental conditions, and explore the predictive power of drought tolerance and carbon economy traits on their growth rate and survival. We aim to answer the following questions: (1) Do leaf functional traits predict the variation in growth and survival of the species planted in anthropogenic vegetation covers with contrasting environmental conditions: abandoned pastures and plantations? (2) What is the minimum set of traits needed to effectively predict species growth rate and survival? and, (3) Does this set of predictors change depending on the vegetation cover? We hypothesized that: (1) Carbon economy and drought resistance traits in combination will predict growth rate and survival of species and (2) The canopy cover composed of fast-growing species can produce drier soil conditions than open pastures, given the high transpiration rates of large fast growing trees, and then that drought resistance traits must be better predictors of young tree performance under the generated canopy than in open pastures. To test these hypothesis, we used a set of ten tropical tree species planted in open pastures and tree plantations in a managed landscape in the humid tropics. We followed the growth and survival of these species over 38 months and measured 17 physiological and morphological leaf traits involved in drought resistance and carbon economy.

2. Methods

2.1. Study site and species

The study was conducted in the Metropolitan Natural Park Cerro El Volador, located in the metropolitan region of the Aburrá Valley in Colombia (6°16'00"N; 75° 35'00" W). The study site is classified as tropical premontane humid forest (Holdridge 1967) with a mean annual temperature of 22.3 °C and a mean annual precipitation of 1629 mm (meteorological data from 1942 to 2014 from Olaya Herrera station at 5 km). Annual rainfall has a binomial distribution with two dry periods (Jul–Aug, 114–140 mm; Dec–Jan, 94–57 mm) and two wet periods (Mar–Apr, 174–194 mm; Sep–Oct, 161–209 mm). According to rainfall data collected during the study period (2013–2016) from a

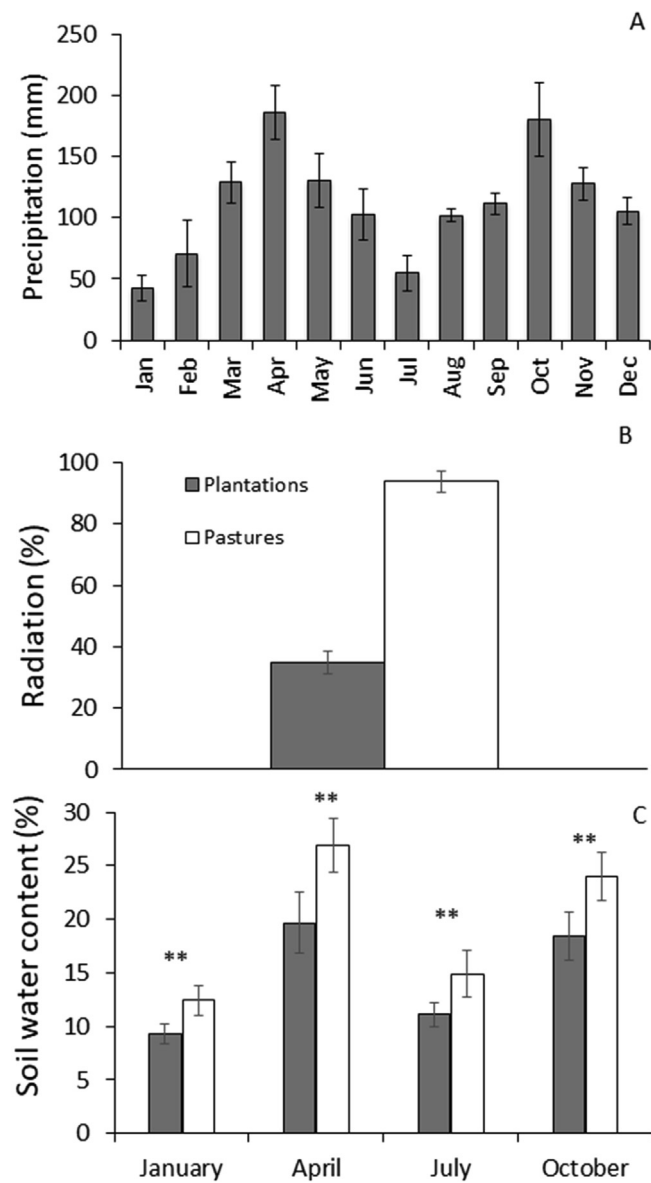


Fig. 1. (a) Mean (\pm SD) monthly rainfall in the study site, (b) Mean (\pm SD) proportion of direct solar radiation and (c) mean (\pm SD) volumetric soil water content in pastures and plantations. Asterisks denote significant differences of species between restoration scenarios (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

weather station installed in the Park in 2012, January and July were the driest months, while April and October exhibited the highest precipitation (Fig. 1a). The study site has a total extension of 109 ha ranging in altitude from 1500 to 1600 masl, which were used for cattle during the past century; however, different vegetation types exist today as a result of vegetation recovery activities executed over the past three decades, where abandoned pastures and tree plantations are the most representative cover types.

As part of a reforestation program carried out in the study site in 2013, more than 5000 saplings of 50 species were planted under different vegetation covers; a total of 30 mixed-species plots were established in areas with similar slope (ranging from 35 to 40%). Plots were set up with an area of 18×15 m and a combination of 165 trees of different species, which were planted at a distance of 1.50 m. Of the 50 species, for this study we select 10 species (Table 1) planted in both abandoned pastures (hereafter, “pastures”) and previously established plantations of fast-growing native and exotic species (hereafter,

“plantations”). Of the 10 species, 645 saplings were planted in eight pasture plots and 331 saplings were planted in six plantation plots.

Pastures are fully exposed to sun and dominated by exotic grasses (mainly *Panicum maximum* (Jacq.)). Plantations are mainly composed of the fast-growing species *Eucalyptus grandis* (W.Hill), *Fraxinus chinensis* (Roxb.) and *Guazuma ulmifolia* (Lam.), which formed dense and homogeneous stands, with a basal area of 27.2 ± 3.6 m² ha⁻¹. To characterize the light environment, we took five hemispherical photographs per plot at two meters above the soil surface in pastures and plantations (30 total photographs in pastures and 40 in plantations). The direct site factor (i.e. the proportion of direct solar radiation reaching a given location, relative to that in a location with no sky obstructions) was obtained from each photograph using the software “Hemiview” (Delta T Devices Ltd., Cambridge, UK), and the mean proportion of radiation reaching the planted sites was estimated. The mean soil moisture of the first 10 cm of soil depth was simultaneously measured in both restoration scenarios at the end of the two lower precipitation and two higher precipitation periods. To characterize the soil moisture during the dry and the wet periods, the soil water content of the first 10 cm of soil was instantaneously measured using a ML3 ThetaKit (Delta T Devices Ltd., Cambridge, UK) in pastures and plantations. Five measurements were taken per plot in random positions during three consecutive days (90 measurements in total for plantations and 120 for pastures) from 06:00 to 08:00 h in the rainier (April and September) and driest months (January and July). In the dry periods measurements were done after seven rainless days.

2.2. Growth and survival measurements

The diameter (d , cm) at 10 cm above the base of the stem and total height (h , cm) of every sapling were measured at the beginning (one month after planting, July 2013) and at the end of the experiment (October 2016). The wood volume (cm³) of saplings was estimated as $V = \pi(d/2)^2 \times h \times f_c$; where f_c is the cylindrical form factor, which represents the ratio of total tree volume to the volume of a cylinder with the same diameter and height as the tree (Kershaw et al., 2017). We used a form factor of 0.7 for all species, which has been reported to be appropriate to calculate the stem volume of young trees (Hess et al., 2015). Then, we calculated the relative growth rate (growth rate hereafter) in volume (cm³ cm⁻³ year⁻¹) for each individual tree as $RGR = (\ln V_2 - \ln V_1)/(t_2 - t_1)$, where V_2 and V_1 are the wood volume at the end of the experiment (t_2) and at the beginning of the experiment (t_1), respectively (Poorter and Garnier, 2007). We used wood volume because it represents a combined response of growth in both diameter and height. The survival of each species was calculated as the proportion of the saplings initially planted that were still alive at the end of the experiment.

2.3. Functional trait measurements

Seventeen functional traits of leaves involve in carbon economy and drought resistance were measured during July 2016 in the ten species in both cover types. Using the automatic light curve program with a LICOR-6400XT (LI-COR Inc., Lincoln, NE, USA) portable photosynthesis system, we measured the gas exchange in response to different light intensities (from 1200 to 800, 500, 200, 50, 20, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The net photosynthesis recorded at each light intensity was corrected for diffusion through the gasket (Bruhn et al., 2002), and the new values were fitted to Thornley’s (1976) nonrectangular hyperbola model to generate light response curves of photosynthesis as a function of photosynthetic active radiation. Measurements were carried out from 08:00 to 12:00 h in two fully expanded healthy leaves from the upper shoots in four randomly selected individuals per species in both restoration scenarios (a total of 80 individuals). During the measurements, CO₂ concentration in the leaf chamber was kept at 400 $\mu\text{mol mol}^{-1}$, and temperature and air humidity were maintained at

Table 1
List of the 10 studied species with their scientific name, family and leaf phenology.

| Species | Code | Family | Leaf phenology | Native/exotic |
|--|------|---------------|----------------|---------------|
| <i>Caryodendron orinocense</i> (H. Karst) | CO | Euphorbiaceae | Evergreen | Native |
| <i>Dipteryx oleifera</i> (Benth) | DO | Fabaceae | Evergreen | Native |
| <i>Genipa Americana</i> (L.) | GA | Rubiaceae | Evergreen | Native |
| <i>Sapindus saponaria</i> (L.) | SS | Sapindaceae | Evergreen | Native |
| <i>Eugenia myrtifolia</i> (Cambess) | EM | Myrtaceae | Evergreen | Exotic |
| <i>Myrcia paivae</i> (O. Berg) | MP | Myrtaceae | Evergreen | Native |
| <i>Lafoesnia speciosa</i> (Kunth.) DC. | LS | Lythraceae | Evergreen | Native |
| <i>Trichanthera gigantea</i> (Bonpl.) Nees | TG | Acanthaceae | Brevideciduous | Native |
| <i>Albizia guachapele</i> (Kunth.) Dugand | AG | Fabaceae | Brevideciduous | Native |
| <i>Samanea saman</i> (Jacq.) Merr. | SSa | Fabaceae | Brevideciduous | Native |

approximately 25 °C and 60%, respectively. The maximum photosynthetic rate at saturating light per unit area (A_m , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and the apparent quantum yield (E_q , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \mu\text{mol m}^{-2} \text{ s}^{-1}$) were derived from the light response curves. The maximal stomatal conductance (g_s , $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) was directly obtained from the gas exchange measurements at 1200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, and the intrinsic water use efficiency (WUE_i , $\mu\text{mol CO}_2 / \text{mol H}_2\text{O}$) was calculated as the $A_m:g_s$ ratio (Cavender-Bares and Bazzaz, 2000).

Morphological traits were measured in five upper-shoot leaves, including those used for photosynthetic measurements. Leaf area was determined using a portable area meter LI-3000C (LI-COR Inc., Lincoln, NE, USA), and specific leaf area (SLA, $\text{cm}^2 \text{ g}^{-1}$), leaf dry matter content (LDMC, g g^{-1}) and leaf thickness (Lt, mm) were determined following the procedures by (Pérez-Harguindeguy et al., 2013). Leaf density (LD, g cm^{-3}) was then calculated as SLA/Lt . The leaf Nitrogen (N, mg cm^{-2}), Phosphorous (P, mg cm^{-2}) and Carbon (C, %) contents were determined from the same leaves using a Flash 2000 Elemental Analyzer (Thermo Fisher Scientific Inc. Waltham, MA; USA); then the C:N ratio was determined. The Photosynthetic N-use efficiency (PNUE, $\mu\text{molCO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$) was calculated as the ratio between A_m and N content (Field and Mooney, 1986). To determine median Leaf Lifespan (LL, days), we marked at least 50 recently formed leaves and monitored them biweekly in 6–10 individuals per species; LL was the time in days at which 50% of the marked leaves had died (Pérez-Harguindeguy et al., 2013).

Leaf drought tolerance traits were determined following the pressure-volume (P-V) technique of (Tyree and Hammel, 1972), using a 1505D-EXP pressure chamber (PMS Instruments company, Albany OR; USA). The potential at turgor loss point (π_{tlp} , Mpa), the osmotic potential at full turgor (π_o , Mpa); the relative water content at turgor loss point (RWC_{tlp} , %) and the modulus of elasticity (ϵ , Mpa) were calculated in four replicates per species per restoration scenario using the P-V curve fitting routine (Microsoft Excel 2000; K.Tu, University of California Berkeley v5.6, <http://landflux.org/Tools.php>), based on the approach of Schulte and Hinckley (1985).

2.4. Statistical analysis

We tested for species differences in mean growth rate and survival between vegetation covers types with a *t*-test and Chi-squared test for binomial proportions, respectively. To explore patterns of covariation between functional traits we performed both, bivariate Pearson correlations, as well as Principal Component Analysis (using standardized values). Since the magnitude of the functional traits and the manner in which they are correlated might change in response to the environmental conditions, we did perform a PCA separately for each vegetation cover. Then, to explore which functional traits significantly contribute to variation along PCA axes, Pearson correlations were performed between individual functional traits and each PCA axis. As functional traits are coordinated to influence plant performance, to assess which functional traits predict variation in the interspecific growth rate, the

individual data of RGR was modeled independently for each cover type as function of principal PCA axes in a mixed model framework with species as random effect using the *lmer()* function in *lme4* package in R (Bates et al., 2015). A stepwise selection with maximum likelihood (ML) fitting procedure was performed to evaluate which PCA axes were significant in the models. Then, the final model was fitted again using restricted maximum likelihood (REML). To discern the minimum set of predictor traits of interspecific growth rate, similar mixed models procedure to that describe for the PCA axes were performed using all functional traits. To assess which functional traits predict the interspecific survival, generalized linear models with binomial error distribution for grouped data (alive/dead count) of each species were performed separately for each cover type using the PCA axes as independent variables. A stepwise procedure was done to evaluate the significant PCA axes. Similar procedures were performed using all traits to detect the minimum set of predictor traits of interspecific survival. All analyses were conducted using R software 3.5.2.

3. Results

3.1. Environmental growth conditions of pastures and plantations

The proportion of direct solar radiation reaching the plantation scenario was significantly lower compared to pastures; while pastures received 94% (SD \pm 3.5) of total radiation, plantations received 35% (SD \pm 3.6) (Fig. 1b). The mean volumetric soil water content was also significantly lower in plantations than in pastures in both dry and wet periods. The soil water content in plantations was of 9% and 20% while in pastures was of 12% and 27% in dry and wet periods respectively (Fig. 1c).

3.2. Variation in growth rate and survival of species between pastures and plantations

Both, RGR and survival were equal or even lower in plantations compared to pastures. Most species exhibited significantly higher growth rates in pastures, while only three species did not differ between the vegetation covers (Fig. 2a). The interspecific variation in RGR was higher under plantations (Coefficient of variation, CV = 46.1%) than in pastures (CV = 33.4%), with an average across all species of 1.35 ($\text{cm}^3 \text{ cm}^{-3} \text{ year}^{-1}$) and 0.78 ($\text{cm}^3 \text{ cm}^{-3} \text{ year}^{-1}$), respectively. The mean survival across all species was 72% and 61% in pastures and plantations, respectively, with higher interspecific variation under plantations (CV = 28.2%) than pastures (CV = 13.1%). Survival of species varied less between vegetation covers; only three species differed, showing significantly higher survival in pastures (Fig. 2b).

3.3. Functional traits variation and relationships in pastures and plantations

Functional traits showed high variation across species in both cover types. Carbon economy traits showed the higher interspecific variation

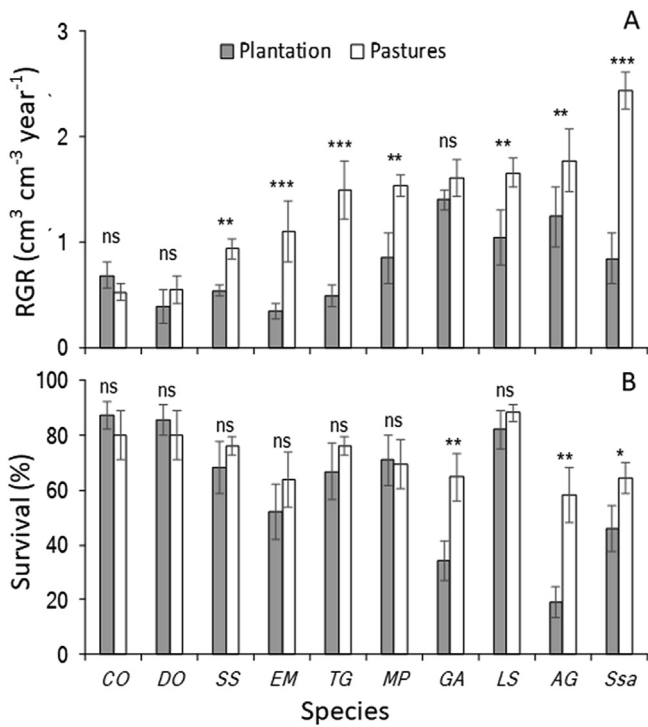


Fig. 2. (a) Mean (\pm SE) relative growth rate (RGR) and (b) mean (\pm SE) survival of species growing in pastures and plantations. Asterisks denote significant differences between restoration scenarios (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$), ns: non-significant differences. Species' code in Table 1.

with values for Am and SLA varying by three and four times in plantations and pastures, respectively. The drought tolerance traits π_{tlp} , π_o and RWC_{tlp} , showed especially low interspecific variation in both cover types; from 0.1 to 0.2 times and from 0.1 to 0.5 times in pastures and plantations, respectively. The ranking of the species with respect to the trait values was similar among plantations and pastures. For instance, the species *C. orinocense* (CO) showed the more negative values of π_{tlp} and lower photosynthetic rates, while *S.saman* (SSa) and *A.guachapelle* (AG) exhibited the less negative values of π_{tlp} and highest photosynthetic rates (Table 1 supplementary material). The patterns of correlation among functional traits were conserved, however the significance of correlations varied among cover types (Table 2). We found higher trait integration between carbon economy traits and drought tolerance traits, as well as, within groups of traits in plantations. The Am was strongly and positively correlated with g_s , Eq, PNUE and SLA in both cover types, while it was negatively correlated with C:N in pastures and Lt in plantations. The SLA correlated positively with g_s , and PNUE, but negatively with C:N in both cover types, but it was also correlated with Lt and LL only in plantations. The π_{tlp} did no correlate with π_o in plantations. π_o negatively correlated with ϵ in pastures with a similar tendency in plantations. Finally, those species with high RWC_{tlp} tended to exhibit low g_s and high ϵ in both cover types (Table 2). Overall, these patterns of traits correlations were also reflected when we performed PCA analysis (Fig. 1 Supplementary Material). In this case, we detected several axis of functional variation. For example, the PC1, the axis synthetizing the highest portion of traits variation, described a continuum of strategies to acquire and use carbon; from acquisitive species with elevated photosynthetic rates, stomatal conductance and thin extended leaves, to conservative species with dense leaves and low physiological rates (Table 2 Supplementary Material). Interestingly, those traits linked with tolerance to drought covaried along PC3, PC4 and PC5, reflecting the relative low variation of those traits compared to carbon economy traits and the low coordination

Table 2
Correlations among functional traits measured in 10 species planted in pastures and plantations. The above and below diagonal represent Pearson's coefficient for pastures and plantations respectively. Significant correlations in bold. * $0.1 > p \geq 0.05$; * $p < 0.05$; ** $p < 0.01$.

| Functional traits | Am | g_s | WUE _i | Eq | PNUE | N | P | SLA | C:N | LDMC | Lt | LD | LL | π_{tlp} | π_o | RWC_{tlp} | ϵ |
|-------------------|---------------|---------------|------------------|--------------|--------------|--------|---|-----|-----|------|----|----|----|-------------|---------|-------------|------------|
| Am | | | | | | | | | | | | | | | | | |
| g_s | 0.87** | | | | | | | | | | | | | | | | |
| WUE _i | -0.08 | -0.51 | | | | | | | | | | | | | | | |
| Eq | 0.81** | 0.75** | | | | | | | | | | | | | | | |
| PNUE | 0.84** | 0.82** | | | | | | | | | | | | | | | |
| N | -0.23 | -0.39 | 0.35 | -0.04 | -0.68* | | | | | | | | | | | | |
| P | -0.31 | -0.28 | -0.13 | -0.21 | -0.35 | 0.36 | | | | | | | | | | | |
| SLA | 0.53* | 0.54* | -0.03 | 0.76* | 0.55* | -0.22 | | | | | | | | | | | |
| C:N | -0.26 | -0.13 | -0.27 | -0.58* | 0.03 | -0.47 | | | | | | | | | | | |
| LDMC | 0.46 | 0.46 | -0.25 | 0.56* | 0.34 | 0.03 | | | | | | | | | | | |
| Lt | -0.75* | -0.73* | 0.17 | -0.91** | 0.08 | 0.12 | | | | | | | | | | | |
| LD | 0.23 | 0.30 | -0.45 | 0.13 | 0.08 | 0.09 | | | | | | | | | | | |
| LL | 0.49 | -0.42 | -0.52 | -0.33 | -0.50 | 0.30 | | | | | | | | | | | |
| π_{tlp} | 0.37 | 0.30 | 0.17 | 0.38 | 0.70* | -0.60* | | | | | | | | | | | |
| π_o | -0.38 | -0.60* | 0.61* | -0.28 | 0.59* | -0.38 | | | | | | | | | | | |
| RWC_{tlp} | 0.03 | -0.11 | 0.36 | -0.21 | -0.03 | -0.14 | | | | | | | | | | | |
| ϵ | | | | | | | | | | | | | | | | | |

Abbreviations: Am: maximal photosynthetic rate, Eq: apparent quantum yield; SLA: specific leaf area; LL: leaf lifespan, LDMC: Leaf dry matter content; LD: leaf density, Lt: leaf thickness, N: leaf Nitrogen content, P: Leaf Phosphorus content, WUE_i: Water use efficiency, g_s : maximal stomatal conductance PNUE: Photosynthetic N-use efficiency, π_{tlp} : leaf potential at turgor loss point, π_o : osmotic potential at full turgor, RWC_{tlp} : relative water content at turgor loss point; ϵ : modulus of elasticity.

Table 3

Results of linear mixed models for species growth rate as a function of PCA axes. Results are shown the the significant PCA axes that predicted interspecific growth rate in pastures and plantations.

| Plantations | | | | | | Pastures | | | | |
|----------------|--------|--------------|-----|-------|----------|--------------|----|------|---------|----------|
| Random effects | | Variance (%) | | | | Variance (%) | | | | |
| Species | | 78.3 | | | | 75.1 | | | | |
| Residual | | 0.91 | | | | 11.3 | | | | |
| Predictors | Coeff. | Df | F | P | Variance | Coeff. | Df | F | P | Variance |
| PC1 | – | – | – | – | – | 0.098 | 1 | 16.1 | < 0.001 | 26.3 |
| PC2 | 0.053 | 1 | 8.7 | 0.006 | 17.2 | – | – | – | – | – |
| PC4 | –0.066 | 1 | 4.9 | 0.035 | 2.5 | – | – | – | – | – |
| PC5 | –0.069 | 1 | 5.3 | 0.028 | 20.1 | – | – | – | – | – |

between gas exchange traits and leaf drought tolerance traits (Table 2 [Supplementary Material](#))

3.4. Prediction of growth rate variation by functional traits

The PCA analyses showed that the first five principal components had eigenvalues greater than one in plantations and pastures. When using these five significant multivariate axes as explanatory variables, we detected that PC1 affected growth rate variation, explaining 26.3% but only in pastures. In this case, species with higher A_m , g_s , N, SLA exhibited higher growth rates (Table 3, Table 2 [Supplementary Material](#)). In contrast, PC5, PC2 and PC4 significantly affected growth rate in plantations but not in pastures, (explaining together 39.8%), with the PC5 explaining most of such variation (Table 3). Together, these correlations indicated that species realizing higher growth rates in plantations tend to have longer leaved leaves (LL), with high mass content (LDMC), and with low water use efficiency (WUE), or leaves that loss turgor at high relative water contents (with high $RWC_{t_{lp}}$). The weak correlation with PC4 suggested that ϵ and P content may also affect growth rate.

When looking for the best minimum set of predictor traits, multiple regressions revealed that three traits together— A_m , SLA and $RWC_{t_{lp}}$ —best predicted the interspecific variation in growth rate in pastures, whereas in plantations, the combination of four traits— A_m , g_s , π_o and $RWC_{t_{lp}}$ —were the best predictors of growth rate (Table 4, Fig. 2 [Supplementary Material](#)). Overall A_m and $RWC_{t_{lp}}$ explained the highest proportion of variance in both types of vegetation cover; however, the relative importance of these traits was different, A_m was more important in pastures, while $RWC_{t_{lp}}$ was more important in plantations (Table 4, Fig. 3 [Supplementary Material](#)).

3.5. Survival variation predicted by functional traits

The GLM models using PCA axis as regressors revealed that in both

Table 4

Results of linear mixed models for species growth rate as a function of functional traits. Results are shown the minimum set of functional traits that predicted interspecific growth rate in pastures and plantations. Information is only given for the significant traits.

| Plantations | | | | | | | Pastures | | | | | |
|----------------|--------|--------------|------|---------|----------|-------|--------------|----|-----|-------|----------|-------|
| Random effects | | Variance (%) | | | | | Variance (%) | | | | | |
| Species | | 74.5 | | | | | 72.4 | | | | | |
| Residual | | 11.1 | | | | | 12.2 | | | | | |
| Predictors | Coeff. | Df | F | P | Variance | v.i.f | Coeff. | Df | F | P | Variance | v.i.f |
| A_m | 0.08 | 1 | 17.3 | < 0.001 | 37.6 | 1.46 | 0.04 | 1 | 4.7 | 0.033 | 65.8 | 1.21 |
| g_s | –3.28 | 1 | 9.3 | 0.005 | 8.4 | 1.56 | – | – | – | – | – | – |
| π_o | 0.54 | 1 | 6.1 | 0.018 | 8.5 | 1.06 | – | – | – | – | – | – |
| $RWC_{t_{lp}}$ | –2.73 | 1 | 7.5 | 0.009 | 26.2 | 1.45 | –8.64 | 1 | 9.9 | 0.003 | 3.3 | 1.19 |
| SLA | – | – | – | – | – | – | 0.01 | 1 | 4.3 | 0.046 | 1.3 | 1.02 |

A_m : maximal photosynthetic rate; g_s : stomatal conductance; π_o : osmotic potential at full turgor; $RWC_{t_{lp}}$: relative water content at turgor loss point; SLA: specific leaf area, v.i.f.: variance inflation factor.

Table 5

Results of generalized linear models for species survival as a function of PCA axes in pastures and in plantations. Information is only given for the significant PCA axes.

| | Predictors | Coefficients | Variance | χ^2 | p |
|-------------|------------|--------------|----------|----------|--------|
| Plantations | PC1 | –0.19 | 22.7 | 13.5 | 0.012 |
| | PC4 | –0.36 | 11.3 | 13.1 | 0.023 |
| | PC5 | 0.64 | 42.3 | 42.3 | 0.004 |
| Pastures | PC1 | –0.12 | 4.9 | 34.9 | 0.0287 |

cover types, those species with low efficiency of carbon gain (low A_m , g_s , Eq, PNUE, SLA) survived better but such relationship was stronger in plantations (Table 5, Table 2 [Supplementary Material](#)). In plantations the best predictor was PC5, indicating that in this condition survival is better predicted by traits related with drought tolerance; survival was enhanced by high values of LDMC and $RWC_{t_{lp}}$. A weak effect of PC4 suggested that high values of ϵ and low P content may also contribute to high survival in plantations (Table 5, Table 2 [Supplementary Material](#)).

Multiple regression showed that three functional traits in combination—SLA, LL and $RWC_{t_{lp}}$ —best predicted survival in pastures (Table 6, Fig. 4 [Supplementary Material](#)). In this case, survival increased among species with lower SLA and LL, but higher $RWC_{t_{lp}}$. In plantations, survival tended to increase towards species with lower Eq and higher LDMC, $RWC_{t_{lp}}$ and ϵ (Table 6, Fig. 5 [Supplementary Material](#)). Albeit in both scenarios $RWC_{t_{lp}}$ was important in predicting survival, this effect was stronger in plantations.

4. Discussion

In this study we hypothesized that carbon economy and drought resistance traits in combination would predict RGR and survival in managed cover types in the humid tropics. Our results support this hypothesis and show that, while there was some variation in which

Table 6

Results of generalized linear models for species survival as a function of functional traits in pastures and plantations. Results are shown the minimum set of functional traits that predicted survival separately for the two cover types. Information is only given for the significant traits.

| | Predictors | Coefficients | Variance | χ^2 | <i>p</i> | v.i.f |
|-------------|-------------|--------------|----------|----------|----------|-------|
| Plantations | <i>Eq</i> | −56.48 | 17.6 | 27.5 | < 0.001 | 1.7 |
| | LDMC | 15.64 | 30.5 | 25.3 | < 0.001 | 1.7 |
| | RWC_{tip} | 24.50 | 30.8 | 21.1 | < 0.001 | 1.6 |
| | ϵ | −0.01 | 3.9 | 3.9 | 0.042 | 1.7 |
| Pastures | SLA | −0.03 | 6.8 | 12.1 | 0.0005 | 2.7 |
| | LL | −0.01 | 6.4 | 10.8 | 0.0010 | 1.2 |
| | RWC_{tip} | 35.6 | 5.6 | 5.6 | 0.0175 | 2.4 |

Eq: apparent quantum yield; LDMC: Leaf dry matter content; RWC_{tip} : relative water content at turgor loss point; ϵ : modulus of elasticity; SLA: specific leaf area; LL: leaf lifespan.

specific predictors were included, both carbon economy and drought resistance traits are necessary to predict interspecific differences in tree performance in pastures and plantations. Although the light use efficiency and carbon conservation traits, which are linked to shade tolerance, contribute to predict the tree performance in plantations, the growth rate and survival were mostly predicted by drought tolerance traits, particularly the capacity of species to sustain high cell hydration (RWC_{tip}). We explain these results from the perspective of resource availability. Despite light conditions inside the tree plantations (35% of full sun-light) do not seem very low, results suggest that they are to some extent limiting for plant performance. Furthermore, our soil moisture data show a greater soil water depletion in plantations compared to pastures in wet and dry seasons, which may explain the important role of drought tolerance traits in predicting growth rate and survival in these conditions. The acclimation of plants to shade possibly restrict the competitive ability for soil water acquisition, since it involves an increase in leaf investment to capture light but also restricts investment for capture of below-ground resources (Sack et al., 2003). This conflict is especially important for tree species from the humid tropics, as their high ability to acclimate to light conditions but narrow range of drought tolerance (da Costa et al., 2010; Mora et al., 2013), likely making plants living under the shade, particularly vulnerable to soil drought. Even though the higher evaporative demand in the pastures, the higher availability of resources (light and soil water) in this condition explained the higher growth rates and survival of species, as well as, why interspecific growth rate and survival are mainly predicted by carbon acquisition and less predicted by drought tolerance traits.

To our knowledge this is the first study in the literature that tests the influence of drought resistance traits on growth rate and survival of a set of tropical species planted in anthropogenic vegetation covers with contrasting environmental conditions; from these results we highlight some important findings. First, in both vegetation covers, the resource-demanding species (i.e. species with high A_m and g_s) grew faster, but at the expense of leaf dehydration (i.e. lower RWC_{tip}). Likewise, species with lower photosynthetic capacity and higher dehydration control exhibited higher survival, suggesting a growth-survival trade-off mediated by a conflicting relationship between carbon gain and water conservation. This trade-off seems to be governed, to some extent, by the stomatal behavior, since the species with higher RWC_{tip} tend to exhibit lower stomatal conductance. These results are in line with other studies which suggest that the maintenance of low stomatal conductance is an important mechanism for preventing water loss and sustaining leaf hydration under drought conditions (Jones and Sutherland, 1991; Martin-StPaul et al., 2017; Meinzer et al., 2017; Yi et al., 2019). In addition, some studies have reported significant correlations between low stomatal conductance and other parameters that confer drought tolerance such as high xylem cavitation resistance (Bartlett et al., 2016; Kursar et al., 2009; Zhu et al., 2018a) suggesting a

whole-plant level coordination among functional traits for drought tolerance, which may explain why leaf level traits can inform on growth and survival. We also found that species with lower photosynthetic capacity and stomatal conductance tended to exhibit more negative π_{tip} in plantations where soils are drier, which reflects a leaf level coordination between functional traits to tolerate drought (see Meinzer et al., 2017; Zhu et al., 2018a for previous findings on leaf traits coordination).

Second, our results show that among the drought tolerance traits the RWC_{tip} is the best predictor of growth and survival of species but not the π_{tip} , which has been considered as a key trait in predicting plant drought tolerance and survival (Bartlett et al., 2012; Maréchaux et al., 2015; Zhu et al., 2018b). Recent studies have questioned whether the maintenance of cell turgor pressure by means of a low π_{tip} or alternatively sustaining the cell hydration by means of a high RWC_{tip} is more important to support leaf functions under drought conditions (Bartlett et al., 2012). As discussed before our results suggest that RWC_{tip} is part of a set of coordinated leaf traits involved in stomatal control and thus on the mechanisms of maintenance of leaf hydric status. The coordinated increment between RWC_{tip} and ϵ as well as, the inverse relation between RWC_{tip} and g_s , detected in this study has been also found by other studies (Corcuera et al., 2002; Binks et al., 2016), which suggest that a high ϵ accompanied by an osmotic adjustment can generate strong gradients between the leaf and soil water potentials with a low leaf water loss, thus maintaining a high RWC_{tip} and preventing cell dehydration (Bartlett et al., 2012). Nevertheless, the lack of published data on the relationships between the leaf drought tolerance traits and plant growth and survival makes it impossible to size any generalization regarding our results. In this sense, more studies are needed to evaluate the importance of cell turgor and cell hydration in support leaf functioning, as well as, the coordination of these attributes with other parameters at plant level that confer drought tolerance.

Third, perhaps counterintuitively, forest plantations were drier habitats than pastures due to higher water consumption of large fast-growing trees. Furthermore, the fact that the importance of drought tolerance traits in predicting growth and survival was higher in plantations than in open sky pastures, suggests that soil water availability may act as an important driver of plant performance in this cover type in the humid tropics. In this study, tree plantations were composed of exotic, fast-growing and highly water demanding species, which may account for high transpiration rates, reducing the water availability for other plants that are only able to extract water from the shallow soil layers (Shi et al., 2012). Several studies have reported that plantations may exhibit up to 10-fold higher transpiration rates per unit area than grasslands (Zhang et al., 2001; Brauman et al., 2012; Dias et al., 2015) which may deplete soil water available for plant uptake (Zhang et al., 2001); hence, while plantations surely reduce atmospheric drought, they may also dramatically increase the risk of soil drought.

Fourth, while the group of traits related to drought tolerance was the most important predictor of growth and survival rates, they also exhibited the lowest magnitude of interspecific variation, as indicated by the fact that the PC5 axis (which only explained 8% of the total interspecific trait variation) was the best predictor of growth rate and survival in plantations. This result strongly suggests that in the humid tropics, while functional differentiation in drought tolerance seems to be relatively restricted in comparison with light use and carbon gain strategies, this differentiation may be of paramount importance in defining species success under pastures and plantations, because plants from the humid tropics are particularly sensitive to drought (Engelbrecht et al., 2007; Comita and Engelbrecht, 2009). More studies comparing the relative importance of carbon gain and drought tolerance traits among multiple species from the humid tropics are needed to test this hypothesis.

4.1. Conclusions

This study revealed that interspecific differences in growth rate and survival of tree species planted under anthropogenic cover types with different environmental conditions are driven by carbon acquisition and leaf drought resistance traits. In particular, tree performance under plantations is, to a large extent, predicted by drought tolerance traits. Such a strong influence of leaf drought-related traits has not previously been described for a set of species planted in the field in anthropogenic vegetation covers in the humid tropics. Our results challenge two common assumptions classically considered for reforestation of pastures and tree plantations in the humid tropics: first, that the use of fast-growing and highly resource-demanding species is the best strategy to reforest abandoned pastures because it is the quickest way to improve the environmental conditions and facilitate colonization by other species; and second, that soil water does not act as a limiting factor on plant performance. We argue that the use of fast-growing species could, perhaps counterintuitively, generate even more stressful conditions for the new species by significantly reducing soil water availability as a consequence of their high water demand. In that sense, species with a combination of water conservative and drought tolerant traits should be selected for reforestation of abandoned pastures. Likewise, if possible, species with a combination of shade and drought tolerance traits should be selected for enrichment of the existing plantations. These new insights from functional ecology represent a complementary approach and an opportunity to move towards more successful species manage for reforestation in the humid tropics.

CRedit authorship contribution statement

Lucas Cifuentes: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **Flavio Moreno:** Conceptualization, Methodology, Validation. **Juan Diego León-Peláez:** Methodology, Validation. **Horacio Paz:** Conceptualization, Formal analysis, Writing - review & editing.

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Appendix A. Supplementary material

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